

SPATIAL DISTRIBUTION AND ASSOCIATION PATTERNS OF *KNEMA PIERREI* WARB. AND ITS NEIGHBORS IN AN EVERGREEN BROADLEAVED FOREST IN CON DAO ISLANDS OF VIETNAM

HIEN, C. T. T.¹ – LONG, N. T.² – HAI, N. H.¹ – CUONG, L. V.³ – QUY, N. V.^{4*}

¹*Vietnam National University of Forestry, Xuanmai, Hanoi 100000, Vietnam*

²*Hung Vuong University, Viettri, Phutho 290000, Vietnam*

³*Vietnam National University of Forestry – Southern Campus, Dongnai 810000, Vietnam*

⁴*Southern Branch of Joint Vietnam-Russia Tropical Science and Technology Research Center, Hochiminh 700000, Vietnam*

**Corresponding author*

e-mail: quyforest@nwafu.edu.cn; phone: +84-988-906-725

(Received 31st Mar 2024; accepted 16th Jul 2024)

Abstract. The spatial pattern of trees can provide information about underlying processes that maintain plant species coexistence. The current study aims to elucidate ecological characteristics and spatial patterns of *Knema pierrei* within the evergreen broadleaved forest stands in Con Dao Islands, southern Vietnam. Data was collected from all woody species with a diameter at breast height (dbh) ≥ 2.5 cm in three two-hectare study plots. Spatial point pattern analysis methods were used to analyze data using Programita 2018 and R 4.2.2 software. The results showed that the spatial distribution of *K. pierrei* shifted from an aggregated pattern at the juvenile stage to a random pattern at the premature stage and a regular pattern at the mature stage. Spatial associations of *K. pierrei* and co-dominant species were mostly independent patterns. The spatial patterns of *K. pierrei* were influenced by habitat heterogeneity and spatial scale. Ecological processes such as dispersal limitation and self-thinning are the main mechanisms that shape the spatial distribution and association patterns of *K. pierrei*. Based on our findings, it is possible to adjust the density, selection of tree species, and planting-hole spacing in restoring or planting new forests with *K. pierrei* and the dominant species.

Keywords: *spatial analysis, intraspecific association, habitat, conservation planning, tropical forest ecology*

Introduction

Most plant species are not randomly distributed on the forest ground (Wiegand et al., 2007; Li et al., 2009) but occupy different niches in the community and have different distribution characteristics and abundance (Yao et al., 2021). Explaining spatial patterns of species and mechanisms to maintain their coexistence is considered central to ecology (Barot, 2004; Wilson, 2011; Fibich et al., 2016; Du et al., 2017). Since Hutchinson (1959) put forward the concept of species coexistence, hundreds of ecologists have proposed various theories and hypotheses to explain this issue (Wrigh, 2002; Robert et al., 2010). Among the proposed theories, niche theory, neutral theory, and Janzen-Connell hypothesis are the most controversial (Chesson, 1991; McGill, 2003; Scott, 2003; Adler et al., 2007; Ryan and Stephen, 2010). The niche theory emphasizes that species can coexist by self-balancing their ecological requirements to match a habitat. The niche theory claims that one species can be in strong competition in this habitat but weak in

another and many different species can coexist in a community (Grinnell, 1917; Gause, 1934; Elton, 2001). Unlike the niche theory, the neutral theory holds that all individuals, regardless of species, are ecologically equivalent such as fertility, mortality rates, migration, and probability of becoming new species (Hubbell, 2001). The neutral theory adds that species diversity is maintained through dispersal limitation and ecological drift (Hubbell, 2006; Zhou and Zhang, 2006). Janzen (1970) and Connell (1971) hypothesized that density limits the survival of seedlings. According to the Janzen-Connell hypothesis, the impact of pests (pathogenic microorganisms and herbivores) and the resource competition between neighbor individuals will reduce the growth rate and increase the death rate of individuals of the same species, providing space and resources for other species and driving species coexistence in the community (Norghauer et al., 2006; Dalling et al., 2009). Although different theories and hypotheses may be right at particular time and space scales, in reality, no unified and complete theory can explain the coexistence of species in different communities on a global scale (Yao et al., 2018). For example, the competitive exclusion principle states that if two species share limited resources, only one dominant species will be left in the long run, with the weaker competitor being eliminated (Hardin, 1960). The competitive exclusion principle is considered appropriate to explain the coexistence of temperate forest plant species (Xiang et al., 2004). Still, this principle cannot explain the coexistence of thousands of plant species in species-rich tropical forests (Li et al., 2020). Therefore, studying the coexistence mechanism of species is still very challenging and needs further clarification.

Space is a final frontier for ecology (Kareiva, 1994), and the spatial pattern of trees refers to the distribution of tree individuals in a horizontal plane (Sun et al., 2016). The spatial pattern of the population results from interactions of tree individuals and their habitat (Fan and Yu, 2016; Quy et al., 2021). The spatial pattern of forest trees reflects species' spatial distribution and ecological relationships in the forest community (Wang et al., 2020). Studying the spatial pattern of forest trees can help to understand the population dynamics, clarify the plant community's formation mechanism, and provide a scientific basis for developing related management and conservation measures (Quy et al., 2021). On the other hand, the spatial association of species is one of the important characteristics of plant communities (Yao et al., 2018). Studying the spatial associations of species can provide knowledge of the internal characteristics of populations and communities and species coexistence (Quy et al., 2022). This information is really helpful in restoring ecosystems, especially in the conservation of threatened species.

Knema pierrei Warb is an evergreen tree belonging to the genus *Knema* in the family Myristicaceae (Hop, 2002); it is indigenous species of Indochina and is naturally distributed in Vietnam and Laos (Pham, 1999). In Vietnam, *K. pierrei* is one of twenty-two recorded members of the Myristicaceae family, and it often grows scattered in natural forests in many provinces such as Lang Son, Yen Bai, Ninh Binh, Thanh Hoa, Nghe An, Dong Nai, and Ba Ria - Vung Tau (Hop, 2002). *K. pierrei* is multi-use species, its wood is preferred in construction (Son et al., 2018), and the seeds can be used medicinally to treat skin diseases (Chi, 2015). *K. pierrei* is shade-tolerant when it is a juvenile tree, but its mature tree is light-demanding, grows well on moist soil, and has poor drought tolerance (Duong et al., 2014). *K. pierrei* is classified as 'Vulnerable' on the IUCN Red List (1998), and its distribution range is increasingly being narrowed by logging and encroachment on forest land (Duong et al., 2020). Studies related to the ecology of the species *K. pierrei* are generally relatively few. According to our knowledge, only a few authors have conducted studies on species identification, analyzing active ingredients in

seeds and the effects of light and fertilizers on the growth of *K. pierrei*. Moreover, the application of the spatial point pattern analysis method in forest research in Vietnam and other countries in Southeast Asia has yet to be given due attention (Tuan et al., 2018).

The current study was conducted to provide additional information on the ecological characteristics of *K. pierrei*, establishing a scientific basis for afforestation and conservation efforts, and expanding the distribution area of this species in Vietnam. We employed the spatial point pattern analysis method to examine the spatial patterns and associations of *K. pierrei* and co-dominant species in the evergreen broadleaved forest stands on the Con Dao Islands. We hypothesized that: (i) the spatial distribution patterns of *K. pierrei* and its associations with other species are influenced by environmental conditions and spatial scale, and (ii) analyzing different diameter at breast height (dbh) classes, which represent the life-history stages of *K. pierrei*, will help illuminate the population dynamics of this tree species. Based on these assumptions, we sought to address the following research questions: (1) Which tree species commonly grow alongside *K. pierrei*, and what is their ecological role in forest stands? (2) What are the spatial patterns of *K. pierrei* at various life-history stages? (3) How does *K. pierrei* coexist with co-dominant species? (4) What mechanisms control the spatial patterns and associations of *K. pierrei* and co-dominant species in forest stands?

Materials and methods

Study area

This study was performed within the evergreen broadleaved forest stands in Con Dao National Park, Con Dao Islands, Ba Ria - Vung Tau province, southern Vietnam. The geographical coordinates of Con Dao National Park is 8°36'-8°48' North latitude and 106°31'-106°46' East longitude, located 80 km from the mainland, including 14 small islands. Con Dao National Park is one of the few national parks in Vietnam where forest resources are almost intact. The total natural area of this National Park is 19883.15 ha, in the forest area is 5145.11ha. The climate regime of the region has two seasons: the rainy season from May to October and the dry season from November to April of next year. The average annual temperature of the area is 26.2°C, while the relative humidity is 90%, and the average annual rainfall is 2,200.3 mm. The topography of Con Dao National Park is a mainly low mountain, with an altitude of 50-200 m above sea level and a slope of 20-25° (Quang, 2020).

The study plots are on two islands of Con Dao National Park, Con Son and Hon Ba. The coordinate positions of the study plots are as follows (Fig. 1):

Plot 1: 8°43'15.33" N of latitude and 106°36'48.62" E of longitude (Con Son Island);

Plot 2: 8°40'57.82" N of latitude and 106°35'12.26" E of longitude (Con Son Island);

Plot 3: 8°40'28.34" N of latitude and 106°40'18.68" E of longitude (Hon Ba Island).

The plant community of the study area has dominant tree species such as *Knema pierrei* Warb., *Pterospermum mucronatum* Tard., *Diospyros maritima* Bl., *Garcinia ferrea* Pierre., *Smilax luzonensis* Presl, *Xerospermum noronhianum* (Bl.) Bl., *Syzygium cumini* (L.) Druce., *Machilus thunbergii* var. *condorensis* Lec., and *Bischofia javanica* Bl.

The study was conducted from January 2022 to June 2022 with three field surveys in Con Dao National Park.

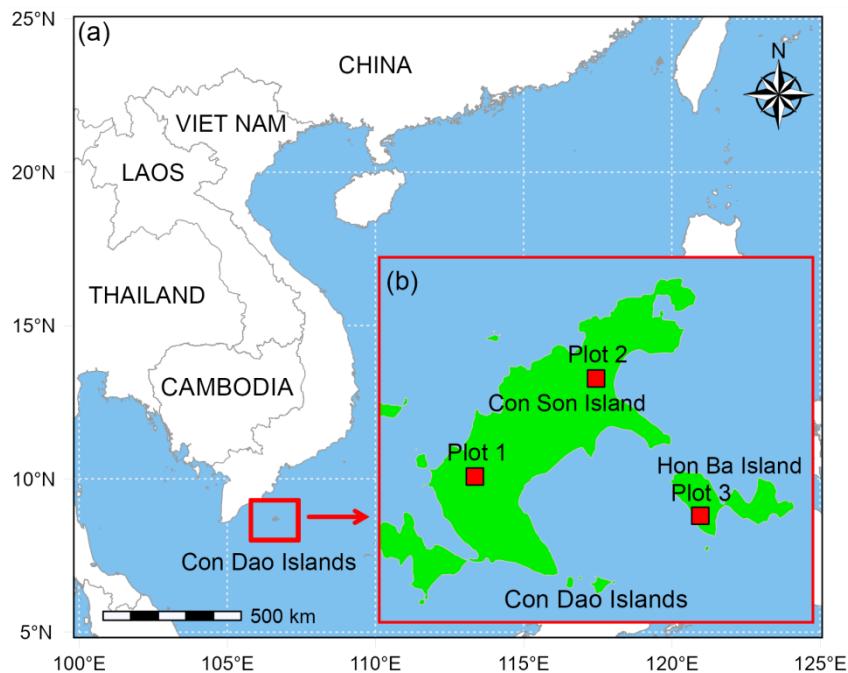


Figure 1. The study area map. Map of Vietnam (a) and the study area (b)

Data collection

Three study plots with an area of 2 ha each (100 m × 200 m) were established in the study area. We used the square grid to divide the study plot into 200 subplots; each subplot's area is 100 m² (10 m × 10 m). The purpose of dividing the study plot into subplots is to facilitate data collection and avoid omitting the survey tree.

In the subplot, all tree individuals with a diameter at breast height (dbh) ≥ 2.5 cm were tapped, numbered, and measured. The coordinates of all trees in the study plot were determined using a laser distance meter (Leica Disto D2) and a compass.

All individual trees of the study plots are divided into one of three basic life-history stages, namely, juvenile (dbh < 5 cm), premature (5 cm ≤ dbh ≤ 10 cm), or mature (dbh > 10 cm) (Quy et al., 2021).

Data analysis

Tree species identification

The tree species name was identified by the plant comparative morphology method; the references used included: Plants of Vietnam (Ho, 1999) and Vietnam Forest Trees (Hop, 2002); the scientific names of species are corrected according to the World Flora Online (<http://104.198.148.243>).

Dominant species identification

This study identified the dominant species based on a species' important value (IV) index. The importance value is a comprehensive quantitative indicator used to characterize the status and role of each species in a community. The formula for calculating the IV index is as follows (Thuy and Patrick, 2016):

$$IVI = \frac{N_i\% + BA_i\%}{2} \quad (\text{Eq.1})$$

where, *IVI* is the important value index of species *i*, $N_i\%$ is the percentage of tree individuals of species *i* compared to the total number of tree individuals in the study plot, and $BA_i\%$ is the percentage of the total basal area of species *i* compared to the total basal area of all species in the study plot. Only species with $IVI \geq 5\%$ must be genuinely ecologically significant (Marmillod, 1982).

Spatial analysis

The spatial point pattern analysis method considers the distance between two adjacent points and the distance between all points in the pattern (Jia et al., 2016). Compared with Ripley's K function, the pair-correlation function $g(r)$ is closely related to the second-order product density and can effectively prevent cumulative effects. In this study, we used the univariate pair-correlation function $g_{11}(r)$ to analyze the spatial pattern of the species *K. pierrei*. Besides, the bivariate pair-correlation function $g_{12}(r)$ was used to analyze the spatial associations of species pairs (*K. pierrei* and co-dominant species) or two tree groups of *K. pierrei* at two different life-history stages.

The function $K(r)$ is the expected number of points in a circle of radius *r* centered at an arbitrary point (which is not counted), divided by the intensity of the point pattern. The pair correlation function $g(r)$, which arises if the circles of Ripley's K-function are replaced by rings (Stoyan and Penttinen, 2000; Dale et al., 2002), gives the expected number of points at distance *r* from an arbitrary point, divided by the intensity of the pattern. Of special interest is to determine whether a pattern is random, aggregated, or regular. Significance is usually evaluated by comparing the observed data with Monte Carlo envelopes from the analysis of multiple simulations of a null model. The formula for calculating the function $K(r)$ is as follows (Ripley, 1981):

$$K(r) = \frac{A}{n^2} \sum_{i=1}^n \sum_{j=1(j \neq i)}^n \frac{I_r(u_{ij})}{w_{ij}} \quad (\text{Eq.2})$$

where, u_{ij} is the distance between two random points *i* and *j*; *A* is the area of the study plot; w_{ij} is a weighting factor correcting for edge effects; *n* is the total number of points in the study plot; $I_r(u_{ij})$ is an indicator function, if $u_{ij} < r$ then the value $I_r(u_{ij}) = 1$, otherwise if $u_{ij} > r$ then the value $I_r(u_{ij}) = 0$.

The function $K(r)$ was linearized by square root transformation $L(r)$ as proposed by Besag to stabilize the variance and simplify the interpretation of $K(r)$. The formula for calculating the function $L(r)$ is as follows (Besag, 1977):

$$L(r) = \sqrt{K(r)/\pi} \quad (\text{Eq.3})$$

where, the value $L(r) = 0$ indicates the points are completely randomly distributed; if the value $L(r) > 0$ indicates the points are aggregated, conversely, the value $L(r) < 0$, the points are regularly distributed up to the distance *r*.

The pairwise correlation function $g(r)$ overcomes the cumulative effect of Ripley's K function on small scales and prevents it on large scales. The pairwise correlation function $g(r)$ is more reliable than Ripley's K function for measuring the degree of deviation

between the actual distribution and its expected value at a given point and scale (Ripley, 1977; Zhu et al., 2011). Therefore, we used the pairwise correlation function $g(r)$, which was developed by Ripley's K function (Ripley, 1976; Wiegand and Moloney, 2004) based on the following forms:

$$g(r) = \frac{K'(r)}{2\pi r} \quad (\text{Eq.4})$$

where, $K'(r)$ is the derivative of the K function with respect to r (also known as scale).

For the univariate function $g_{11}(r)$ (the same tree species or a group of trees): if the value of $g_{11}(r) = 1$ indicates the points are randomly distributed; if the value of $g_{11}(r) > 1$ indicates the points are aggregated and vice versa if the value of $g_{11}(r) < 1$ means the points are regularly distributed at the distance r between the points of the pattern (Nguyen et al., 2014; Quy et al., 2022).

For the bivariate function $g_{12}(r)$ (describing the expected density of species 2 at a distance r from any point of species 1): if the value of $g_{12}(r) = 1$ means the association pattern of two species is independent; if the value of $g_{12}(r) > 1$ indicates the association pattern of two species is an attraction (facilitation); conversely if the value of $g_{12}(r) < 1$ indicates the association pattern of two species is repulsion at distance r (Quy et al., 2022).

In spatial analysis, it is necessary to select a null model (simulation model of observed values) based on the habitat homogeneity in the study plot to eliminate errors in spatial pattern judgment. The null models used in this study include: (1) the null model of complete spatial randomness (CSR) (also known as homogeneous Poisson Process) for the functions $g_{11}(r)$ and the $L_{11}(r)$ of the mature trees in the study plots. (2) The null model of the inhomogeneous Poisson process (IPP) was used to analyze the spatial pattern of the species *K. pierrei* when the habitat of the study plot was inhomogeneous; conversely, if the habitat of the study plot was homogenous, the null model of CSR was used. (3) The null model of random superposition (RS) was used to analyze the spatial association patterns of *K. pierrei* at different life-history stages and the spatial association patterns of *K. pierrei* and co-dominant species in the forest stand (Quy et al., 2022). The RS null model assumes that the two-point patterns were created by two independent processes (Wiegand and Moloney, 2004). It is largely used to investigate the relationship between two species, size classes, or life-history stages (Ben-Said, 2021).

As a basic rule in spatial analysis, the maximum analyzed spatial scale does not exceed half of the shortest side length of the study plot (Tian and Lu, 2022). Therefore, this study's spatial point model analysis scale is 50 m. All spatial analyzes were performed on Programita 2018 software with 199 Monte Carlo simulations (Wiegand and Moloney, 2014). We used the fifth maximum and the fifth minimum values of 199 Monte Carlo simulations to construct approximate 95% confident intervals and to evaluate significant departures from the null models. The distribution map of forest trees was built by Package 'spatstat' (Baddeley and Turner, 2005) and 'ggplot2' (Wickham, 2016) on R software version 4.2.2 (R Core Team, 2021).

The habitat homogeneity was tested based on the spatial pattern of mature trees in the study plot. Mature trees were selected as analyzed objects because they can live in all possible locations in the study plot and have undergone natural selection (Getzin et al., 2006). The spatial pattern of mature trees will reflect the habitat homogeneity in the study plot. If the mature trees are relatively uniformly distributed over the study plot, which indicates that the study plot's habitat is homogeneous. On the contrary, if the mature trees are not uniformly distributed, the habitat of the study plot is not homogeneous.

Results

Woody species grow with *K. pierrei* and their ecological role

The study identified seventy-two woody species within three study plots of evergreen broadleaved forest in Con Dao National Park. While the number of species among the study plots showed minimal variation, there was a clear contrast in the number of tree individuals between them. The study plots on Con Son Island (Plots 1 and 2) had more trees than on Hon Ba Island (Plot 3). The number of species recorded was fifty-four species with 2806 individuals in Plot 1, forty-three species with 2847 individuals in Plot 2, and fifty-three species with 1729 individuals in Plot 3. The species composition according to the IV index is shown in *Table 1*.

Table 1. Species composition in the stands

Plot	S	N	Species composition by IV index
1	54	2806	16 <i>Knema pierrei</i> + 11.4 <i>Pterospermum mucronatum</i> + 10.3 <i>Diospyros maritima</i> + 7.5 <i>Garcinia ferrea</i> + 6.9 <i>Smilax luzonensis</i> + 6.6 <i>Xerospermum noronhianum</i> + 5.6 <i>Syzygium cumini</i> + 4.4 <i>Alangium salvifolium</i> + 3.0 <i>Aglaia poulocondorensis</i> + 2.4 <i>Sandoricum koetjape</i> + 2.2 <i>Sageraea elliptica</i> + 2.1 <i>Pithecellobium marcrocarpum</i> + 2.1 <i>Dipterocarpus condorensis</i> + 2.0 <i>Xylopia vielana</i> + 1.7 <i>Memecylon scutellatum</i> + 1.4 <i>Litsea pierrei</i> + 14.4 Others.
2	43	2847	14.2 <i>Syzygium cumini</i> + 13.8 <i>Garcinia ferrea</i> + 11.7 <i>Xerospermum noronhianum</i> + 10.8 <i>Knema pierrei</i> + 6.8 <i>Machilus thunbergii</i> var. <i>condorensis</i> + 5.4 <i>Smilax luzonensis</i> + 4.3 <i>Bischofia javanica</i> + 3.3 <i>Diospyros maritima</i> + 2.9 <i>Schefflera octophylla</i> + 2.1 <i>Dipterocarpus condorensis</i> + 1.7 <i>Alstonia scholaris</i> + 1.3 <i>Lagerstroemia indica</i> + 1.2 <i>Litsea pierrei</i> + 1.0 <i>Aglaia littoralis</i> + 1.0 <i>Alangium salvifolium</i> + 0.9 <i>Memecylon scutellatum</i> + 0.8 <i>Aglaia poulocondorensis</i> + 16.8 Others.
3	53	1729	29.5 <i>Xerospermum noronhianum</i> + 13.4 <i>Knema pierrei</i> + 8.5 <i>Bischofia javanica</i> + 5.5 <i>Machilus thunbergii</i> var. <i>condorensis</i> + 4.9 <i>Alstonia scholaris</i> + 4.4 <i>Schefflera octophylla</i> + 4.2 <i>Sandoricum koetjape</i> + 4.0 <i>Syzygium cumini</i> + 3.5 <i>Aporusa tetrapleura</i> + 2.6 <i>Aglaia poulocondorensis</i> + 1.6 <i>Diospyros maritima</i> + 1.4 <i>Barringtonia macrostachya</i> + 16.5 Others.

S - Number of species; N - number of individuals; IV index - importance value index expressed as a percentage

Table 1 shows that the IV index of *K. pierrei* is different between the study plots; this species had the highest IV index (16%) in Plot 1, followed by Plot 3 (13.4%) and the lowest in Plot 2 (10.8%). This result indicated that the predominant ability of *K. pierrei* is different in different habitats. In addition, the results also showed that *K. pierrei* is an ecologically significant species (IVI > 5%) in all three study plots and often occurs with some species such as *P. mucronatum*, *D. maritima*, *G. ferrea*, *S. luzonensis*, *X. noronhianum*, *S. cumini*, *M. thunbergii* var. *condorensis*, and *B. javanica*, forming an ecologically dominant species group in the islands of Con Dao National Park.

Habitat heterogeneity effects

The analysis result of the function $L_{11}(r)$ showed that the cumulative density of all mature trees in two study plots, Plots 1 and 2, was the same, there was no aggregation at scales of 0-50 m, and their spatial patterns were randomness (*Fig. 2d, e*); Conversely, mature trees of Plot 3 showed aggregated pattern at scales from 15-50 m (*Fig. 2f*). In

addition, the function $g_{11}(r)$ also showed that mature trees only have a random distribution at all scales from 5-50 m in two Plots 1 and 2 (Fig. 2g, h). Still, mature trees of Plot 3 have two distribution patterns: aggregation and randomness at scales of 0-50 m. The distribution map of all mature trees also indicated that most of the locations in the two study plots, Plots 1 and 2, have mature trees (Fig. 2a, b); meanwhile, Plot 3 has many locations where there was no mature trees distribution (Fig. 2c). From the result of two functions, $g_{11}(r)$ and $L_{11}(r)$, it can be confirmed that the original hypothesis about habitat homogeneity of Plot 3 is rejected; for Plots 1 and 2, this hypothesis is accepted. Therefore, the null models selected to perform the spatial pattern and association analysis of *K. pierrei* is the null model of IPP for Plot 3 and CSR for Plots 1 and 2.

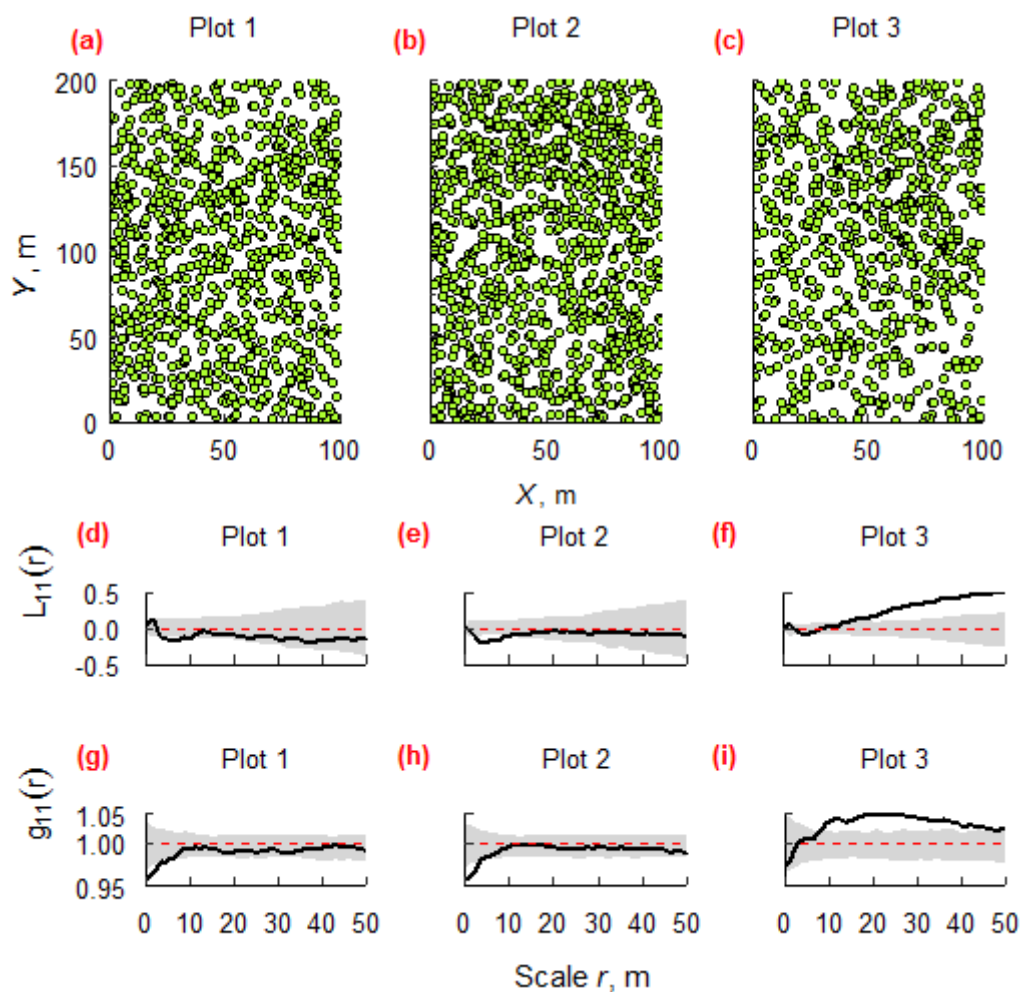


Figure 2. Locations of mature trees in the study plots (a-c). The plot of the empirical univariate L - and g -functions as solid black lines (d-i). The grey shading areas are acceptance regions, bounded by 95% pointwise envelopes based on 199 Monte Carlo simulations of homogeneous Poisson processes. The horizontal dashed red lines show the theoretical functions of a homogeneous Poisson process

Spatial pattern of *K. pierrei*

The spatial patterns of all *K. pierrei* trees in the study plots showed a difference between homogeneous and heterogeneous habitats. Under homogenous habitat (Plots 1 and 2), *K. pierrei* tends to aggregate at small scales ($r < 10$ m) and then shift to a random

or regular distribution at large scales ($r > 10$ m) (Fig. 3d, e). In contrast, the spatial pattern of all *K. pierrei* trees under heterogeneous habitats showed aggregation at both small-scale and large-scale (Fig. 3f). This result indicated that in addition to the influence of habitat and spatial scale were also a factor affecting the spatial patterns of the species *K. pierrei*. On the other hand, the tree distribution map of *K. pierrei* (Fig. 3a-c) showed that most of the locations of Plot 1 have *K. pierrei* trees (Fig. 3a); meanwhile, many locations of the remaining two study plot, Plots 2 and 3 did not have *K. pierrei* trees distributed (Fig. 3b, c); this result did not contradict to the analyzed results of the IV index. Hence, the IV index of one species, besides indicating its dominant degree, can also reflect the ability to occupy the space of the species.

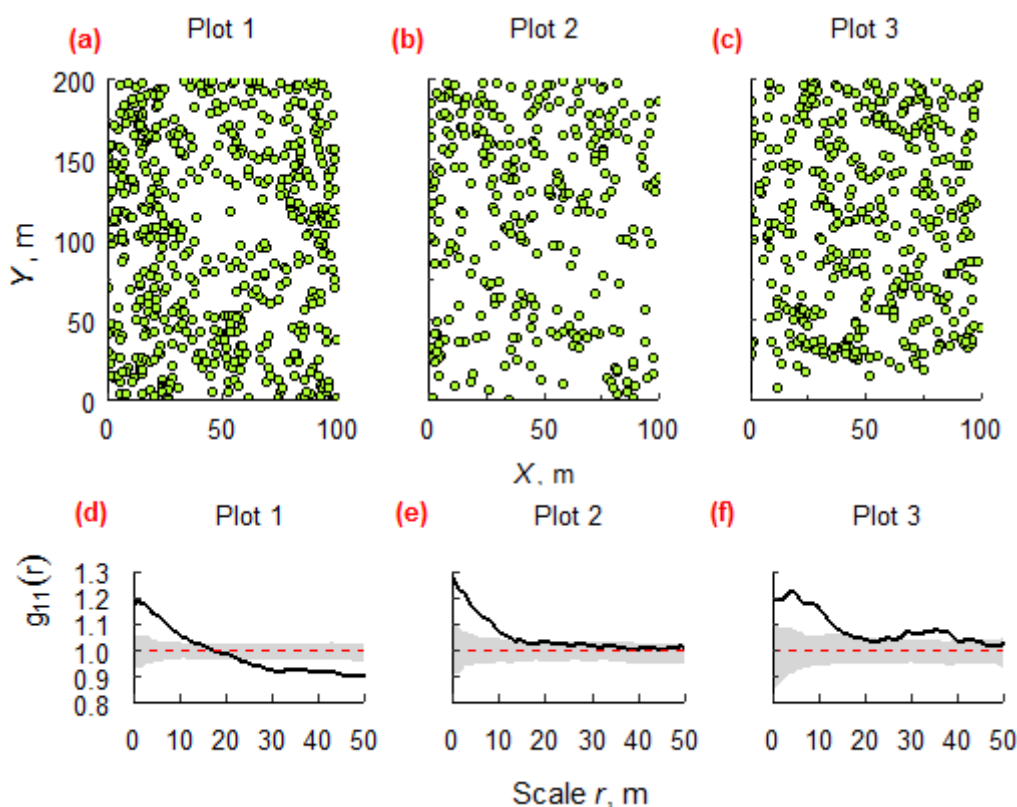


Figure 3. Locations of *K. pierrei* trees in the study plots (a-c). The plot of the empirical univariate g -function as solid black lines (d-f). The grey shading areas are acceptance regions, bounded by 95% pointwise envelopes based on 199 Monte Carlo simulations of homogeneous Poisson process (d, e) and inhomogeneous Poisson process (f). The horizontal dashed red lines show the theoretical functions of Poisson processes

As with the spatial pattern of all *K. pierrei* trees, the spatial pattern of this species at life-history stages has differences between homogeneous and heterogeneous habitats (Fig. 4). The spatial pattern of *K. pierrei* tended to shift from aggregation at the juvenile stage to randomness at the premature stage and regularity at the mature stage under homogenous habitat (Fig. 4a-f). In contrast, the premature and mature trees of *K. pierrei* had only aggregated and random patterns under heterogeneous habitats (Fig. 4g-i). These results showed that, ignoring the influence of habitat conditions, the spatial pattern of *K. pierrei* was not the same at different growth stages.

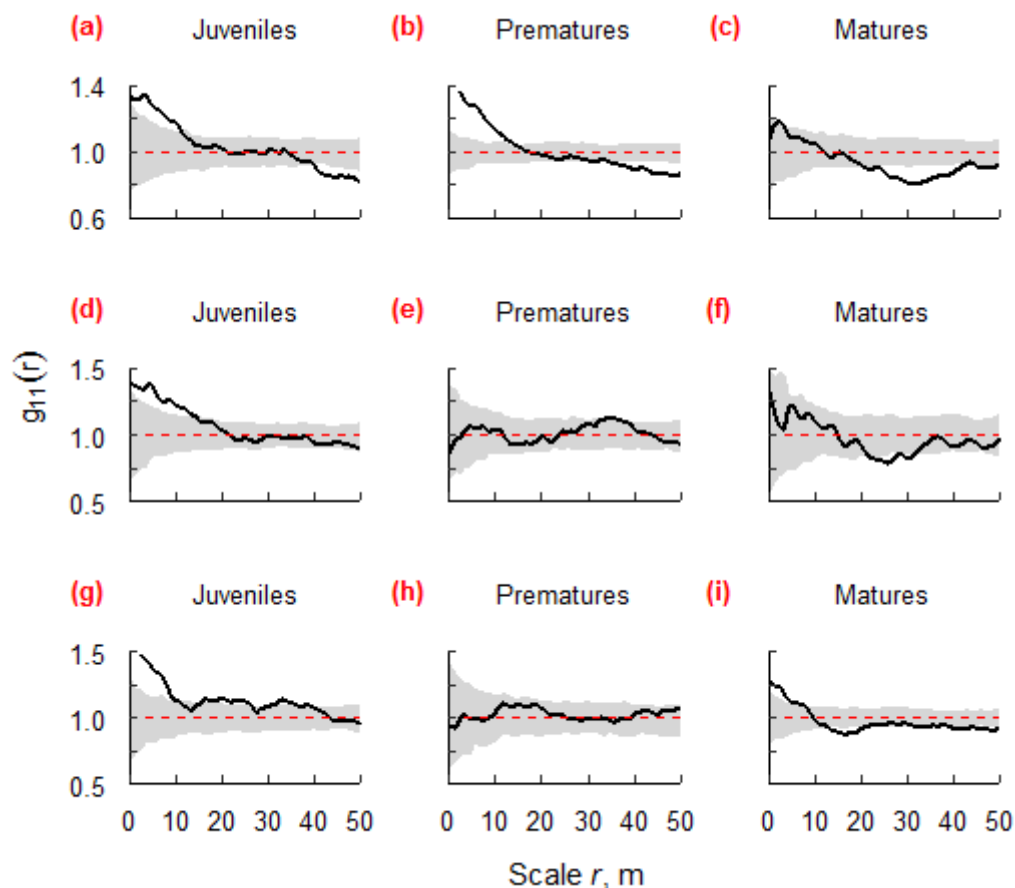


Figure 4. Spatial distribution patterns of *K. pierrei* at different life-history stages in Plot 1 (a-c), Plot 2 (d-f), and Plot 3 (g-i). The solid black lines represent the univariate g -function for the observed distribution. The grey shading areas are acceptance regions, bounded by 95% pointwise envelopes based on 199 Monte Carlo simulations of homogeneous Poisson process (a-f) and inhomogeneous Poisson process (g-i). The horizontal dashed red lines show the theoretical functions of Poisson processes

Intraspecific associations of K. pierrei

The spatial association patterns of *K. pierrei* are shown in *Figure 5*. The results showed that regardless of the difference in habitat, the association patterns of *K. pierrei* species had common characteristics at all life-history stages. For example, the spatial associations between mature and juvenile trees of *K. pierrei* showed an attraction (*Fig. 5a, d, g*); vice versa, the spatial associations between premature and juvenile trees showed independence (*Fig. 5c, f, i*), and between mature and premature trees of this species showed a repulsion (*Fig. 5b, e, h*). This result indicated among *K. pierrei* individuals had competition for nutrient space when the tree size increased. On the other hand, our findings also showed that intraspecific interaction of *K. pierrei* individuals had a very clear difference between the two spatial scales $r < 30$ m and $r > 30$ m; the positive interaction (attraction) or negative interaction (repulsion) mainly appear at spatial scales $r < 30$ m.

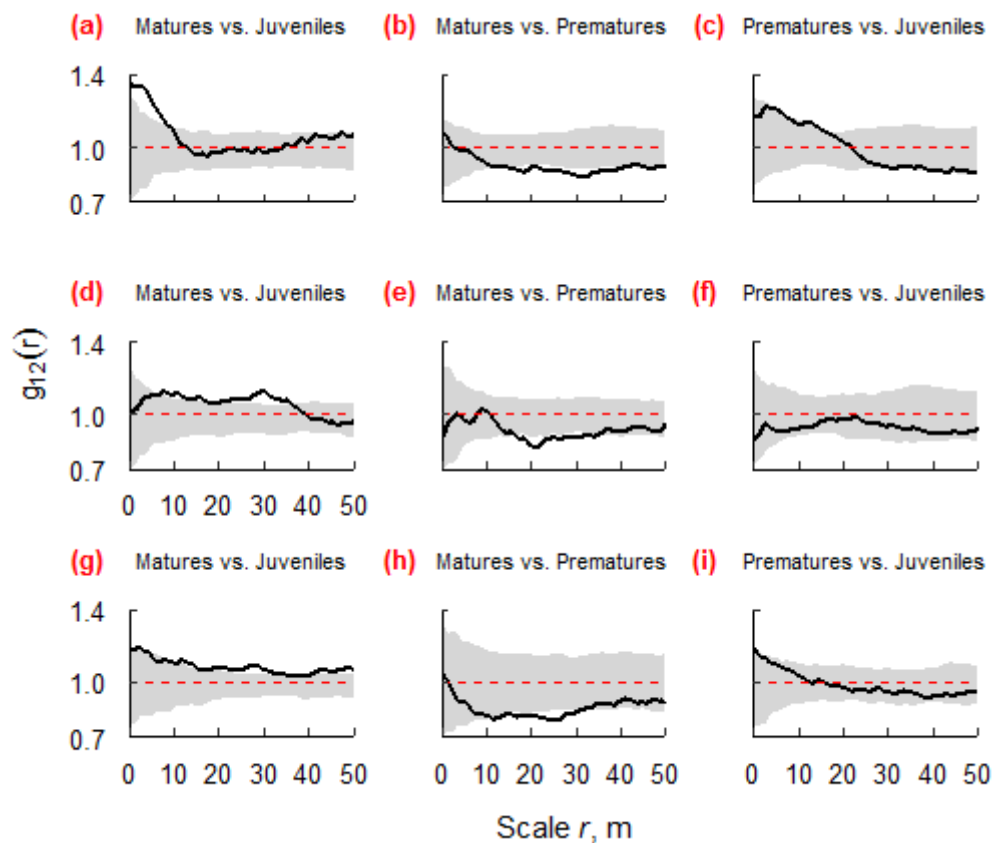


Figure 5. Intraspecific association patterns of *K. pierrei* in Plot 1 (a-c), Plot 2 (d-f), and Plot 3 (g-i). The solid black lines represent the bivariate g -function for the observed distribution. The grey shading areas are acceptance regions, bounded by 95% pointwise envelopes based on 199 Monte Carlo simulations. The horizontal dashed red lines are the values of the function when the two types of point are spatially independent

Interspecific associations of *K. pierrei*

The spatial association patterns of *K. pierrei* and co-dominant species showed that the independent association accounted for a higher proportion than attraction and repulsion at all scales of 0-50 m (Fig. 6, A1, A2, and A3). Similar to the intraspecific associations of *K. pierrei*, the interspecies interactions between *K. pierrei* and co-dominant species had a significant difference at the two spatial scales $r < 30$ m and $r > 30$ m; especially, this difference is more obvious in heterogeneous habitats. The independent association between *K. pierrei* and co-dominant species tends to increase with the increase of scale under homogenous habitat; on the contrary, the independent association tends to decrease in heterogeneous habitat conditions. Attraction at small scales ($r < 10$ m) accounted for a higher proportion than at large scales ($r > 10$ m) in homogenous habitats (Plot 2), which is evidence of the dispersal limitation of species. The attraction between *K. pierrei* and co-dominant species tends to increase at the scales $r > 30$ m when the habitat of the study plot was heterogeneous. This result showed that habitat heterogeneity affects the spatial association pattern of *K. pierrei* and co-dominant species in the forest stand; it also indicates that species interaction mainly occurs on small scales.

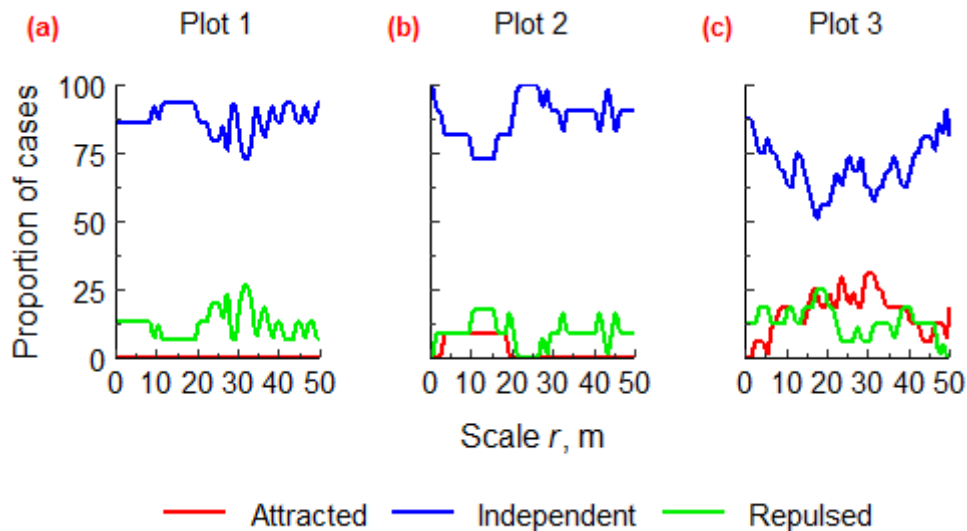


Figure 6. Interspecific association patterns of *K. pierrei* and co-dominant species as analyzed by the bivariate g -function under the null model of random superposition

Discussion

Tree species often grow with K. pierrei

Tropical forests are complex ecosystems regarding structure and species composition diversity (Thin, 2004). Some plant species are more adapted than others due to extreme habitat conditions or under certain soil conditions; their individuals are ecologically dominant in the forest stand (Trung, 1978). These species form one group with a high or continuous presence in the community, called plant associations (Lan et al., 2006). Under normal circumstances, the tropical forest community usually has only one group of species with relative dominance, the number of individuals of each species accounts for about 5% of the total number of individuals in the stand, and this species group is called the group of dominant species (Trung, 1978). Because tropical forests have a high diversity in species composition, but the density of each species is often low, identifying the dominant tree species group can accurately reflect the status of the stand (Quy et al., 2022). The dominant species of the stand are usually identified based on the number of individuals and their relative spatial relationships (Lan et al., 2006). The traditional method determines the dominant degree of species mainly using a species' ecological criteria, such as relative density, relative coverage, and basal area. In addition, some authors also believe that the species composition can reflect a stand's structural stability (Huang and Zhao, 2009).

Each vegetation type is formed under different environmental conditions, so dominant species appear (Thin, 2004). The species composition of three study plots showed that *K. pierrei* often grows with twenty-three other species, including *L. pierrei*, *S. octophylla*, *B. macrostachya*, *D. condorensis*, *A. salvifolium*, *L. indica*, *A. poulocondorensis*, *P. macrocarpum*, *M. thunbergii* var. *condorensis*, *S. luzonensis*, *P. mucronatum*, *A. scholaris*, *A. littoralis*, *B. javanica*, *G. ferrea*, *M. scutellatum*, *S. elliptica*, *S. koetjape*, *A. tetrapleura*, *D. maritima*, *S. cumini*, and *X. noronhianum*. *K. pierrei* is a species with real ecological dominance in forest stands; this species and twenty-three co-dominant species have created a typical forest ecosystem on the Con Dao Islands of Vietnam.

Habitat heterogeneity effects

Plant habitat combines many factors, such as topography, soil, light, water, and climate (Getzin et al., 2008). The interaction of these factors is different in time and space, which has created habitat heterogeneity (Li et al., 2020). Many studies have shown that habitat heterogeneity directly affects species distribution, or, in other words, their spatial patterns are affected by habitat heterogeneity (Shen, 2010). The population will have different spatial patterns in different habitats, such as randomness, aggregation, or regularity (Wu et al., 2018). Some studies also often use spatial patterns of mature trees to reflect habitat heterogeneity on the study plot indirectly (Getzin et al., 2006; Dien and Hai, 2016; Quy et al., 2022). These authors believe that if mature trees are clustered at scales of $r > 10$ m, it proves that the habitat is heterogeneous. Habitat heterogeneity within the same study plot has proven to be a fairly common phenomenon (Wiegand et al., 2007). Liu et al. (2021) used two types of null models to evaluate the spatial pattern of woody species in the secondary temperate forest of northeastern China; they found that habitat heterogeneity significantly affects the aggregated intensity of tree species in the study plot. Tuan et al. (2018) indicated that habitat heterogeneity is one of the main factors that govern spatial patterns and associations of woody species in the evergreen broadleaved forest stand of Dong Nai Culture and Nature Reserve, Vietnam. Having the same above opinion, Phuong et al. (2022) also suggested that habitat heterogeneity plays an important role in forming the evergreen broadleaved forest plant community in Central Vietnam.

In our study, the spatial pattern of mature trees is also used to evaluate habitat heterogeneity in the study plots indirectly. The analysis results showed that the spatial pattern of mature trees was not the same; the habitat of the study plots is evaluated to be relatively homogeneous for the two study plots on Con Son Island (Plots 1 and 2) and heterogeneous for the study plot on Hon Ba Island (Plot 1). Considering the spatial pattern of *K. pierrei*, we found that aggregated intensity of this species in homogeneous habitat conditions tended to decrease as the spatial scale increased. Still, the aggregated intensity of *K. pierrei* was not changing if the habitat was heterogeneous. From the analysis results of habitat effects, we concluded that the environmental conditions of the study plot significantly influence the *K. pierrei* population's spatial pattern, namely aggregated intensity of this species at different spatial scales.

Spatial pattern of *K. pierrei*

The spatial pattern of the plant population is determined by the biological characteristics and the interaction between species with their habitat (Zhu et al., 2020). In addition, spatial patterns of populations can reflect intraspecific interactions of individuals (Li et al., 2003). The aggregated pattern indicates that the interactions between individuals are positive; they aggregate due to similarities in ecological needs or to dealing with adverse environmental conditions, which help improve their survival ability (Akhavan et al., 2012). The regular pattern indicates that intraspecific interactions of individuals are negative, compete for nutritional space, or have different responses to habitat (Long et al., 2015). The random pattern indicates that individuals' intraspecific interaction is less clear than positive or negative (Wu et al., 2018). Previous studies have shown that aggregation of plant species tends to decrease as the tree size increases; asymmetric competition occurs between individuals of the same or different species; large trees compete more strongly in the vicinity than small trees (Weiner, 1990). Juvenile

trees often have a higher aggregation intensity than premature and mature trees due to dispersal limitations and habitat heterogeneity (Lara-Romero et al., 2016).

In this study, the spatial patterns of *K. pierrei* have been analyzed, and the result was consistent with previous studies on the spatial pattern of tropical forest tree species. *K. pierrei* has fleshy fruit (Son et al., 2018), so its seed dispersal mechanism is short-distance dispersal and is influenced by Earth's gravity. For this reason, juveniles of *K. pierrei* are often distributed near the mother tree. On the other hand, the ecological characteristics of *K. pierrei* indicated that it is a shade-tolerant tree when juvenile and light-demanding in the mature stage (Ho, 1999). Hence, the cluster distribution of juvenile trees and random distribution of premature trees can be explained by the aggregation of juveniles in the shade and changes in light requirements at premature and mature tree stages. The spatial pattern of *K. pierrei* matures indicated competition for nutrient space and light requirements, manifested by the appearance of a regular pattern. Competition of mature trees will lead to natural self-thinning, increasing the distance between mature trees, thus reducing the cluster distribution at this stage.

From the spatial pattern of *K. pierrei* by life-history stages, we found that environmental conditions and underlying processes such as dispersal limitation and natural self-thinning influence this species' spatial pattern.

Spatial associations of K. pierrei

Forest tree species' spatial distribution and association patterns often change according to their life-history stages (Liu et al., 2021). In tropical forests, intraspecific interactions between individuals of species change from a positive interaction at the juvenile stage to a negative interaction at the mature tree stage (Long et al., 2015). Previous studies suggested that the spatial association of individuals in a population and between populations are also affected by environmental conditions, individual size, and species interactions (Li et al., 2003; Wu et al., 2018). In our study, an intraspecific association of *K. pierrei* between juveniles and matures was attraction (positive interaction); premature and mature trees of this species showed a repulsion (negative interaction). In contrast, the spatial association of its juvenile and premature trees was independent. These results were consistent with the ecological characteristics of *K. pierrei* were previously published by some authors. *K. pierrei* is not only a shade-tolerant tree when it is juvenile but also a moisture-loving tree with very poor drought resistance (Duong et al., 2014). In addition, *K. pierrei* is an evergreen tree, so its juvenile trees distributed near the mother tree will improve their survival in the dry season on Con Dao National Park islands. Having the same opinion as our study, Tian and Lu (2022) also showed that the closed canopy environment of mature trees is essential for the growth and development of juvenile trees as shade-tolerant species. During the growth and development of forest trees, the demand for light, water, and nutrients will increase as the tree age increases. Competition for resources is the cause of changes in the spatial patterns and associations among individuals of the same species (Yue et al., 2008).

Interspecific associations of species can reveal the ecological processes of forest tree populations, providing insight into community dynamics and a reference for forest vegetation restoration (Luambua et al., 2021). The spatial associations of *K. pierrei* and co-dominant species showed that it has independent and attractive patterns with many species at spatial scales of 0-50 m; this proves that it can use many co-dominant species to plant with *K. pierrei* in areas has similar soil and climate conditions to the study area. In the restoration and enrichment of forests in the ecological restoration zones of Con Dao

National Park, adjusting the density of tree species that grow together with *K. pierrei* can focus on increasing the density of species that have a positive interaction and reducing the density of species that compete with it.

Conclusion

Our study result indicated that *K. pierrei* was a tree species that played an important ecological role within the stands on the Con Dao Islands of Vietnam. The spatial patterns and associations of *K. pierrei* play an important role in population formation and maintenance of the coexistence of this tree species with other species in the stands. The spatial association analysis of *K. pierrei* and co-dominant species is significant in preserving and expanding the distribution area for *K. pierrei*. Measures for forest restoration and enrichment can be through adjusting species density that has positive and negative interactions with *K. pierrei*. Still, all silviculture measures should be done strictly with the current legislation about special-use forest management in Vietnam. This study has clarified the ecological characteristics of *K. pierrei*, making it possible for species conservation and afforestation with native trees in Vietnam to be more effective.

Acknowledgements. The authors are deeply thankful to the Con Dao National Park staff for their indispensable support during the fieldwork. Furthermore, we sincerely appreciate the valuable insights provided by Prof. Dr. Kang Yong Xiang from Northwest A&F University, China, and Assoc. Prof. Nguyen Thanh Tuan from Vietnam National University of Forestry – Southern Campus, Vietnam, on the manuscript. We also extend our special gratitude to Assoc. Prof. Nguyen Hong Hai for his valuable assistance in analyzing spatial point patterns.

REFERENCES

- [1] Adler, P. B., HilleRisLambers, J., Levine, J. M. (2007): A niche for neutrality. – Ecology letters 10(2): 95-104.
- [2] Akhavan, R., Sagheb-Talebi, K., Zenner, K. E., Safavimanesh, F. (2012): Spatial patterns in different forest development stages of an intact old-growth Oriental beech forest in the Caspian region of Iran. – European Journal of Forest Research 131: 1355-1366.
- [3] Baddeley, A., Turner, R. (2005): Spatstat: an R package for analyzing spatial point patterns. – Journal of Statistical Software 12(6): 1-42.
- [4] Barot, S. (2004): Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? – Oikos 106(1): 185-192.
- [5] Ben-Said, M. (2021): Spatial point-pattern analysis as a powerful tool in identifying pattern-process relationships in plant ecology: an updated review. – Ecological Processes 10(56): 1-23.
- [6] Besag, J. (1977): Contribution to the discussion of Dr. Ripley's paper. – Journals of the Royal Statistical Society B39: 193-195.
- [7] Chesson, P. (1991): A need for niches? – Trends in Ecology & Evolution 6(1): 26-28.
- [8] Chi, V. V. (1997): Dictionary of Medicinal Plants in Vietnam. – Medical Publishing House, Hanoi, Vietnam.
- [9] Connell, J. H. (1971): On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. – Dynamics of Populations 298: 312.
- [10] Dale, M. R. T., Dixon, P. M., Fortin, M. J., Legendre, P., Myers, D. E., Rosenberg, M. S. (2002): Conceptual and mathematical relationships among methods for spatial analysis. – Ecography 25: 558-577.

- [11] Dalling, J. W., Pearson, T. R., Ballesteros, J., Sanchez, E., Burslem, D. F. R. P. (2009): Habitat partitioning among neotropical pioneers: a consequence of differential susceptibility to browsing herbivores? – *Oecologia* 161(2): 361-370.
- [12] Dien, P. V., Hai, N. H. (2016): Spatial pattern and associations of tree species in a tropical evergreen broadleaved forest A Luoi, Thua Thien Hue. – *Science and Technology Journal of Agriculture and Rural Development, Vietnam Ministry of Agriculture and Rural Development* 1(2016): 122-128.
- [13] Du, H., Hu, F., Zeng, F., Wang, K. L., Peng, W. X., Zhang, H., Zeng, Z. X., Zhang, F., Song, T. Q. (2017): Spatial distribution of tree species in evergreen-deciduous broadleaf karst forests in southwest China. – *Scientific Reports* 7(1): 15664.
- [14] Duong, N. T., Trieu, D. T., Dung, N. A., Dung, L. T. (2014): The effect of light intensity to survival rate and growth of *Knema pierrei* Warb. – *Vietnam Journal of Forest Science* 4: 3590-3598.
- [15] Duong, N. T., Belyaeva, N. V., Danilov, D. A., Kazi, I. A. (2020): Lighting effect on growth *Knema pierrei* Warb. – *Proceedings of the Saint Petersburg Forestry Research Institute* 2020: 14-24.
- [16] Elton, C. S. (2001): *Animal ecology*. – University of Chicago Press, Chicago, United States.
- [17] Fan, D. X., Yu, X. X. (2016): Spatial point pattern analysis of *Quercus variabilis* and *Pinus tabulaeformis* populations in a mountainous area of Beijing. – *Acta Ecologica Sinica* 36(2): 318-325.
- [18] Fibich, P., Leps, J., Novotny, V., Klimes, P., Tesitel, J., Molem, K., Damas, K., Weiblen, G. D. (2016): Spatial patterns of tree species distribution in New Guinea primary and secondary lowland rain forest. – *Journal of Vegetation Science* 27(2): 328-339.
- [19] Gause, G. F. (1934): Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. – *Science* 79(2036): 16-17.
- [20] Getzin, S., Dean, C., He, F., Trofymow, J. A., Wiegand, K., Wiegand, T. (2006): Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. – *Ecography* 29(5): 6782.
- [21] Getzin, S., Wiegand, T., Wiegand, K., He, F. (2008): Heterogeneity influences spatial patterns and demographics in forest stands. – *Journal of Ecology* 96(4): 807-820.
- [22] Grinnell, J. (1917): The niche-relationships of the California Thrasher. – *The Auk* 34(4): 427-433.
- [23] Hardin, G. (1960): The competitive exclusion principle. – *Science* 131(3409): 1292-1297.
- [24] Ho, P. H. (1999): *Plants of Vietnam*. – Youth Publishing House, Hanoi, Vietnam.
- [25] Hop, T. (2002): *Vietnam Forest Trees*. – Agriculture Publishing House, Hanoi, Vietnam, 2002.
- [26] Huang, S. X., Zhao, X. H. (2009): Structure and spatial patterns of main woody plant populations in a natural *Pinus tabulaeformis* forest in Taiyue Mountain, Shanxi Province. – *For Resour Manage* 4: 41-47.
- [27] Hubbell, S. P. (2001): *The unified neutral theory of biodiversity and biogeography*. – Princeton University Press, Princeton, New Jersey, United States.
- [28] Hubbell, S. P. (2006): Neutral theory and the evolution of ecological equivalence. – *Ecology* 87(6): 1387-1398.
- [29] Hutchinson, G. E. (1959): Homage to Santa Rosalia or why are there so many kinds of animals? – *The American Naturalist* 93: 145-159.
- [30] Janzen, D. H. (1970): Herbivores and the number of tree species in tropical forests. – *The American Naturalist* 104(940): 501-528.
- [31] Jia, G., Yu, X., Fan, D., Jia, J. (2016): Mechanism underlying the spatial pattern formation of dominant tree species in a natural secondary forest. – *PLoS One* 11(3): e0152596.
- [32] Kareiva, P. (1994): Space: the final frontier for ecological theory. – *Ecology* 75(1): 1.
- [33] Lan, P. N., Hong, P. N., Hung, T. V., Thin, N. N., Chan, L. T. (2006): Natural forest ecosystem in Vietnam. – Vietnam Ministry of Agriculture and Rural Development, Hanoi, Vietnam.

- [34] Lara-Romero, C., de-la-Cruz, M., Escribano-Ávila, G., Garcia-Fernandez, A., Iriondo, J. M. (2016): What causes conspecific plant aggregation? Disentangling the role of dispersal, habitat heterogeneity and plant-plant interactions. – *Oikos* 125(9): 1304-1313.
- [35] Li, J. G., Ning, H. S., Liu, B. (2003): Study on character structure and distribution pattern of *Haloxylon ammodron*. – *Journal of Xinjiang Agricultural University* 26(3): 51-64.
- [36] Li, L., Huang, Z., Ye, W., Cao, H. L., Wei, S. Q., Wang, Z. G., Lian, J. Y., Sun, I. F., Ma, K. P., He, F. L. (2009): Spatial distributions of tree species in a subtropical forest of China. – *Oikos* 118(4): 495-502.
- [37] Li, L., Wei, S. G., Ma, J. M., Ye, W. H., Lian, J. Y. (2020): Relative effects of habitat heterogeneity and dispersal limitation on species diversity maintenance in south subtropical evergreen broad-leaved forest. – *Scientia Silvae Sinicae* 56(10): 1-10.
- [38] Liu, J., Bai, X., Yin, Y., Wang, W., Li, Z., Ma, P. (2021): Spatial patterns and associations of tree species at different developmental stages in a montane secondary temperate forest of northeastern China. – *PeerJ* 9: e11517.
- [39] Long, C., Yang, X. B., Long, W. X., Li, D. H. (2015): Stand thinning based on species diversity and spatial patterns. – *Chinese Journal of Ecology* 34(2): 571-581.
- [40] Luambua, N. K., Hubau, W., Salako, K. V., Amani, C., Bonyoma, B., Musepena, D., Rousseau, M., Bourland, N., Nshimba, H. S. M., Ewango, C., Beeckman, H., Hardy, O. J. (2021): Spatial patterns of light-demanding tree species in the Yangambi rainforest (Democratic Republic of Congo). – *Ecology and Evolution* 11(24): 18691-18707.
- [41] Marmillod, D. (1982): *Methodology and Results of Studies on the Composition and Structure of a Terrace Forest in Amazonia*. – The University of Göttingen, Göttingen, Germany, 1982.
- [42] McGill, B. J. (2003): A test of the unified neutral theory of biodiversity. – *Nature* 422(6934): 881-885.
- [43] Nguyen, H., Wiegand, K., Getzin, S. (2014): Spatial patterns and demographics of *Streblus macrophyllus* trees in a tropical evergreen forest, Vietnam. – *Journal of Tropical Forest Science* 26(3): 309-319.
- [44] Norghauer, J. M., Malcolm, J. R., Zimmerman, B. L., Felfili, J. M. (2006): An experimental test of density- and distant-dependent recruitment of mahogany (*Swietenia macrophylla*) in southeastern Amazonia. – *Oecologia* 148: 437-446.
- [45] Pham, H. H. (1999): *An illustrated the flora of Vietnam*. – Youth Publisher, Ho Chi Minh City, Vietnam.
- [46] Phuong, P. M., Quy, N. V., Huong, T. M. N., Tuan, N. T., Ha, P. T. (2022): Spatial distribution patterns and associations of woody plant species in the evergreen broad-leaved forests in Central Vietnam. – *Biol Bull Russ Acad Sci* 49(5): 369-380.
- [47] Quang, T. M. (2020): Morphology, abundance and the invasiveness of coral-killing sponge *Chalinula nematifera* (Porifera: Demospongiae) from Con Dao National Park, Vietnam. – *Vietnam Journal of Marine Science and Technology* 20(4): 95-103.
- [48] Quy, N. V., Kang, Y. X., Khot, C., Hop, N. V., Tuan, N. T. (2021): Spatial distribution and interspecific association patterns between *Shorea roxburghii* G. Don and other tree species in a South Vietnam evergreen forest. – *Applied Ecology and Environmental Research* 19(6): 4665-4681.
- [49] Quy, N. V., Ha, P. T., Tuan, N. T., Hop, N. V. (2022): Spatial distribution and association patterns of woody species in the broadleaved evergreen of Kon Ka Kinh National Park, Gia Lai Province. – *Can Tho University Journal of Science* 58(3): 191-203.
- [50] R Core Team (2021): *R: A language and environment for statistical computing*. – R Foundation for Statistical Computing, Vienna, Austria.
- [51] Ripley, B. D. (1976): The second-order analysis of stationary point processes. – *Journal of Applied Probability* 13(2): 255-266.
- [52] Ripley, B. D. (1977): *Modelling spatial patterns*. – *Journal of the Royal Statistical Society: Series B (Methodological)* 39(2): 172-192.
- [53] Ripley, B. D. (1981): *Spatial statistics*. – John Wiley Sons, New York.

- [54] Robert, B., Press, M. C., Scholes, J. D. (2010): Evolutionary history and distance dependence control survival of dipterocarp seedlings. – *Ecology Letters* 13(1): 51-59.
- [55] Ryan, A. C., Stephen, W. P. (2010): Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. – *Proceedings of the National Academy of Sciences* 107(36): 15821-15825.
- [56] Scott, N. (2003): Neutral theory: a new, unified model for ecology. – *BioScience* 53(2): 124-129.
- [57] Shen, G. C. (2010): The effects of habitat heterogeneity and dispersal limitation on species diversity in subtropical and tropical forests. – Zhejiang University, Hangzhou, China.
- [58] Son, H. T., Bon, T. N., Trung, V. Q., Linh, N. V., Dong, T. L. (2018): Handbook: Identification of some plant species in Dong Nai Biosphere Reserve. – The agricultural publishing house, Hanoi, Vietnam.
- [59] Stoyan, D., Penttinen, A. (2000): Recent application of point process methods in forest statistics. – *Statist. Sci.* 15: 61-78.
- [60] Sun, S. X., Wei, Z. J., Wu, X. H. (2016): Point pattern and spatial association of primary plant populations in the seasonal regulation of grazing intensity in desert grassland. – *Acta Ecologica Sinica* 36(23): 7570-7579.
- [61] Thin, N. N. (2004): Tropical Forest Ecosystems. – Hanoi National University Publishing House, Hanoi, Vietnam.
- [62] Thuy, T. N., Patrick, J. B. (2016): Structure and composition of deciduous dipterocarp forest in Central Vietnam: patterns of species dominance and regeneration failure. – *Plant Ecology & Diversity* 9(5-6): 589-601.
- [63] Tian, Y., Lu, J. (2022): Analysis methods of plant population structure and quantity dynamics. – *Journal of Green Science and Technology* 24(3): 89-94.
- [64] Trung, T. V. (1978): Forest Vegetation of Vietnam. – Agriculture Publishing House, Hanoi, Vietnam.
- [65] Tuan, N. T., Trang, B. T. T., Binh, N. T., Duy, V. D., Xuan, B. T. (2018): Spatial pattern and associations of predominant tree species in the unstable forest in the Dong Nai Culture and Nature Reserve. – *Journal of Vietnam Agriculture and Rural Development* 1(2018): 106-114.
- [66] Wang, Y. F., Qu, M. X., Lan, H. Y. (2020): Spatial pattern and interspecific correlation of dominant population in Spruce-fir-Korean pine forest. – *Journal of Central South University of Forestry & Technology* 40(1): 49-58.
- [67] Weiner, J. (1990): Asymmetric competition in plant-populations. – *Trends in Ecology & Evolution* 5: 360-364.
- [68] Wickham, H. (2016): *ggplot2: Elegant Graphics for Data Analysis*. – Springer-Verlag New York, United States.
- [69] Wiegand, T., Moloney, K. A. (2004): Rings, circles, and null-models for point pattern analysis in ecology. – *Oikos* 104(2): 209-229.
- [70] Wiegand, T., Gunatilleke, S., Gunatilleke, N. (2007): Species associations in a heterogeneous Sri Lankan dipterocarp forest. – *The American Naturalist* 170(4): 77-95.
- [71] Wiegand, T., Moloney, K. A. (2014): *A handbook of spatial point pattern analysis in ecology*. – Chapman and Hall/CRC press, Boca Raton, FL.
- [72] Wilson, J. B. (2011): The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. – *Journal of Vegetation Science* 22(1): 184-195.
- [73] World Conservation Monitoring Centre (1998): *Knema pierrei*. – The IUCN Red List of Threatened Species 1998: e.T37091A10030576.
- [74] Wright, S. J. (2002): Plant diversity in tropical forests: a review of mechanisms of species coexistence. – *Oecologia* 130: 1-14.
- [75] Wu, C. P., Yuan, W. G., Sheng, W. X., Huan, Y. J., Chen, Q. B., Shen, A. H., Zhu, J. R., Jiang, B. (2018): Spatial distribution patterns and associations of tree species in typical

- natural secondary forest communities in Zhejiang Province. – *Acta Ecologica Sinica* 38(2): 537-549.
- [76] Xiang, H. J., An, S. Q., Wang, Z. S., Zheng, J. W., Xin, L., Zhuo, Y. W. (2004): Plant diversity and the mechanism for its maintenance in tropical forests. – *Biodiversity Science* 12(2): 290-300.
- [77] Yao, L. J., Yao, L., Yi, Y. M., Ai, X. R., Feng, G., Liu, Y. C., Chen, S., Huang, W., Ding, Y., Zang, R. G. (2018): Spatial patterns of dominant species *Carpinus fargesiana* and *Cyclobalanopsis multinervis* in a subtropical evergreen and deciduous broad-leaved mixed forest. – *Scientia Silvae Sinicae* 54(12): 1-11.
- [78] Yao, H. F., Lu, J., Wang, C. (2021): Spatial pattern and correlation of dominant plants in *Pinus armandii* forest in Bomji Gang Township. – *Journal of Northwest Forestry University* 36(4): 110-117.
- [79] Yue, Y. J., Yu, X. X., Wu, J. (2008): Point pattern analysis of spatial distribution of natural secondary forest population in mountainous area of Beijing: A case study of Wuling Mountain nature reserve. – *Science of Soil and Water Conservation* 6(3): 59-64.
- [80] Zhou, S. R., Zhang, D. Y. (2006): Neutral theory in community ecology. – *Journal of Plant Ecology* 30(5): 868-877.
- [81] Zhu, Y., Bai, F., Liu, H. F., Li, W. C., Li, L., Li, G. Q., Wang, S. Z., Sang, W. G. (2011): Population distribution patterns and interspecific spatial associations in warm temperate secondary forests, Beijing. – *Biodiversity Science* 19(2): 252.
- [82] Zhu, Q., Ai, Z. R., Yao, L. (2020): Species abundance distribution pattern of evergreen and deciduous broad-leaved mixed forest in the subtropical mountains of southwestern Hubei. – *Acta Botanica Boreali-Occidentalia Sinica* 40(6): 1061-1069.

APPENDIX

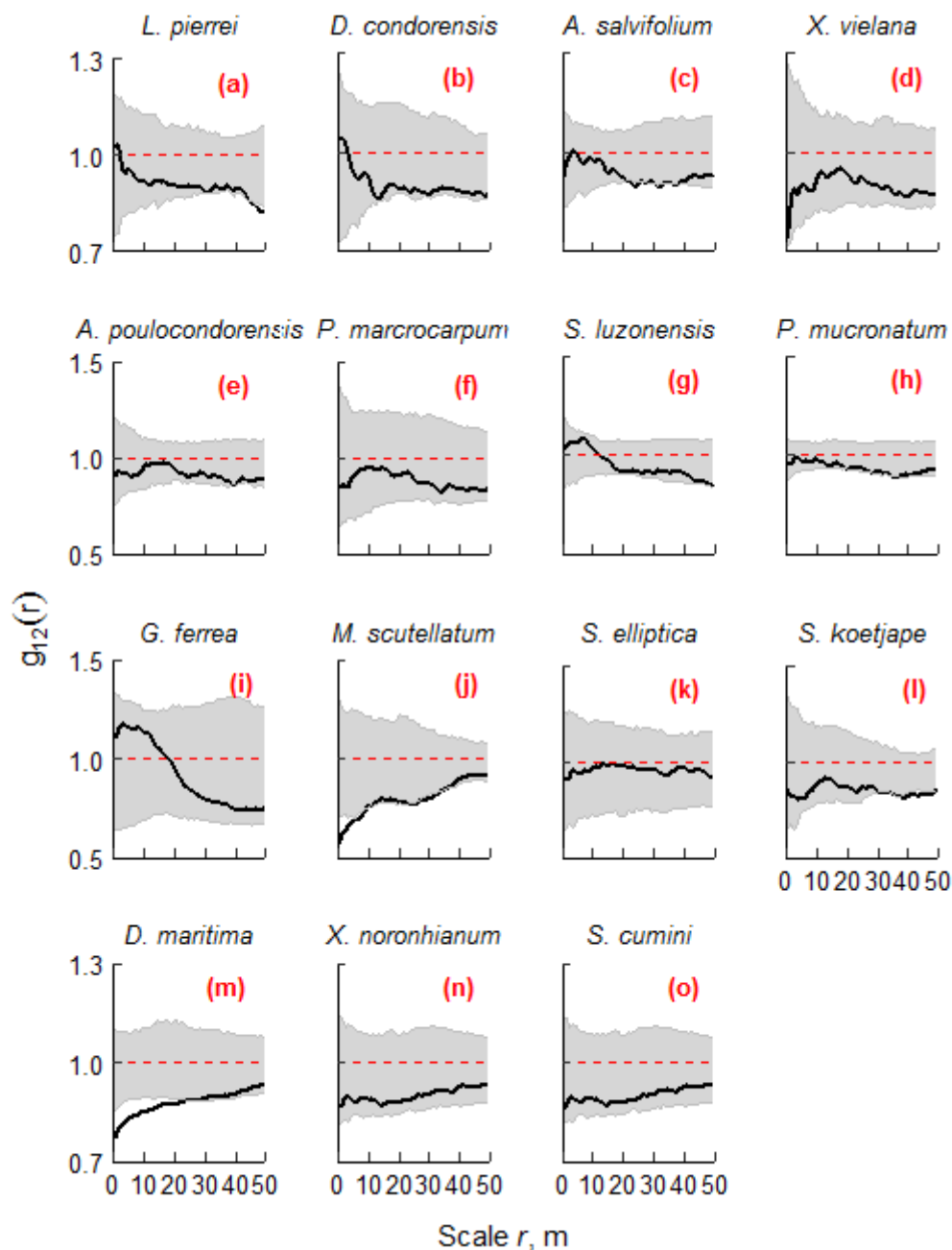


Figure A1. Interspecific association patterns of *K. pierrei* and co-dominant species in Plot 1. The solid black lines represent the bivariate g -function for the observed distribution. The grey shading areas are acceptance regions, bounded by 95% pointwise envelopes based on 199 Monte Carlo simulations. The horizontal dashed red lines are the values of the function when the two types of point are spatially independent

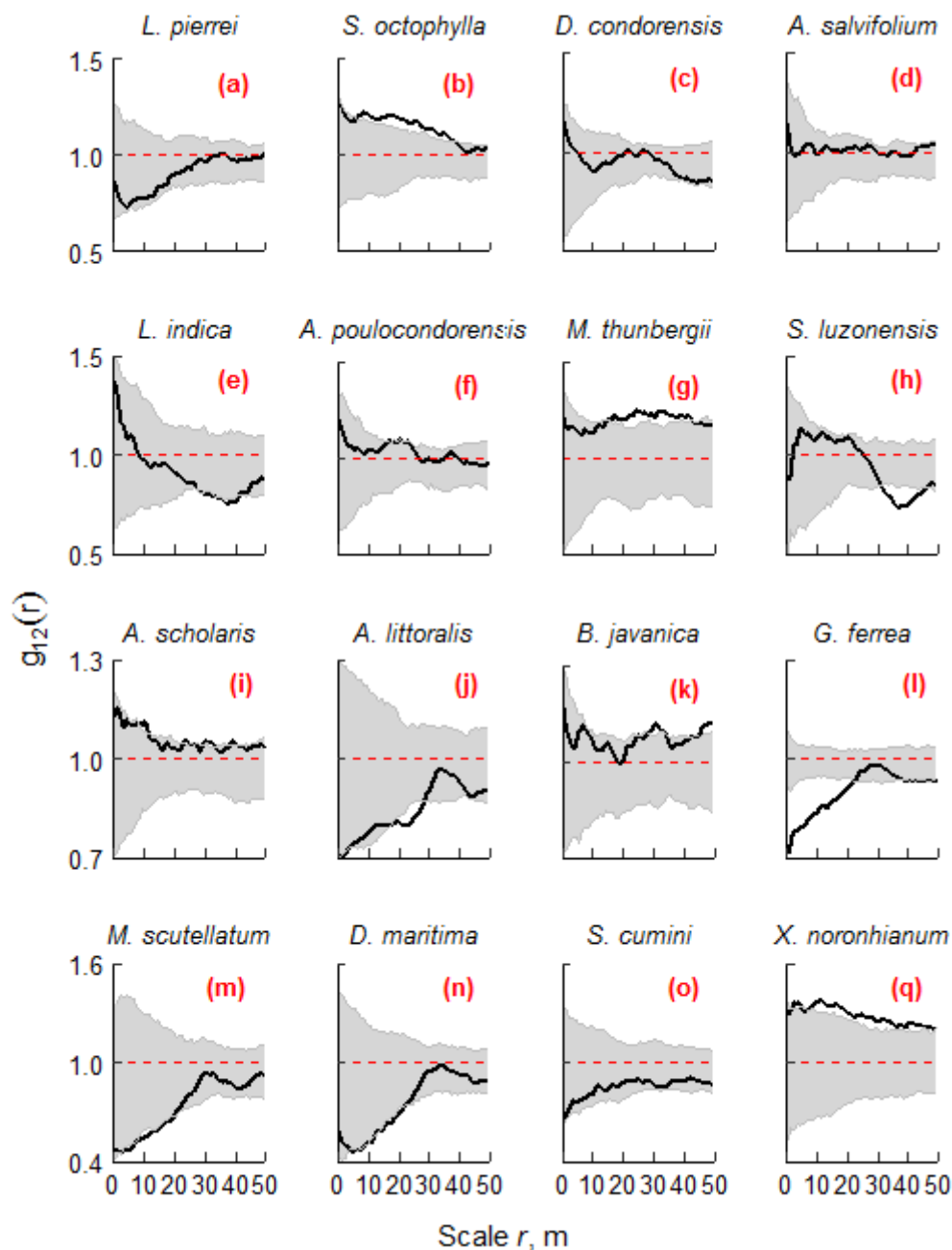


Figure A2. Interspecific association patterns of *K. pierrei* and co-dominant species in Plot 2. The solid black lines represent the bivariate g -function for the observed distribution. The grey shading areas are acceptance regions, bounded by 95% pointwise envelopes based on 199 Monte Carlo simulations. The horizontal dashed red lines are the values of the function when the two types of point are spatially independent

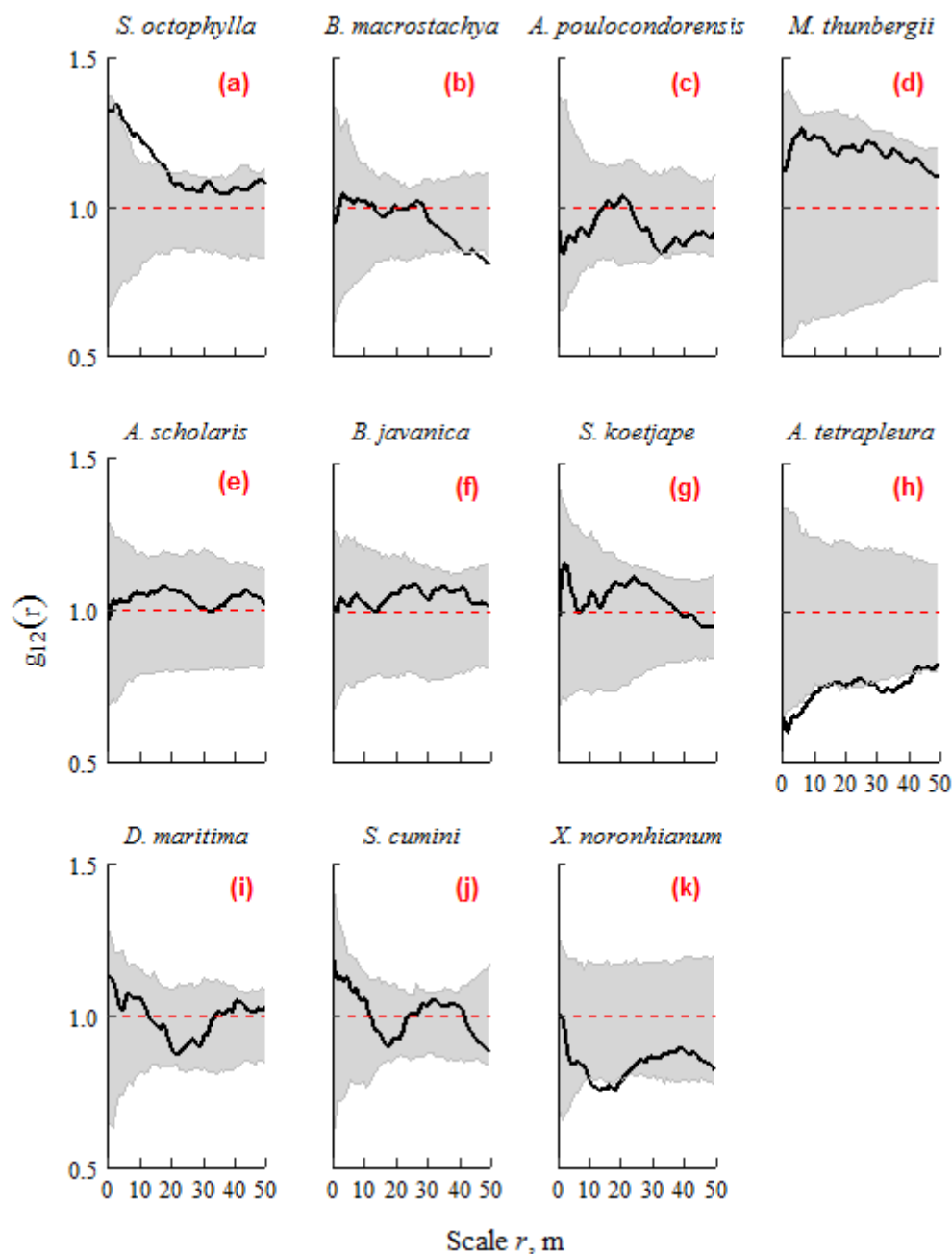


Figure A3. Interspecific association patterns of *K. pierrei* and co-dominant species in Plot 3. The solid black lines represent the bivariate g -function for the observed distribution. The grey shading areas are acceptance regions, bounded by 95% pointwise envelopes based on 199 Monte Carlo simulations. The horizontal dashed red lines are the values of the function when the two types of point are spatially independent



Figure A4. Field Investigation Images (a) Branches bearing leaves and fruit of *K. pierrei*; (b) Stem and leaves of *K. pierrei*; (c) Forest stand on the Con Dao Islands where *K. pierrei* is found (Photos by Le Van Cuong)