

Spatial Distribution Patterns and Associations of Woody Plant Species in the Evergreen Broad-Leaved Forests in Central Vietnam

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Received April 4, 2022; revised April 23, 2022; accepted April 25, 2022

Abstract—The present study was conducted to elucidate the underlying processes that have maintained and promoted the coexistence of tropical forest tree species. Three 1-ha study plots (100 × 100 m) were established in the evergreen broad-leaved forest in Pu Hoat Nature Reserve, Nghe An Province, Central Vietnam. Uni- and bivariate spatial analyses were performed using the Programita November 2018 software to analyze the spatial patterns and associations of the co-dominant species at a distance of 0–50 m. The results showed that spatial patterns of species were mostly aggregated at a small scale of $r < 15$ m; randomness and regularity tend to increase at a large scale of $r > 15$ m. The number of species pairs with independent association accounted for an extremely high proportion (75–90%); attraction and repulsion accounted for a lower proportion (5–12.5%). Spatial association patterns of co-dominant species in the stands were primarily independent or segregated at large scales of $r > 30$ m. Processes such as limited seed dispersal, habitat heterogeneity, and density-dependent mortality adjusted the spatial distribution patterns and associations of the tree species in the study area.

Keywords: spatial pattern, limited dispersal, species coexistence, evergreen forest, Pu Hoat Nature Reserve

DOI: 10.1134/S1062359022050132

INTRODUCTION

Understanding the rules and mechanisms of species coexistence is one of the focused contents of ecological research (Liu et al., 2021). Studying spatial distribution patterns of species helps to explain the forest plant communities' formation and the underlying processes that have taken place in the community, such as limited dispersal, habitats' heterogeneity, and species competition (Ripley, 1977; Barot et al., 1999). In particular, the spatial distribution pattern of populations can reflect the forest dynamics and biodiversity maintenance mechanisms (Greig-Smith, 1983). Spatial pattern of a population changes according to the stages of forest development (Gu et al., 2019). Tree species are not randomly distributed on the forest ground but follow specific rules (Condit et al., 2000). Previous studies have shown that species tend to be aggregate at the juvenile tree stage, randomness or regularity at the subadult and adult tree stages (Stoll and Bergius, 2005). The species interactions are believed to be one

of the leading causes of spatial distribution patterns of a forest tree population (Quy et al., 2021). Negative interactions among species reduce the density of neighboring trees at a small scale, whereas positive interactions increase aggregation intensity (Martínez et al., 2010). Ecologists used the spatial point pattern analysis method to understand the arrangement of forest trees in the stand as well as their interactions (Quy et al., 2022). The spatial distribution of forest tree populations not only shows the spatial distribution characteristics of species at present but also helps to predict the development trend of forest communities in the future; from that, it can promptly correct adverse effects in the relationship between people, organisms, and the environment (Condit et al., 1994; He and Duncan, 2000; Plotkin et al., 2000). Studying the spatial associations of species also provide information on the interactions of populations and the differences in their spatial distribution patterns under different habitat conditions (Wiegand et al., 2007), this

information is helpful in selecting species and densities when afforestation or reforestation.

The evergreen broadleaved forest is one of the main vegetation types in Vietnam, with considerably rich and diverse plant resources. This forest type distributed in Cao Bang, Thanh Hoa, Nghe An, Ha Tinh, Quang Nam, Central Highlands, etc. (Phung Ngoc Lan et al., 2006). In Vietnam's forest research history, many studies mentioned the structure and biodiversity of evergreen broadleaf forests (Quy et al., 2021). Still, few publications on distribution patterns and spatial associations of tree species in this forest type.

In this study, we established three study plots, 1 ha each, belonging to the evergreen broadleaved forest in Pu Hoat Nature Reserve, Nghe An Province, Vietnam. The method of spatial point pattern analysis based on univariate and bivariate pairwise correlation functions was used to analyze the spatial distribution patterns and associations of co-dominant species (species with the number of individuals from 30 individuals ha^{-1} or more) in the stands.

Two research hypotheses are put forth: (i) The first hypothesis: the formation of spatial distribution patterns of forest tree populations is affected by limited dispersal, density-dependent mortality, and habitat heterogeneity. If the research results show that the spatial distribution patterns of species at small scales are mainly aggregation while they tend to switch to randomness or regularity at large scales, the hypothesis is accepted; otherwise, the hypothesis will be rejected. (ii) The second hypothesis: The spatial distribution of forest tree species is closely related to the habitat, and different species have different habitat needs. If the research results show that independence dominates in the spatial association patterns of species at small scales and the spatial associations are mostly non-association or segregated at large scales, then the second hypothesis is accepted; otherwise, the hypothesis will be rejected.

The study results will intensify our understanding of forest structure and dynamics as well as processes that maintain and promote species' coexistence in Vietnam's evergreen broadleaf forest. Hence, our study provides a scientific basis for managers to develop sustainable forest management, protection, and development plans in the study area.

MATERIALS AND METHODS

Study Area

Pu Hoat Nature Reserve is located in Que Phong District of Nghe An Province, Central Vietnam. The geographical coordinates of the Nature Reserve are from $19^{\circ}27'46''$ to $19^{\circ}59'55''$ N, $104^{\circ}37'46''$ to $105^{\circ}11'11''$ E. The total natural area of the Nature Reserve is 34589 ha, of which the strict protection zone is 26183.87 ha, and the ecological restoration subdivision is 8406.02 ha. Pu Hoat Nature Reserve is

located in the tropical monsoon climate, hot and humid, with a lot of rain, influenced by the Northern Truong Son Mountain range climate. The area's average annual temperature is 23.1°C , the yearly average rainfall is 1734.5 mm, and the average annual humidity is 86%. The topography of Pu Hoat Nature Reserve has three main types: high mountain terrain (1600–1828 m above sea level), medium and low mountain terrain (300–1700 m), and flat and low terrain (Vietnam Administration of Forestry, 2021) (Fig. 1).

Study plots are designed at positions with coordinates:

- (1) Plot 1: $19^{\circ}48'20.81''$ N, $104^{\circ}52'33.85''$ E;
- (2) Plot 2: $19^{\circ}44'54.19''$ N, $104^{\circ}47'44.06''$ E;
- (3) Plot 3: $19^{\circ}46'29.38''$ N, $104^{\circ}55'28.04''$ E.

The plant community in the study area is located in a lowland tropical moist evergreen closed forest with a wide range of species belonging to the family Myrtaceae, Lauraceae, Magnoliaceae, Fagaceae, etc. (Vietnam Administration of Forestry, 2021).

The study was carried out from June 2021 to September 2021 with six field surveys.

Research Methods

Investigation and data collection method. At the study area, three study plots were established with each plot area being 1 ha (100×100 m). The square grid method was employed to divide the study plot into 100 subplots; each subplot area is 100 m^2 (10×10 m). In the subplot, we collected information on tree individuals with a diameter at breast height (DBH) ≥ 2.5 cm, including the name of tree species and DBH. A tree caliper was used to determine DBH; we defined the relative coordinates of each tree individual in the study plot by Laser Distance Meter (Leica Disto D2) and compass.

All individual trees in the study plot were divided into one of three life-history stages: juvenile (DBH < 10 cm), subadult ($10 \text{ cm} \leq \text{DBH} \leq 30$ cm), and adult (DBH > 30 cm).

Data processing methods. *Identify the species name.* The name of the tree species were determined by the comparative morphological method. The reference documents used include Plants of Vietnam (Pham Hoang Ho, 1999–2003), Forest trees of Vietnam (Tran 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>).

Analyze the homogeneity of environmental conditions in the study plots. The homogenate environmental conditions in the plots were tested through a spatial distribution pattern of all mature trees with DBH ≥ 15 cm in the study plot by comparing the results of two functions, $g(r)$ and $L(r)$ (Pham and Nguyen, 2016). We selected trees with DBH ≥ 15 cm because they can live

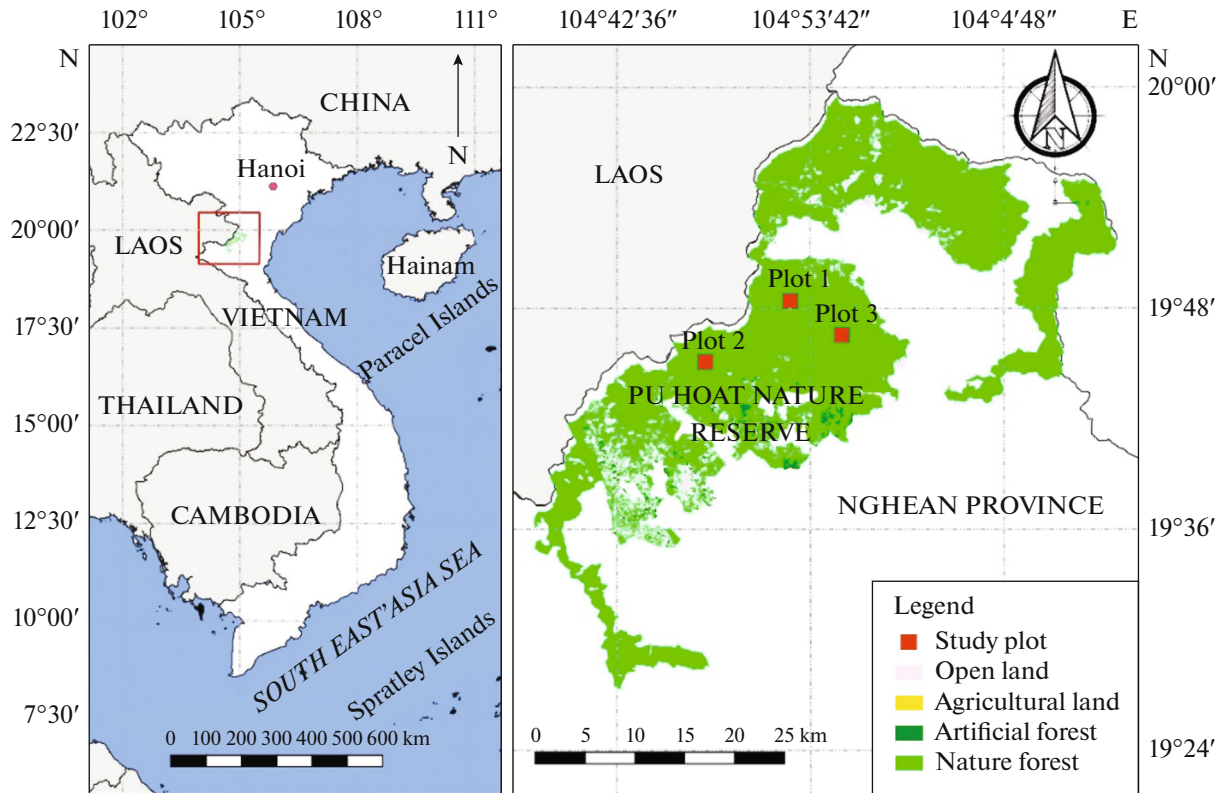


Fig. 1. The research area map. Map of Vietnam (left) and Pu Hoat Nature Reserve (right).

in all possible areas in the study plot; these trees have undergone natural selection. If the environmental conditions in the study plot were heterogeneous, it will be reflected by the heterogeneous distribution of mature trees (Hai et al., 2014).

Spatial distribution patterns analysis of the forest tree species. We use the univariate pairwise correlation function $g_{11}(r)$ to analyze spatial distribution patterns of species. The pairwise correlation function $g(r)$ is the derivative of the Ripley K with $g(r) = K'(r)/(2\pi r)$, which gives the expected intensity of points at a distance r from any point (Ripley, 1976). For the univariate pairwise correlation function $g_{11}(r)$ (same tree species or a group of tree species), if $g_{11}(r) = 1$, the distribution points are complete spatial randomness; if $g_{11}(r) > 1$, the distribution points are aggregate, and vice versa, if $g_{11}(r) < 1$, the points are regular distribution at the distance r between the points of the pattern.

Null models are employed in this study include: the null model of complete spatial randomness (CSR) was used for the functions $g_{11}(r)$ and $L_{11}(r)$ of all mature trees in the study plots, the null model of inhomogeneous Poisson process (IPP) was used to analyze the spatial distribution of tree species when the habitat in the study plot was heterogeneous; conversely, if the habitat in the study plot was homogeneous, the CSR model is applied.

Spatial association patterns analysis of species. The bivariate pair-correlation function $g_{12}(r)$ and null model of independence were used to analyze the spatial associations of species pairs; in which species 1 was fixed and species 2 was moved randomly around species 1 to estimate the simulation value from the null model (Wiegand et al., 2007). By comparing the calculated value $g_{12}(r)$ and the simulated value, the spatial distribution of species 2 around species 1 will be tested.

If the $g_{12}(r)$ value is larger than the simulated value, it proves that the spatial association of the two species has a positive correlation (attraction). If $g_{12}(r)$ value is not significantly different from the simulated value, it means that the two species were completely spatially independent (independence). In contrast, if the $g_{12}(r)$ value is smaller than the simulated value, the spatial association of the species pair is a negative correlation (repulsion).

Besides, we also used the classification P – M axis (Fig. 2a) to classify the spatial association types of species pairs. The values P and M were calculated as follows (Wiegand et al., 2007):

$$P = -\hat{P}_0(r) + P_0^h(r), \quad (2.1)$$

$$M = \ln(\hat{K}_{12}(r)) - \ln(K_{12}^h(r)), \quad (2.2)$$

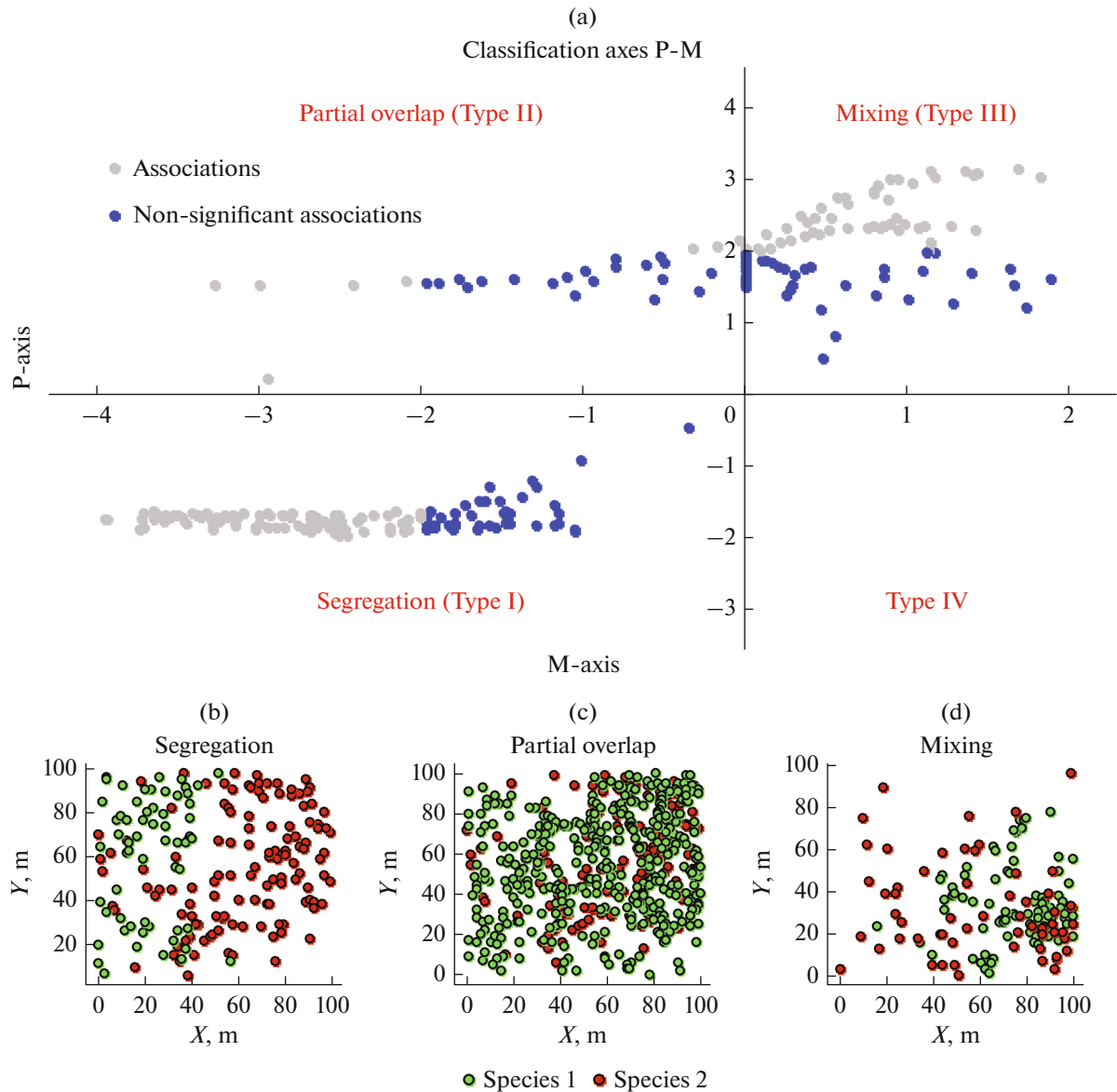


Fig. 2. Classification axes P–M (a) and the spatial association types of a pair of species (b–d) were created by the values of P and M.

where $P_0(r)$ is the probability that species 2 does not appear in a circle of radius r containing an individual of species 1 (Diggle, 2003).

$$P_0(r) = 1 - D_{12}(r).$$

$D_{12}(r)$ is the bivariate nearest neighbor distance function $K_{12}(r)$ of Ripley. $P_0^h(r) = \exp(-\lambda_2 \pi r^2)$ and $K_{12}^h(r) = \pi r^2$ are the expected values of $P_0(r)$ and $K_{12}(r)$. The symbol “ $\hat{}$ ” indicates the actual observed value (Wang et al., 2010).

The classification axes P–M allows to identify of four types of spatial association of two tree species as follows: (1) $P < 0, M < 0$ indicates two segregated species (segregation, Type I), which means the individu-

als of species 2 appear fewer around individuals of species 1 than would be expected in neighborhoods of radius r (Fig. 2b). (2) $P < 0, M \geq 0$ indicates the partial mix of species 2 with species 1 (partial overlap, Type II), some neighborhoods around species 1 appear with more individuals of species 2 and others fewer (Fig. 2c). (3) $P \geq 0, M \geq 0$ indicates a mix of the two species (mixing, Type III); the individuals of species 2 occur more frequently in the vicinity of species 1 within a radius of r ; in other words, the 2 species intertwine to high intensity on a specific scale (Fig. 2d). (4) $P \geq 0, M < 0$ shows that the individuals of species 1 are mainly distributed in clusters, and a few individuals of species 2 are distributed close to the clusters of species 1 (Type IV), which only happens when there is a secondary effect (competition between the two species is extreme) and

this type of association is scarce in natural forests (Wiegand et al., 2007). In addition, the two species will not be spatially associated (non-association or independence) when the values $K_{12}(r)$ and $P_0(r)$ have no significant difference from the null model (Wiegand et al., 2007; Wang et al., 2010; Martínez et al., 2010; Nguyen and Cao, 2019). Testing the difference between the observative model and the null model is done through the rank (rank) of the spatial statistical function $L(r)$ and $D(r)$; if the rank >195 , then the spatial association of the two species is significant, conversely, rank <195 means that the species pair is not spatially associated (Wiegand, 2018).

In analyzing spatial distribution patterns and associations of tree species, the Epanechnikov kernel was used for the intensity function with a moving window radius $R = 50$ m and spatial resolution (bins) of 1 m. All spatial patterns were analyzed using Programita Noviembre 2018 software with 199 Monte Carlo simulations, using the 5th maximum value and 5th minimum value of 199 simulations to build an approximate confidence interval of approximately 95% (<http://programita.org>); The distribution map of forest tree species was built through Package “spatstat” and Package “ggplot2” on R software version 4.1.1 (R Development Core Team, 2021).

RESULTS

Tree Species Composition in the Study Plots

The study identified 84 tree species belonging to 49 plant families in Plot 1, while in Plot 2, 81 species belonging to 43 families were recorded, and in Plot 3, there were 94 species belonging to 56 families. Density, average DBH, and the importance value index of species in the study plot are shown in Table 1. Among the species appearing in the study plots, there are eight species in Plot 1, 8 species in Plot 2, and 14 species in Plot 3 with the number of tree individuals >30 . Therefore, they were the main species in the stands and been selected for in-depth study on spatial distribution characteristics, association patterns, and spatial association types. Of the eight major tree species in Plot 1, only five species have ecological significance (IVI% $>5\%$), namely *Helicia tonkinensis*, *Symplocos lancifolia*, *Wrightia annamensis*, *Schima superba*, and *Litsea glutinosa*. In Plot 2, there were two ecologically important species, namely *Vatica odorata*, and *Syzygium zeylanicum*. Plot 3 showed four ecologically significant species, including *Ormosia pinnata*, *Quercus platycalyx*, *Lithocarpus annamensis*, and *Cinnamomum parthenoxylum*. Although the number of species between the three plots is not differential high (3–10 species), there was a noticeable difference in the density of tree individuals between study plots. The highest density was Plot 3 with 1053 trees ha^{-1} , and the lowest density was Plot 1 with 862 trees ha^{-1} .

The Heterogeneity of Habitat on the Study Plots

All mature trees' spatial patterns (DBH ≥ 15 cm) in the study plots were compared to the CSR null model to test the difference between observational and theoretical models at large scales. We used both cumulative and non-cumulative densities of two functions, $L_{11}(r)$ and $g_{11}(r)$, for all mature trees in each study plot when conducting this analysis (Fig. 3). The results showed that, for the function $g_{11}(r)$, all mature trees in Plot 1 were aggregated at a distance of 18–20, 25–27 m (Fig. 3d); while in Plots 2 and 3, the mature trees only have a random distribution at all scales (Figs. 3e, 3f). The function $L_{11}(r)$ also showed a difference in the cumulative density of the mature tree individuals in three study plots. In Plot 1, the mature trees were aggregated at all scales of $r > 20$ m (Fig. 3g); in Plots 2 and 3, the spatial distribution patterns of mature trees mainly were random; aggregation was found (Figs. 3h, 3i). Moreover, the mature trees' distribution map showed that many locations within Plot 1 do not have distributed mature trees (Fig. 3a); in contrast, in Plots 2 and 3, mature trees were distributed relatively regularly across the plots (Figs. 3b, 3c). Therefore, there was a significant difference in Plot 1 between the observational model and the null model of CSR, the hypothesis of habitat homogeneity in Plot 1 was not accepted. In Plots 2 and 3, no significant difference was found between the observational models and the null models of CSR at large scales, so it can conclude that the habitat conditions in these two plots were homogeneous. Based on the mature tree spatial distribution pattern analysis results, we used the IPP null model for Plot 1 and the CSR null model for Plots 2 and 3 to further analyze the selected tree species' spatial model in the three study plots.

Spatial Distribution of Tree Species in Forest Stands

Analyzing the spatial distribution patterns of tree species with the number of individuals >30 trees in the three study plots (Fig. 4), the results showed that at the scale r of 0–15 m, most species have cluster distributions (accounted for 50–75% of the species analyzed). As the scale increases, the tree species' spatial distribution patterns on the study plots gradually shift from aggregation to randomness and regularity (about 50–90% of the total number of species analyzed at scales of r 15–50 m). Furthermore, the study results showed that in Plot 1 (nonhomogeneous habitat), there was no regularity at all scales (Fig. 4a). Conversely, on the other two plots (homogeneous habitat conditions), there was no regularity at small scales of $r < 15$ m; but at large scales of $r > 30$ m in Plot 2 and $r > 15$ m in Plot 3, there was regularity (Figs. 4b, 4c).

Table 1. Characteristics of species composition in the study plots

Plot	No.	Species name	<i>N</i> , trees ha ⁻¹	DBH, cm	IVI, %
1	1	<i>Helicia tonkinensis</i>	122	12.4 ± 5.6	9.8
	2	<i>Symplocos lancifolia</i>	84	15.5 ± 7.2	7.8
	3	<i>Wrightia annamensis</i>	50	18.9 ± 8.3	5.4
	4	<i>Schima superba</i>	45	19.6 ± 10.1	5.2
	5	<i>Litsea glutinosa</i>	37	13.9 ± 8.2	3.3
	6	<i>Cinnamomum parthenoxylum</i>	33	20.2 ± 13	4.1
	7	<i>Gironniera subaequalis</i>	33	20.1 ± 12	4
	8	<i>Aglaia dasyclada</i>	30	25 ± 19.5	5.3
		Eight co-dominant species	434	18.3 ± 5.5	44.9
		76 other species	428	21.4 ± 7.2	55.1
	All (84 species)	862	17.9 ± 12.7	100	
2	1	<i>Vatica odorata</i>	130	22.1 ± 19.6	18.5
	2	<i>Syzygium zeylanicum</i>	90	13.7 ± 6.1	7
	3	<i>Carallia brachiata</i>	49	11.6 ± 4.2	3.4
	4	<i>Polyalthia jucunda</i>	45	13.9 ± 5.2	3.4
	5	<i>Diospyros sylvatica</i>	40	13.1 ± 4.4	2.9
	6	<i>Cinnamomum parthenoxylum</i>	34	24.6 ± 15.7	4.7
	7	<i>Ormosia pinnata</i>	33	20.2 ± 8.3	3.4
	8	<i>Helicia tonkinensis</i>	32	12.2 ± 7.3	2.4
		Eight co-dominant species	453	16.5 ± 4.7	45.7
		73 other species	457	15.9 ± 4.9	54.3
	All (81)species	910	17.8 ± 15.1	100	
3	1	<i>Ormosia pinnata</i>	86	17.3 ± 8.5	7.7
	2	<i>Diospyros sylvatica</i>	73	11.3 ± 5.3	4.7
	3	<i>Syzygium wightianum</i>	64	11.5 ± 4.8	4.1
	4	<i>Quercus platycalyx</i>	53	24.7 ± 13.8	7.3
	5	<i>Cinnamomum ovatum</i>	53	14.6 ± 8.9	4.2
	6	<i>Lithocarpus annamensis</i>	48	23.8 ± 14	6.4
	7	<i>Syzygium jambos</i>	45	12.9 ± 6	3.1
	8	<i>Symplocos laurina</i>	42	10.4 ± 5.1	2.6
	9	<i>Polyalthia jucunda</i>	38	12.9 ± 5.7	2.6
	10	<i>Cinnamomum parthenoxylum</i>	35	24.1 ± 19.3	5.4
	11	<i>Vatica odorata</i>	35	19 ± 18.7	4.4
	12	<i>Ormosia laosensis</i>	33	25.2 ± 13.7	4.6
	13	<i>Nephelium melliferum</i>	32	13.2 ± 6.6	2.3
	14	<i>Archidendron eberhardtii</i>	31	23.2 ± 9.9	3.7
		14 co-dominant species	668	17.5 ± 10.1	63.1
	80 other species	385	18.2 ± 9.7	36.9	
	All (94 species)	1053	16.6 ± 11.7	100	

N—Density (trees ha⁻¹), DBH—Mean Diameter at Breast Height (cm), IVI (%)—Importance value index = (relative density + relative tree basal area)/2 (m²).

Spatial Associations of Tree Species

The spatial association analysis results of species pairs (Fig. 5) showed that the association patterns of species were mainly independent in all three research plots (accounted for 75–90% of the total number of

species pairs). The proportion of attraction and repulsion between species pairs was deficient (about 5–12%). The species-species interactions at distances of $r < 30$ m were more robust than those at $r > 30$ m (Figs. 5a–5c).

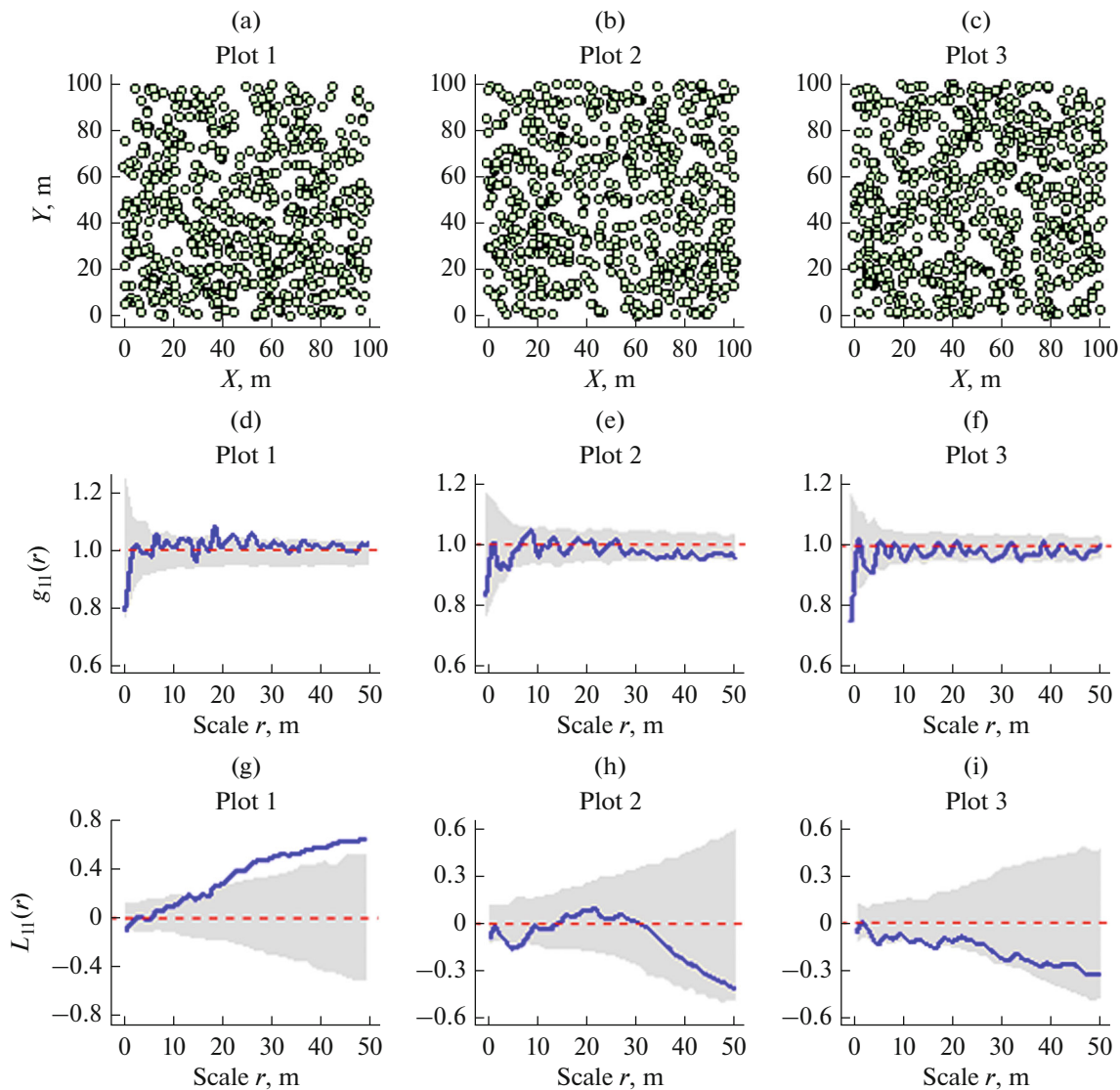


Fig. 3. The distribution map of all mature trees (a–c) and their spatial patterns (d–g) in the study plots were analyzed by functions $g_{11}(r)$ and $L_{11}(r)$. The blue line lying beyond the confidence envelope region (a gray area) indicates a significant departure from the null model of CSR. The gray envelope region is the $p = 0.05$ confidence intervals from 199 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 mature tree individuals.

When analyzing the spatial association patterns of species pairs in the study plots by the classification axes P–M (Fig. 6), the results showed that there were differences in spatial association patterns of species in the heterogeneous habitat (Fig. 6a) and the homogeneous habitats (Figs. 6b, 6c). Besides, Figure 6 also showed that at small scales ($r < 15$ m) and large scales ($r > 15$ m), the spatial associations between species were not the same. When the environment of the study plot is nonhomogeneous, at small scales, species pairs were mainly segregated (accounting for about 45% of the total number of species pairs); at large scales, the association was primarily independent (accounting for about 50% of the total number of species pairs). When

the plot habitat was homogenous, the spatial association pattern was independent primarily at small and large scales (the number of species pairs with independent association accounts for about 40% of the total number of species pairs). However, the spatial association patterns were segregated, increasing as the spatial scale increased.

DISCUSSION

Environmental Heterogeneity Effects

Spatial distribution patterns of plant populations can be affected by habitat heterogeneity such as exposed rock, slope, canopy cover, nutrients in the

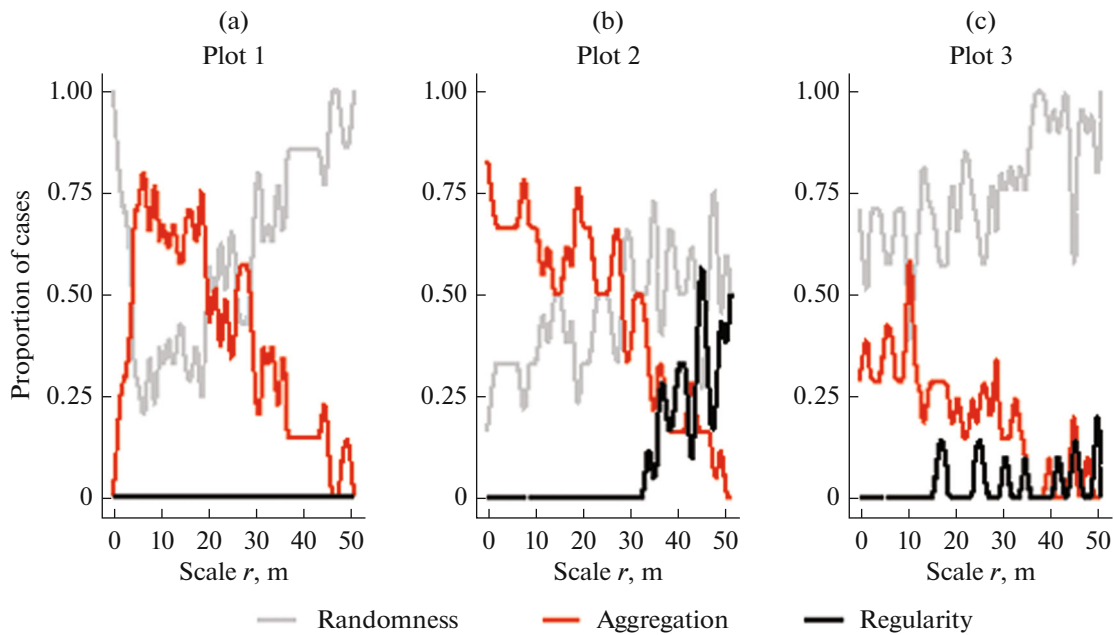


Fig. 4. The spatial distribution patterns of tree species were analyzed by the function $g_{11}(r)$ under the null model of IPP (a) and the null model of CSR (b, c).

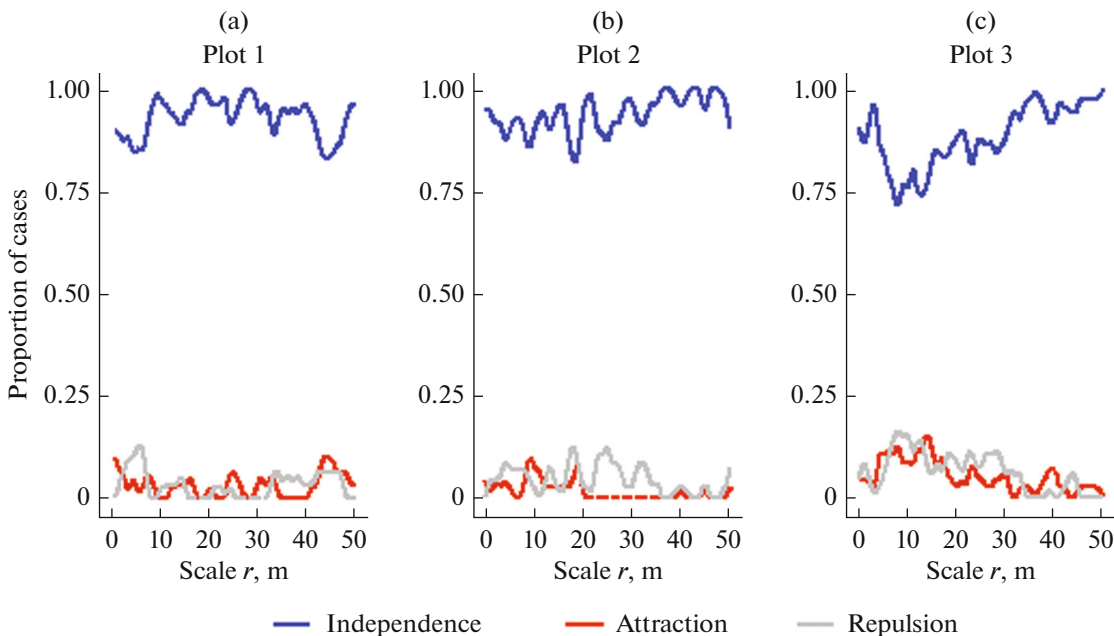


Fig. 5. The pair number of tree species with interspecific interaction was analyzed by the function $g_{12}(r)$ under the null model of independence.

soil. The population can exhibit spatial distribution patterns that are not the same in different habitats, such as randomness, aggregation, or regularity (Hu et al., 2019). Getzin et al. (2008) suggested that, at distances >10 m, if the forest trees are aggregated, it can be explained by the influence of the heterogeneity of the habitat. Habitat heterogeneity in the same study

plot in tropical rainforests was a widespread phenomenon when the cumulative intensity of mature individuals tends to shift from randomness to aggregation at distances greater than 20 m (Wiegand et al., 2007).

When studying the spatial distribution patterns and associations of the major tree species in the evergreen broadleaf secondary forest in Zhejiang Province,

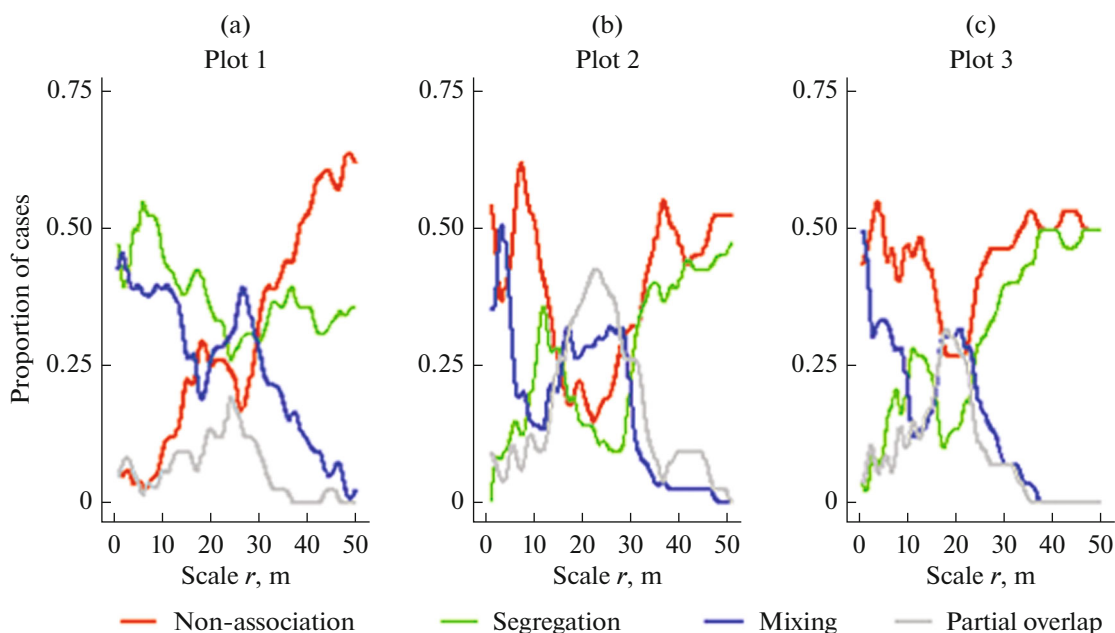


Fig. 6. Spatial associations of forest tree species in the plots were analyzed by P–M classification axes under the null model of independence.

China, Wu et al. (2018) also suggested that habitat heterogeneity plays a vital role in the formation of forest plant communities. Nguyen et al. (2018) have the same opinion when studying spatial distribution and interactions between some dominant species of unstable forest in Dong Nai Nature–Culture Reserve. Many other authors also found that the heterogeneity of habitats in the study plot was the main reason for the significant variation between the characteristics of the stand at different locations in the research plot (Liu et al., 2021). This matter creates the diversity of the spatial structure of the research object.

In our study, after testing all mature trees' spatial distribution patterns on each plot by the null model of CSR, we also found that in Plot 1, there was heterogeneity in environmental conditions, it was manifested by the cumulative intensity of mature trees was higher compared with the simulated value at all distances from 0–50 m; in Plot 2 and Plot 3, reversely, the habitat conditions on these two plots were homogeneous.

Spatial Distribution Patterns of Tree Species in the Forest Stands

Our study analyzed the spatial distribution patterns of selected 30 tree species on three study plots. Most of them have aggregated patterns at small scales of 0–15 m, and individuals of the same species tend to be distributed closer together. This result is consistent with the spatial distribution of populations in natural forest communities, proved in previous studies. Studying the spatial distribution and associations of evergreen broadleaved forest species in A Luoi of Thua Thien

Hue Province, Vietnam, Dien and Hai (2016) found up to 16 of 18 of the studied trees species with the aggregated distribution at different scales and the aggregated spatial distribution was mainly found at small scales r of <15 m. Yan et al. (2011) conducted a study on the spatial distribution of tree species in the Beijing–China secondary forest; they also found a similar result, most tree species have cluster distribution (aggregation) at a small scale, which manifests as the highest population density at distances from 1–3 m; at larger scales, mature trees tend to have a random or uniform distribution, but they are still aggregated at small scales <15 m.

Limited seed dispersal has also been shown to be one of the main factors influencing spatial distribution patterns of forest tree species (Hubbell and Foster, 1983; He et al., 1997; Murrell et al., 2002). Limited seed dispersal causes most seeds to fall under the parent tree stump. Therefore, the further away from the parent trees, the fewer the seeds number (Janzen, 1970). Although affected by the constrained effect of nutrient space, the mortality risk of new regenerative plants around the parent plant is increased. However, most newly regenerated individuals are still aggregated around mature trees due to limited dispersal mechanisms, making the population density at small scales higher than at large scales. The resultant study on spatial distribution patterns of species in the Pu Hoat evergreen broadleaved forest proved that the first hypothesis is accepted. This result confirmed the formation of spatial distribution patterns of forest tree populations is affected by restrictions on seed dispersal and habitat heterogeneity.

Spatial Associations of Tree Species

Habitat heterogeneity and limited dispersal affect spatial distribution patterns of species. These processes lead to association patterns of different species that are often spatially independent or segregated. The spatial relationship between them is, therefore, primarily independent. Our study found that the populations were mainly aggregated at small scales and randomly or regularly distributed at large scales. This evidence showed that the spatial distribution of tree species is closely related to habitat and that different species have different habitat needs. We found 30 selected tree species in the three plots were primarily distributed in separate arrays, leading to spatial segregation or non-association between species when considered at large scales. These spatial association types (segregation and non-association) accounted for 40% with each type at a large scale. This finding is entirely consistent with the studies of Wiegand et al. (2007) and Wang et al. (2010). The results of our research (spatial associations of tree species in the evergreen broadleaf forest in Pu Hoat Nature Reserve) have proven that the hypothesis of habitat separation between different species (second hypothesis) was accepted.

In addition, the analysis results of spatial association types of species in this study show that the proportion of partial mixing and interspecies mixing is much lower than that of two segregated and independent associations at large scales, which indicates that there is little chance of interaction between species. It is equivalent to not being easy to appear attraction or repulsion between species at distances above 15 m. Moreover, the independent relationship between species accounts for a considerable proportion compared to attraction and repulsion. Therefore, it was evident that repulsion between species is not the cause that adjusted the spatial distribution pattern of the evergreen broadleaf forest tree species in the study area. Wiegand et al. (2007) analyzed the spatial associations of 2070 tropical forest tree species pairs in Sri Lanka. These authors found that about 50% of species pairs had independent associations, and only 6% showed interspecific interactions (attraction and repulsion). Wiegand et al. (2007) also concluded that interspecific interaction is not enough to affect the structure of plant communities. Peters (2003) studied the effect of density on the spatial distribution of tropical forest tree species in Panama and Malayan. The author found that more than 80% of species studied at each survey site had density-dependent mortality; a high density of individuals of the same species in the vicinity of the target tree could increase the mortality of the target tree.

In contrast, the heterogeneity of species composition in neighboring scales increased the survival rate of target plants. This process is because the effects of neighboring trees of different species on the target tree are not the same, but if the neighboring trees are of the same species, the impact on the target tree is equal

(Stoll and Newbery, 2005). When considering the spatial associations of species pairs, our study found that three independent associations accounted for most of the three types of spatial associations (independence, attraction, and repulsion). This result also proves that the neutral theory is suitable to explain spatial distribution patterns of tropical forest trees.

In the natural forest, the aggregated intensity of species will decrease during the development of populations as tree age or tree diameter increases (Liu et al., 2021). The general trend is aggregated distribution pattern at the juvenile tree stage—randomly distributed at the subadult tree stage—regularly distributed at the adult tree stage (Wiegand et al., 2007). The change in the spatial distribution pattern of forest trees in the community at different growth stages originates from the impact of specific ecological processes (Gavrikov and Stoyan, 1995). Habitat heterogeneity is an essential factor affecting the change in spatial distribution patterns of populations, but after excluding habitat heterogeneity, limited dispersal and density-dependence regulate the spatial structure of forest tree populations (He and Duncan, 2000; Zhu et al., 2010). Density-dependent mortality often regulates the spatial distribution of neighboring trees of the same species; as the mortality rate of neighboring individuals of the same species increases, the distance between them will increase, after a long time or when the diameter of forest trees increases, the aggregated intensity of the population will decrease (Condit et al., 1992; Barot et al., 1999; Zhu et al., 2009).

CONCLUSIONS

In Pu Hoat Nature Reserve, three study plots of 1 ha were established to study the spatial distribution and association patterns of tree species in the evergreen broadleaf forest type. The primary characteristics of the study plots have been determined; there are 53 species of trees belonging to 31 families in Plot 1, 64 species of 34 families in Plot 2, and 58 species of 27 families in Plot 3. Among those, the density of forest stands was different, with the highest density being 1053 individuals ha^{-1} (Plot 3), and the lowest one was 862 individuals ha^{-1} (Plot 1). In three study plots, 30 species were selected for in-depth study on spatial distribution and association patterns (species with more than 30 individuals in the plot).

The results showed that the difference in the spatial pattern of the species was huge between the heterogeneous habitat (Plot 1) and the homogeneous habitat (Plot 2 and Plot 3). When the habitat was heterogeneous, the species' spatial distribution had no regular distribution pattern at all scales of 0–50 m. On the contrary, in the homogeneous habitat conditions, there is no regular pattern at small scales <15 m, but at the large scale >15 m, this distribution pattern appears. The results of spatial distribution pattern analysis of

species also showed that, in addition to the influence of heterogeneous environmental conditions, the formation of spatial patterns of species was also influenced by limited dispersal and density-dependent mortality. Spatial patterns of species mostly were aggregation at small scales (accounting for about 50–75% of total species); randomness and regularity tend to increase at large scales (accounting for about 50–90% of entire species).

Analyzing the spatial association patterns of species showed that independent association accounted for a high proportion (accounting for 75–90% of the total number of species pairs). Attraction and repulsion between species accounted for a deficient proportion (5–12.5%). The species have separate habitats and different species with different habitat needs. At the same time, the results of this analysis also showed that the neutral theory is suitable to explain spatial distribution models of tropical forest trees. From the obtained results, our study showed that the three underlying processes that maintain and promote the coexistence of species in Pu Hoat Nature Reserve as density-dependent mortality, habitat heterogeneity, and limited dispersal. If these three mechanisms are combined into a model that predicts the spatial distribution of plant populations will help to understand better the dynamics of evergreen broadleaf forest communities in Vietnam.

ACKNOWLEDGMENTS

We are grateful to the laboratory of the Institute of Tropical Ecology of Vietnam–Russia Tropical Centre. We thank forest managers at Pu Hoat Nature Reserve and some local people at Hanh Dich commune for their support of our survey.

FUNDING

The study was partly supported by the project “Application of Geographic Information Method (Gis) and Molecular Biology for Investigation, Monitoring and Development *Cunninghamia konishii* Hayata Species of Vietnam” of the Joint Russian-Vietnamese Tropical Research and Test Center, Hanoi, Vietnam (Vietnam–Russia Tropical Center) for stage 2020–2022. We are grateful for the survey supported by task E1.2 conducted in Pu Hoat Nature Reserve in 2021. We thank the forest rangers in Hanh Dich and Thong Thu communes for all of our appropriate.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

The authors declare that they have no conflicts of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

AUTHOR CONTRIBUTIONS

All authors participated in samples collection, QVN did the data analyses and wrote the main part of paper, MPP, HTMN, TTN together wrote paper and prepared illustrations; MPP organized most part of our field expedition in Vietnam and assure our contacts with Pu Hoat NR and other organizations.

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