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Seedling Distribution and Genetic Diversity of *Rubroshorea acuminata*, *Shorea guiso*, and *Rubroshorea leprosula* in the Harapan Rainforest: A Crucial Study for Conservation Efforts

Iskandar Zulkarnaen Siregar[1], Laswi Irmayanti[2], Ulfah Juniarti Siregar[1], Fifi Gus Dwiyanti[1*]

[1]Department of Silviculture, Faculty of Forestry and Environment, IPB University, Academic Ring Road Campus IPB Dramaga, Bogor, Indonesia 16680
[2]Study Program of Forestry, Faculty of Agriculture, University of Khairun, South Ternate, North Maluku, Indonesia 97719

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Abstract

The genera Rubroshorea *and* Shorea *are ecologically and commercially important timber species in Indonesia. Genetic diversity is essential for maintaining the long-term stability of forest ecosystems where these species occur. Furthermore, genetic diversity is linked to the flowering system and seed dispersal methods, which play a crucial role in determining population dynamics. However, studies on genetic diversity and seed dispersal in these genera in Indonesia remain limited. This study mapped the seedling distribution of* Rubroshorea acuminata*,* Shorea guiso*, and* Rubroshorea leprosula *in the Harapan Rainforest. It also assessed the genetic diversity and genetic structure of the three species using ten microsatellite markers. The results showed that the three species used the gyration method for seed dispersal, which helps explain the decline in seedling density with increasing distance from the putative mother tree. Among these species,* R. leprosula *exhibited the highest seedling density and slightly greater genetic diversity than the others. The genetic relationship analysis revealed that* R. leprosula *and* R. acuminata *were closely related and formed a separate group from* S. guiso*. The study's findings provide valuable insights into seed dispersal methods and genetic diversity, which can aid in developing conservation management strategies for the three* dipterocarp *species.*

Keywords: *dipterocarps, genetic diversity, Harapan Rainforest, microsatellite, seedling distribution*

**Correspondence author, email*: *fifi_dwiyanti@apps.ipb.ac.id*

Introduction

In Indonesia (Kalimantan, Sumatra, and Java), the Malay Peninsula, and the wetter regions of the Philippines, large trees from the Dipterocarpaceae family dominate the forests in both number and biomass (Corlett & Primack, 2005). The genera *Shorea* and *Rubroshorea,* part of this family, include several timber species of important ecological and commercial value in Indonesia. Unfortunately, these important trees are threatened by illegal logging, forest fires, and overexploitation, which jeopardize the genetic resources in forest ecosystems where the species are prevalent.

One notable rainforest in Indonesia that hosts *Shorea* and *Rubroshorea* species, but has experienced extensive logging and other human activities, is the Harapan Rainforest. This forest is situated in the lowlands of East Sumatra, spanning the regions of Jambi and South Sumatra Provinces (Mansur et al., 2010). Before 2010, this rainforest spanned 100,000 ha of ex-logging concessions managed by PT Asialog. By 1997, only 3.34% of it remained intact (Laumonier, 1997). However, since 2010, the area has been managed by PT REKI (PT. Indonesian Ecosystem Restoration) and the Indonesian Forest Ecosystem Conservation Foundation, whose primary objective is to conserve and restore the remaining forest. Currently, the Harapan Rainforest encompasses 101,000 ha (Mansur et al., 2010) and is dominated by three dipterocarp species: *Rubroshorea acuminata* (Dyer) P.S. Ashton & J. Heck. (syn. *Shorea acuminata* Dyer), *Shorea gui*so (Blanco) Blume, and *Rubroshorea leprosula* (Miq.) P.S. Ashton & J. Heck. (syn. *Shorea leprosula* Miq.) (Mansur et al., 2010; Rangkuti et al., 2021). According to the International Union for Conservation of Nature (IUCN) red list of threatened species, *Rubroshorea acuminata* is classified as Least Concern (Barstow, 2019), *S. guiso* as Vulnerable (Khou et al., 2017), and *R. leprosula* as Near Threatened (Pooma & Newman, 2024). In Indonesia, *R. acuminata* is found on Sumatra Island (in areas such as Langsa, Pulau Mursala, from south to north Palembang, as well as Lingga) (Newman et al., 1996), *S. guiso* is found on Sumatra Island (in Aceh, North Sumatra, and South Sumatra) and Borneo Island (Newman et al., 1998a), while *R. leprosula* is distributed across Sumatra Island, Bangka Island, Belitung Island, and throughout Borneo Island (Newman et al., 1998b).

These three species exhibit distinct characteristics, particularly in leaf morphology (Rangkuti et al., 2021; Murfahatun et al., 2023) and in flower and fruit morphology. *R. acuminata*, which can produce light red *meranti* timber and resin (*damar*), has elliptical or ovate leaves with a long-acuminate apex and a wedge-shaped or rounded base; it also lacks domatia, and the stipules and young shoots are

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distinguishable by their bright red color (Subiakto et al., 2016). The flower petals of *R. acuminata* are dark wine-red, with 15 stamens. The calyx of the fruit features three longer wings (3.9–4.7 cm × 0.7–0.9 cm), two shorter wings (1.5–2.3 cm × 0.2–0.3 cm), and a nut measuring 7–12 cm × 45 mm (Newman et al., 1996). *S. guiso*, which can produce red balau timber, has elliptical or ovate leathery leaves with short hairs on the surface and nervation, and its upper surface dries reddish or purplish brown. It possesses axillary domatia and small flowers with 2028 stamens; the buds are elongate. The calyx of its fruits has three longer wings (4.0–5.5 cm × 0.6–1.0 cm), two shorter wings (2.0–3.0 cm × 0.20.5 cm), and a nut measuring 5–8 cm × 3–5 mm (Newman et al., 1998a). While *R. leprosula*, which can also produce light red meranti timber and resin (damar), has oblong, elliptical, or obovate leaves. The upper surface of the leaves dries to reddish brown, purplish brown, or brown and features scaly, flat, axillary domatia along secondary nerves. This species has small flowers with yellow petals and 15 stamens; the calyx of the fruits has three longer wings (5.0–6.7 cm × 1.0–1.4 cm), two shorter wings (1.9–2.5 cm × 0.15–0.25 cm), and a nut measuring 12–14 mm × 7–9 mm (Newman et al., 1998b).

These three species are ecologically valuable for the success of the ecosystem conservation program, the biodiversity protection program, and the restoration program in the Harapan Rainforest. However, information regarding their seed dispersal, genetic diversity, and genetic structure, which are critical for successful ecosystem restoration because they determine the adaptability and resilience of plant populations (Thomas et al., 2014; Aavik et al., 2021), is currently lacking. Without this knowledge, restored ecosystems are less likely to be self-sustaining and may fail in the long term. Additionally, understanding the genetic status of dipterocarp species is important for developing their effective tree-breeding programs and conserving genetic resources.

Seed dispersal facilitates the establishment of new plants in varied locations, as flowering plants, especially dipterocarp species, have evolved various adaptations. These adaptations enable their seeds to be dispersed far from the parent plant by wind, animals, or water (particularly for species growing near rivers) (Takeuchi et al., 2005). Seed dispersal is also crucial for the demographic dynamics of tree species (Takeuchi et al., 2005). Theories regarding tropical tree diversity suggest that dispersal limitation may be a key factor in creating spatial separation among species and minimizing competitive exclusion (Seidler & Plotkin, 2006). Furthermore, Duncan and Chapman (1999) reported that various tree characteristics can affect seed dispersal. The flowering system determines the pollination pattern, which, along with seed dispersal, shapes gene flow and ultimately influences the genetic structure and diversity of the population. The genetic diversity provides the raw material for populations and is essential for maintaining stability and health, enabling them to adapt to future environmental changes, such as climate change (Zulfahmi et al., 2010). Genetic structure describes how genes are distributed in space, and studying seed dispersal, genetic diversity, and genetic structure together provides a complete picture of the dynamics and genetic health of a tree species' population (Clair & Johnson, 2004).

Many studies have investigated the genetic diversity and genetic structure of plant species using microsatellite markers (Lemes et al., 2011; Mantello et al., 2012; Zalapa et al., 2012; Goetze et al., 2013), including dipterocarp species (Ng et al., 2009a; 2009b; Dwiyanti et al., 2014a; 2014b; Dwiyanti et al., 2015; Ng et al., 2022; Dwiyanti et al., 2025) as these markers combine several suitable features for evaluating genetic diversity, such as high polymorphism (Varshney et al., 2007), high reproductive rates, and co-dominance (Weising et al., 2005). Furthermore, Perez et al. (2005) reported that microsatellite genetic markers are highly effective for studying genetic diversity in various plant species. Thus, this study aims to address several key objectives: i) to evaluate the distribution of seedlings, ii) estimate the amount of genetic diversity, and iii) examine the genetic structure of *R. acuminata, S. guiso*, and *R. leprosula* using microsatellite markers as references.

Methods

Study site and plant materials Populations of *R. acuminata*, *S. guiso*, and *R. leprosula* were sampled in lowland tropical forests of the Harapan Rainforest, which is managed by PT Restorasi Ekosistem Indonesia/PT REKI (PT. Indonesian Ecosystem Restoration) in Jambi Province on Sumatra Island, Indonesia (Figure 1, Table 1). The sampling took place in September 2015. In this month, the average daily precipitation was approximately 7.22 mm day^{-1}. The recorded maximum occurred at 13:00 (Indonesian Western Time), when the evapotranspiration rate reached 23.28 mm day^{-1} (Malau, 2024). The average wind speed ranges from 1.89 m s^{-1} to 2.82 m s^{-1} (Malau, 2024). The average annual temperature is approximately 26 °C, and the average annual precipitation is about 2,235 mm (Drescher et al., 2016; Nguyen et al., 2023). The climate in this region is influenced by El Niño–Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD) (Saji et al., 1999; Aldrian & Susanto, 2003). During the warm phase of ENSO, Sumatra typically experiences reduced rainfall, whereas during the cold phase it

Figure 1 Sampling location of *Rubroshorea acuminata*, *Shorea guiso*, and *Rubroshorea leprosula* in Harapan Rainforest-PT Restorasi Ekosistem Indonesia (REKI).

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Table 1 Tree coordinates of parent trees of *Rubroshorea acuminata*, *Shorea guiso*, and *Rubroshorea leprosula* in Harapan Rainforest

Species	Tree code	Latitude	Longitute
Rubroshorea acuminata	SA1	S2°9'58.263"	E103°19'45.012"
Shorea guiso	SG2	S2°7'52.930"	E103°22'23.653"
	SG3	S2°7'53.742"	E103°22'21.937"
	SG4	S2°7'54.231"	E103°22'22.099"
Rubroshorea leprosula	SL2	S2°7'53.742"	E103°22'21.970"
	SL3	S2°7'49.675"	E103°22'23.624"

experiences increased rainfall (Philander, 1990; Cane, 2005). Likewise, the IOD is characterized by fluctuations in sea surface temperatures and wind patterns across the Indian Ocean, exhibiting both positive and negative phases. In the negative phase, the western Indian Ocean experiences cooler temperatures, while the eastern region is warmer than usual; conversely, during the positive phase, the opposite occurs. This temperature differential establishes a gradient that affects rainfall distribution, leading to increased precipitation over western Indonesia during the negative phase and decreased rainfall during the positive phase (Saji et al., 1999; Iskandar et al., 2022). The Harapan Rainforest predominantly consists of low-fertility loam Acrisol soil (Schneider et al., 2015).

The seed dispersal method of each species was examined following the methods of Seidler and Plotkin (2006) and Ribbens et al. (1994). Initially, purposive sampling was performed through intentional visits to the mother trees of each species to confirm the accurate sourcing of seedlings from their designated parent trees. A total of three mother trees of *R. acuminata*, three mother trees of *S. guiso*, and two mother trees of *R. leprosula* were identified in the field and designated as the mother trees for all known seedlings of the respective target species. All seedlings located within distances of 5 m, 10 m, 15 m, 20 m, 25 m, and 30 m from each mother tree of each species were mapped using the Global Positioning System (GPS; Garmin 360). In total, 23 seedlings of *R. acuminata*, 17 seedlings of *S. guiso*, and 43 seedlings of *R. leprosula* were documented. For a genetic study, a single leaf was collected from three parent trees of *R. acuminata*, three parent trees of *S. guiso*, and two parent trees of *R. leprosula* (Table 1), focusing on trees with a diameter at breast height (dbh) greater than 20 cm. Additionally, leaves were also collected from 10 seedlings (< 1.3 m tall) growing beneath each parent tree. In total, 88 leaf samples from the three species were selected for genetic analysis. The collected leaf samples were preserved in plastic ziploc bags containing silica gel and were transported to the Forest Genetics and Molecular Forestry Laboratory at the Department of Silviculture, Faculty of Forestry and Environment, IPB University in Bogor, West Java, Indonesia, for further genetic analysis.

DNA extraction and microsatellite genotyping Genomic DNA extraction was performed on leaf tissues of *R. accuminata*, *S. guiso*, and *R. leprosula* using a modified protocol of the DNeasy 96 Plant Kit (QIAGEN, Hilden, Germany). This modification involved extending the incubation time to 30 minutes at -20 °C after adding Buffer P3, which is often necessary when the plant sample contains high levels of secondary metabolites. These secondary metabolites can complicate the DNA extraction process (Sari & Restanto, 2022). Tropical plants such as *R. leprosula* and *R. acuminata* frequently contain these compounds, making the modification essential for improving both the quantity and quality of the extracted DNA (Rachmat et al., 2024). The concentration and integrity of the extracted DNA were assessed through 1% (w/v) agarose gel electrophoresis, with visualization performed using a UV transilluminator (Weising et al., 2005).

The present study employed a total of ten microsatellite loci, selected following an initial screening of multiple loci developed for *Shorea leprosula* syn. *Rubroshorea leprosula* (Miq.) P.S.Ashton & J.Heck and *Shorea curtisii* syn. *Rubroshorea curtisii* (Dyer ex King) P.S. Ashton & J. Heck. Loci that demonstrated successful amplification across the three studied species were carefully chosen for subsequent analysis. Among them, three loci (*SleE02*, *SleE07*, and *SleE14*) were initially developed for *S. leprosula* by Ng et al. (2009a), four loci (*Sle267*, *Sle280*, *Sle562*, and *Sle566*) were originally developed for *S. leprosula* by Lee et al. (2004), and three loci (*Shc01*, *Shc07*, and *Shc09*) were previously developed for *S. curtisii* by Ujino et al. (1998). Multiplex Polymerase Chain Reaction (PCR) was carried out using a VeritiTM thermal cycler (Applied Biosystems) to amplify the genomic DNA of the three studied *Shorea* species. The PCR mixture in a volume of 10 µl, contained 5 µl of 2× Multiplex PCR Master Mix, 1 µl of each primer mix (2 µM each), 3 µl of RNase-free water, and 1 µl of genomic DNA (± 40 ng). The PCR conditions included an initial denaturation step at 94 °C for 3 minutes, followed by 35 cycles consisting of denaturation at 94 °C for 1 minute, annealing at either 45 °C or 49 °C for 30 seconds (Table 2), and extension at 72 °C for 45 seconds. Fragment size analyses were performed on an ABI PRISM 310 Genetic Analyzer (Applied Biosystems).

Data analysis The distributions and distances of seedlings from their putative mother trees were estimated using GPS data and analyzed using Minitab 14 (McKenzie, 2004). Statistical analysis of genetic diversity was performed, including polymorphic loci percentage, observed number of alleles (N_a), effective number of alleles (N_e), observed heterozygosity (H_o), and expected heterozygosity (H_e). These calculations were performed using GenAlEx version 6.41

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Scientific Article
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Table 2 Primer information for the 10 microsatellite loci used for *Rubroshorea acuminata*, *Shorea guiso*, and *Rubroshorea leprosula* from Harapan Rainforest

Locus	Length (bp)	Annealing temperature (°C)	Number of alleles	H_e	F
SleE02	134–183	45	13	0.165	−0.409
SleE07	178–192	45	5	0.472	−0.600
SleE14	194–253	45	17	0.448	−0.508
Sle267	100–130	45	11	0.195	−0.333
Sle280	106–152	45	11	0.342	−0.510
Sle562	156–199	45	20	0.466	−0.385
Sle566	68–102	45	18	0.462	−0.408
Shc01	134–183	49	12	0.295	−0.462
Shc07	128–185	49	17	0.398	−0.377
Shc09	180–212	49	9	0.314	−0.398

Note: H_e = Nei's expected heterozygosity; F = fixation index

(Peakall & Smouse, 2006). Nei's genetic distance (D) (Nei et al., 1983) was calculated in POPGENE version 1.31 to estimate genetic distances between populations (Yeh & Yang, 1999). The dendrogram was constructed based on the resulting distance matrix generated from the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) implemented in NTSYS version 2.02 (Rohlf, 2008).

The population genetic structure of the three species was analyzed using the Bayesian model-based clustering approaches in STRUCTURE version 2.3.3 (Evanno et al., 2005; Pritchard et al., 2010). This approach allows for determining the number of populations (clusters) and the extent of membership of each individual within those clusters (including cases of admixture or introgression). This enables an analysis of direct genetic relationships based on molecular data (Dillon et al., 2013). The entire dataset was processed using a burn-in of 20,000 steps followed by 100,000 steps of MCMC (Markov chain Monte Carlo) simulation, with 8 replications each, over a range of K-values from 1 to 10. To identify the appropriate number of clusters (K), the statistic ΔK [18] was calculated based on the rate of change in the log probability of data across the specified parameters and assumptions between successive K-values using STRUCTURE HARVESTER (Earl & vonHoldt, 2012).

Results

Seedling distributions of *Rubroshorea acuminata, Shorea guiso,* and *Rubroshorea leprosula* The present study demonstrated that *R. acuminata, S. guiso*, and *R. leprosula* within the Harapan Rainforest employed the gyration method for seed dispersal (Figure 2). This mechanism may play a significant role in the distribution pattern of seedlings around their respective mother trees. Specifically, the study found that seedling density decreases with increasing distance from the mother tree across all three species (Figure 3). Although the three studied species employ the same gyration method for seed dispersal and exhibit a slightly similar pattern of seedling distribution in the Harapan Rainforest, variations in seedling density are evident among them, with *R. leprosula* exhibiting the highest density (Figure 3).

Genetic diversity of *Rubroshorea acuminata, Shorea guiso,* and *Rubroshorea leprosula* This study demonstrated that ten microsatellite primer pairs that were previously developed for *Shorea leprosula* syn. *Rubroshorea leprosula* and *S. curtisii* syn. *Rubroshorea curtisii* was successfully amplified across three species (*R. acuminata*, *S. guiso*, and *R. leprosula*). Primer information and genetic diversity, as represented by expected heterozygosity (H_e), across three species are summarized in Table 2. The total number of alleles varied between 5 and 20, with the lowest number observed at locus *SleE07* and the highest at locus *Sle562*. All microsatellite loci exhibited low expected heterozygosity, with values ranging from H_e = 0.165 in *SleE02* to H_e = 0.472 in *SleE07*. Furthermore, the ten microsatellite primer pairs were used to estimate genetic diversity in both seedlings and mother trees of the studied *R. acuminata, S. guiso*, and *R. leprosula* (Table 3).

The genetic diversity in seedlings was found to be greater than that in mother trees across all examined species (Table 3). Specifically, the mean expected heterozygosity (H_e) for seedlings was 0.450, 0.461, and 0.544 for *R. acuminata, S. guiso*, and *R. leprosula*, respectively. In contrast, the mean expected heterozygosity (H_e) for mother trees was 0.167, 0.267, and 0.350 for *R. acuminata, S. guiso*, and *R. leprosula*, respectively. At the species level, *R. leprosula* exhibited slightly higher mean genetic diversity in both seedling (H_e = 0.544) and mother tree (H_e = 0.350) populations compared to *R. acuminata* (H_e seedlings = 0.450, H_e mother trees = 0.167) and *S. guiso* (H_e seedlings = 0.461, H_e mother trees = 0.267) (Table 3).

Genetic structure among *Rubroshorea acuminata, Shorea guiso*, and *Rubroshorea leprosula* The UPGMA dendrogram revealed that the populations of *R. acuminata, S. guiso*, and *R. leprosula* can be clustered into three distinct groups based on species (Figure 4). In the dendrogram, *R. leprosula* and *R. acuminata* form a sister group, distinct from *S. guiso* (Figure 4).

A model-based clustering analysis was performed using STRUCTURE to further investigate the genetic relationship among populations of the three species. The analysis revealed that the highest ΔK value, which suggests the most likely number of genetic clusters, occurred at K = 3. This suggested that the seedlings of the three species studied here can be distinctly categorized into three genetically distinct

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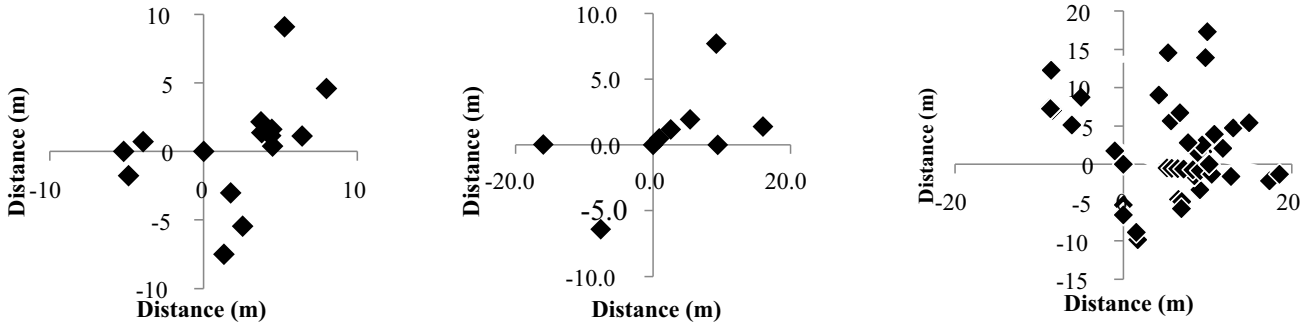

(a) (b) (c)

Figure 2 Seed dispersal in three dipterocarp species in Harapan Rainforest: (a) *Rubroshorea acuminata*, (b) *Shorea guiso*, and (c) *Rubroshorea leprosula.*

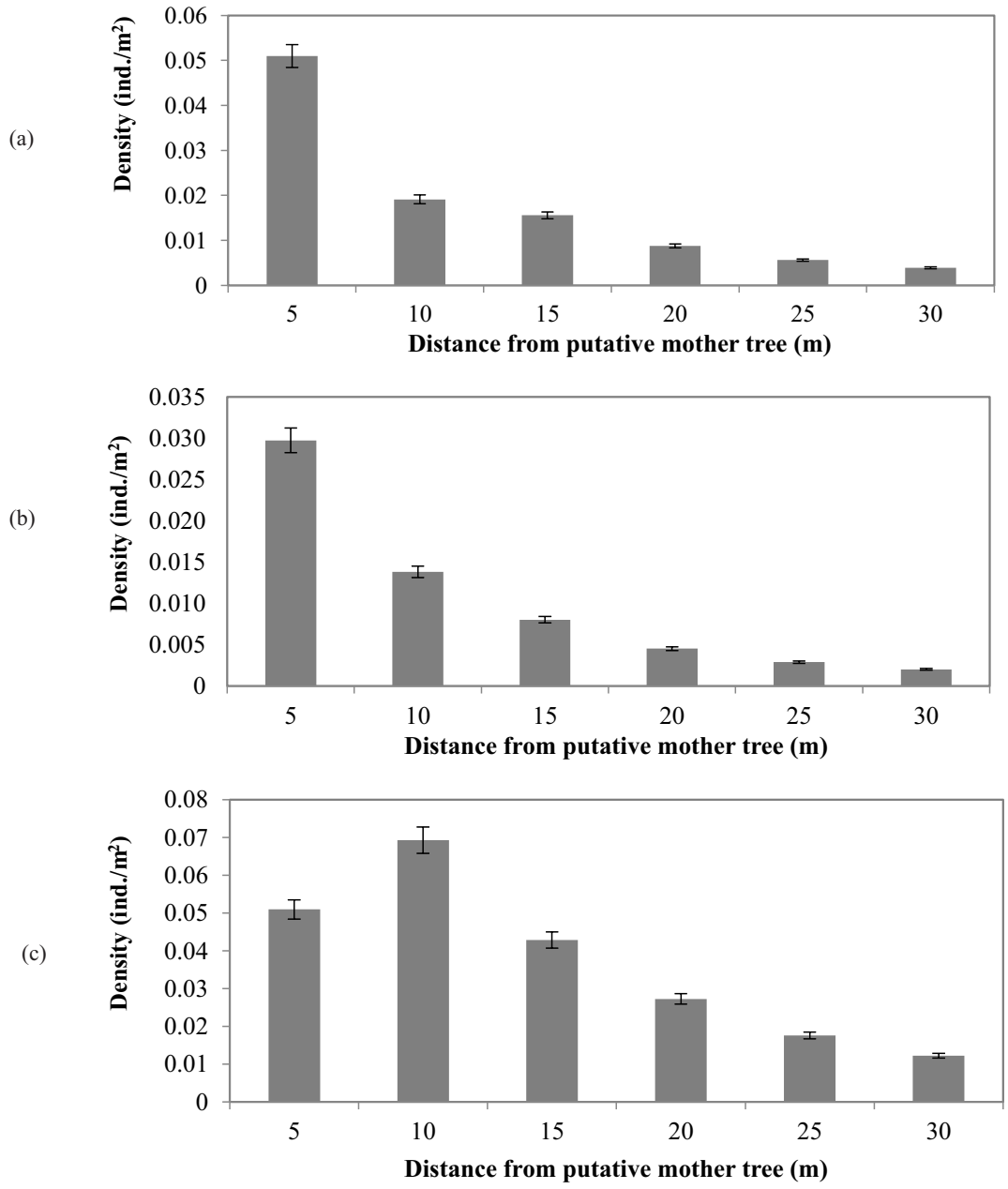

Figure 3 Distance of seedlings of three dipterocarp species from their putative mother tree in Harapan Rainforest: (a) *Rubroshorea acuminata,* (b) *Shorea guiso,* and (c) *Rubroshorea leprosula.*

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Scientific Article
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Table 3 Summary of genetic diversity within populations of *Rubroshorea acuminata*, *Shorea guiso,* and *Rubroshorea leprosula* in Harapan Rainforest

Population	N	N_a	N_e	PLP (%)	H_o	H_e
Seedling						
R. acuminata-1 (SA1)	10	2.4	1.839	70	0.530	0.407
R. acuminata-2 (SA2)	10	3.3	2.186	80	0.360	0.442
R. acuminata-3 (SA3)	10	4.3	2.903	80	0.353	0.502
Mean	*10*	*3.3*	*2.309*	*77*	*0.414*	*0.450*
S. guiso-2 (SG2)	10	2.9	2.120	90	0.500	0.482
S. guiso-3 (SG3)	10	2.5	1.942	80	0.520	0.413
S. guiso-4 (SG4)	10	3.0	2.334	80	0.540	0.488
Mean	*10*	*2.8*	*2.132*	*83*	*0.520*	*0.461*
R. leprosula-2 (SL2)	10	3.7	2.449	100	0.617	0.540
R. leprosula-3 (SL3)	10	4.9	2.529	90	0.590	0.547
Mean	*10*	*4.3*	*2.489*	*95*	*0.604*	*0.544*
Mother Tree						
R. acuminata-1 (SA1)	1	1.2	1.200	30	0.300	0.150
R. acuminata-2 (SA2)	1	1.2	1.200	30	0.300	0.150
R. acuminata-3 (SA3)	1	1.3	1.300	40	0.400	0.200
Mean	*1*	*1.2*	*1.233*	*33*	*0.333*	*0.167*
S. guiso-2 (SG2)	1	1.5	1.500	60	0.600	0.300
S. guiso-3 (SG3)	1	1.8	1.800	80	0.800	0.200
S. guiso-4 (SG4)	1	1.5	1.500	60	0.600	0.300
Mean	*1*	*1.6*	*1.600*	*67*	*0.667*	*0.267*
R. leprosula-2 (SL2)	1	1.7	1.700	70	0.700	0.350
R. leprosula-3 (SL3)	1	1.7	1.700	70	0.700	0.350
Mean	*1*	*1.7*	*1.700*	*70*	*0.700*	*0.350*

Note: N = number of individuals; N_a = mean number of observed alleles; N_e = mean number of effective alleles; PLP = percentage of polymorphic loci; H_o = mean observed heterozygosity; H_e = mean expected heterozygosity

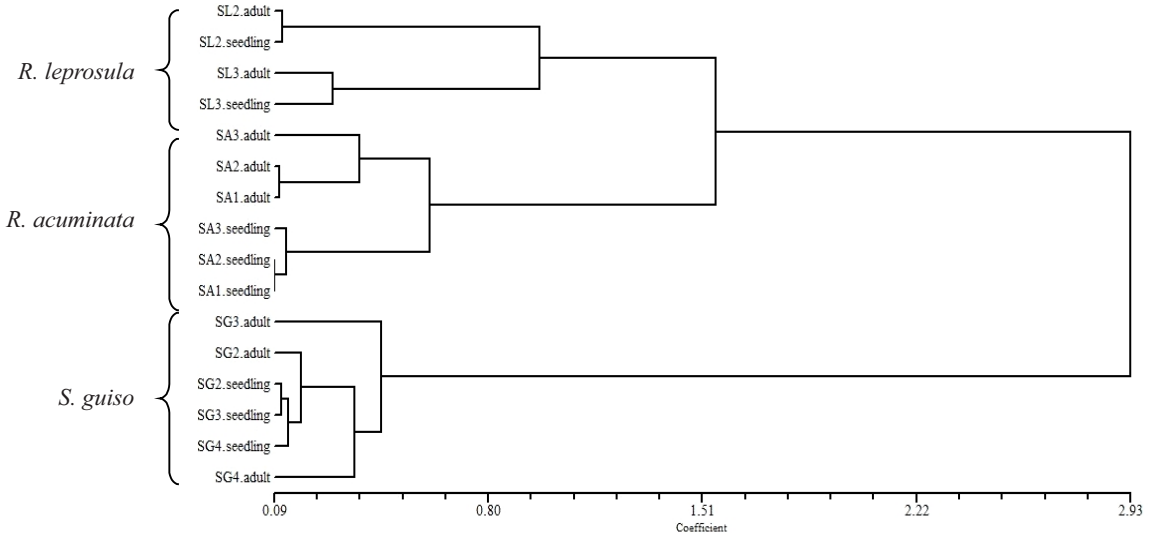

Figure 4 Unweighted pair group method with arithmetic mean dendogram representing the genetic distances among populations of *Rubroshorea acuminata, Shorea guiso*, and *Rubroshorea leprosula* in Harapan Rainforest.

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groups (Figure 5). Although several individual seedlings from each species exhibit bars with multiple colors, the case of the *R. acuminata* individual is particularly noteworthy. This individual displays nearly 50% of the *S. guiso* bar color, suggesting.

Discussion

Plant regeneration is influenced by biotic and abiotic factors, especially seed dispersal, which influences the process of forest regeneration (Freund, 2012). Tree species with limited seed dispersal frequently exhibit distinctly clustered spatial patterns, in contrast to those with mechanisms for long-distance dispersal. The effectiveness of seed dispersal varies among species, significantly influenced by their specific dispersal strategies. When seed dispersal is restricted, the patterns of seed and seedling recruitment become notably clustered, underscoring the critical role of dispersal methods in shaping forest dynamics (Datta & Rawat, 2008). The way seeds are dispersed affects how seedlings grow near the mother tree. Seidler and Plotkin (2006) reported that there are seven seed dispersal methods: ballistic, gravity, gyration, wind, and animals (for small, medium, and large fruit sizes). Fruits that lack edible pulp or flesh and have characteristics suited for abiotic dispersal are categorized as mechanically dispersed (Datta & Rawat, 2008). In most dipterocarps, fruits are specifically classified as winged fruits, which disperse by wind through a process called auto-gyration (Ashton, 1982; Nagamitsu et al., 2001).

The present study highlighted that the species *R. acuminata, S. guiso*, and *R. leprosula* in the Harapan Rainforest employed the gyration method for seed dispersal (Figure 2). This finding is consistent with research by Varshney et al. (2012), which identified that winged seeds exhibit a gyration-type of fall to the forest floor. Commonly, species that depend on gyration for seed dispersal can occasionally achieve long-distance dispersal by means of strong winds; however, such fruits generally possess limited lift due to their high mass-to-wing area ratio (Seidler & Plotkin, 2006). Cao et al. (2006) reported that the maturation of fruits of the genera *Rubroshorea* or *Shorea* occurs approximately 14 weeks following mass-flowering events. If a dry spell transpires during this maturation period, it may delay fruit drop and adversely affect fruit development. During mast-fruiting events, seeds frequently evade predation by overwhelming predators (Janzen, 1974) or by germinating rapidly before migratory predators arrive (Curran & Leighton, 2000). Therefore, the impact of secondary dispersal by seed predators on seed aggregation is likely to be minimal (Seidler & Plotkin, 2006). Furthermore, these species experience limited seed dispersal due to the considerable weight of their seeds (Cao et al., 2006). This mechanism may contribute to the observed distribution pattern of seedlings surrounding the mother trees of the three studied species in the Harapan Rainforest, where seedling density declines with increasing distance from the putative mother tree in all three species (Figure 3). Although wind disperses the fruits, they infrequently travel beyond 50 meters from the mother tree. This constrained dispersal significantly contributes to the clumped distribution of *R. leprosula* (Chan, 1980). Such a distribution pattern likely accounts for the notable density of *R. acuminata*, *S. guiso*, and *R. leprosula* seedlings observed near the mother tree in this study, thereby highlighting the unique ecological dynamics of these species.

Although the three studied species employ the same gyration method for seed dispersal and have a slightly similar pattern of seedling distribution in the Harapan Rainforest, seedling density varied among them, with *R. leprosula* exhibiting the highest density (Figure 3). This pattern may be attributable to the elevated survival rate of *R. leprosula* seedlings, indicating strong potential for natural regeneration in *R. leprosula*. Numerous studies have reported that *Shorea leprosula* syn. *Rubroshorea leprosula* seedlings exhibit higher survival rates in plantation environments and superior growth performance compared to other dipterocarp species, such as *Shorea acuminata* syn. *Rubroshorea acuminata* (Nurfaeiza et al., 2022), *Shorea stenoptera, S. mecisopteryx, S. pinanga,* and *S. palembanica* (Dwiyanti et al., 2024), particularly in the flat slope class area (Malinda et al., 2022). The high survival rate of *R. leprosula*'s natural regeneration is primarily due to its adaptability to various environmental conditions, including those in the Harapan Rainforest, which features a high-rainfall climate conducive to its growth. Furthermore, *R. leprosula* is well-suited to shaded environments, especially on flat slopes with dense canopy cover, and demonstrates a preference for well-drained soil (Pamoengkas et al., 2014; Nurfaeiza et al., 2022; Attarik et al., 2024). This elevated survival rate not only enhances seedling abundance but may also influence the genetic diversity of *R. leprosula* within this ecosystem. Seed dispersal affects genetic diversity by influencing gene flow,

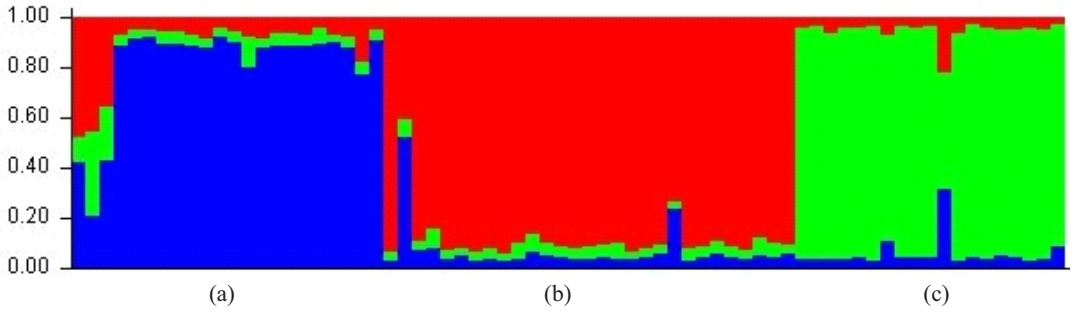

Figure 5 Clustering results for three dipterocarp species in Harapan Rainforest obtained from the STRUCTURE analysis: (a) *Rubroshorea acuminata,* (b) *Shorea guiso,* and (c) *Rubroshorea leprosula.*

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Scientific Article
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with long-distance dispersal generally increasing diversity within a population by introducing new genetic material and mixing populations. In contrast, short-distance dispersal or clumped dispersal can lead to greater genetic structure within a local population because offspring (seedlings) are more closely related to their neighbors (Hamrick et al., 1993). Effective dispersal mechanisms can help maintain genetic diversity and prevent local populations from becoming too genetically isolated, while the loss of dispersal mechanisms, such as the disappearance of a seed-dispersing animal, can lead to reduced diversity and genetic differentiation.

The genetic study demonstrated that ten microsatellite primer pairs that were previously developed for *Shorea leprosula* syn. *Rubroshorea leprosula* and *S. curtisii* syn. *Rubroshorea curtisii* could be successfully used to estimate genetic diversity in the studied *R. acuminata, S. guiso*, and *R. leprosula,* indicating potential cross-amplification of microsatellite markers between the two genera. A previous study has reported the successful cross-amplification of microsatellite markers from *Shorea leprosula* syn. *Rubroshorea leprosula* and *S. curtisii* syn. *Rubroshorea curtisii* in *Shorea guiso* from the Philippines (Tinio et al., 2014) and *Shorea acuminata* syn. *Rubroshorea acuminata* from Malaysia (Naito et al., 2008). Additionally, the primer pairs for *R. leprosula* developed by Lee et al. (2004) were also effectively employed for *S. curtisii* (Abasolo et al., 2009; Ho et al., 2006). This suggested that the flanking regions of these microsatellite loci are conserved across various *Shorea* and *Rubroshorea* species, as indicated by Ng et al. (2004).

In this study, seedling genetic diversity exceeded that of the mother trees across all species examined (Table 3). This observation corroborates findings by Dwiyanti et al. (2014a) in their study on *Dipterocarpus littoralis*, which attributed this phenomenon to the reduced number of mother trees available in the field. Commonly, increased genetic diversity among seedlings is attributed to genetic mixing from multiple parents during sexual reproduction, resulting in novel combinations of genetic material. Consistent with the characteristics of dipterocarp species, the three species investigated exhibit a sporadic flowering pattern throughout the year in natural forests (Ashton, 1988). These species typically flower every 2 to 5 years (Soerianegara & Lemmens, 1993; Joker, 2002), with numerous trees producing abundant and synchronized blooms during flowering years. The flowers of these species typically open in the evening, emitting a strong fragrance that attracts flower thrips, which are essential for pollination. Most members of the Dipterocarpaceae family are pollinated by pollenivores such as bees and thrips (Ashton, 2014). Specifically, within the genera *Shorea* and *Rubroshorea,* these species depend on small insects, particularly thrips, for effective pollination (Cao et al. 2006). Furthermore, Nagamitsu et al. (2001) also reported that the outcrossing rate of thrips-pollinated *Rubroshorea leprosula* was equal to or exceeded that of species pollinated by bees in Pasoh Forest Reserve, Malaysia, suggesting a high likelihood of mating opportunities among reproductive trees and/or a strong post-pollination selection against selfing in *R. leprosula*. In the context of *R. acuminata*, the big-eyed bug has been identified as a critical pollinator (Kondo et al., 2016). Outbreaks of flower thrips have been observed to attract big-eyed bugs to various flowering *R. acuminata* trees, facilitating the dispersal of outcross pollen. Given their longer generation times and lower reproductive rates compared to flower thrips (Naranjo & Stimac, 1985), it is plausible that big-eyed bugs face challenges in responding rapidly to irregular and intense flowering events, as they do not significantly increase their populations during bloom periods. However, like giant honey bees, stingless bees, and herbivorous beetles, big-eyed bugs can respond promptly to the sudden availability of abundant floral resources during mass-flowering periods by sustaining their populations during intervals between such events (Kondo et al., 2016). This reliance on insect pollinators may facilitate extensive gene flow among the existing mother trees of the three species within the Harapan Rainforest during reproductive periods. However, greater distances from each reproductive tree may reduce outcrossing rates because there are fewer opportunities for cross-pollination. Consequently, conserving existing mother trees in the Harapan Rainforest is important.

This study also found that *R. leprosula* exhibited slightly higher average genetic diversity in both seedling and mother-tree populations than *R. acuminata* and *S. guiso* (Table 3). This finding is anticipated, given the nature of cross-species amplification, as the microsatellite markers were specifically developed for *R. leprosula* and subsequently applied to other species. It is also possible that the observed variation may have been influenced by the presence of null alleles in *R. acuminata* and *S. guiso*, which were not assessed in the present study. Additionally, the allelic diversity and heterozygosity of the three species in the present study were found to be higher than those reported for *S. curtisii* by Ho et al. (2006) in the Ulu Sedili Forest Reserve, Johor, Malaysia, where heterozygosity values (H_e) were 0.285 for seedlings and 0.223 for adult trees, but lower than those reported for *Shorea acuminata* syn. *Rubroshorea acuminata* adult trees in Pasoh Forest Reserve, Negeri Sembilan, Malaysia (H_e = 0.676) (Naito et al., 2008) and *S. guiso* adult trees from natural forest in the Philippines (H_e = 0.75) (Tinio et al., 2014).

The greater genetic diversity in *R. leprosula* in the Harapan Rainforest compared to other studied species in the present study may be associated with its outcrossing event. As a diploid and predominantly outcrossed species (Ng et al., 2009b), *R. leprosula* is characterized by a high outcrossing rate (0.77 to 1.00) in the natural forest compared to other dipterocarp species, such as *S. acuminata* (0.61) (Naito et al., 2008), *S. trapezifolia* (0.54–0.62), and *S. megistophylla* (0.71–0.87) (Murawski et al., 1994a; 1994b; Nagamitsu et al., 2001). Notably, a single logging event could contribute to genetic erosion in this species and also other dipterocarps (Ng et al., 2009b). Moreover, previous studies indicate that the density of flowering conspecifics can significantly affect outcrossing rates in certain dipterocarp species (e.g., Lee et al., 2000; Murawski et al., 1994b; Obayashi et al., 2002). The low outcrossing rate, such as in *S. acuminata,* is likely due to the very low density of conspecifics flowering in that population (Naito et al., 2008). Due to a lack of available data, a comparison of outcrossing rates with *S. guiso* remains unfeasible. For predominantly outcrossing species such as dipterocarps, maintaining high outcrossing rates is crucial in order to mitigate the risk of inbreeding depression in future

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generations (Naito et al., 2008). Furthermore, a study by Chan (1981) demonstrated self-incompatibility in *R. leprosula* through controlled pollination experiments, revealing the complexities of its reproductive strategies.

The high genetic diversity observed in both the mother trees and the seedlings of *R. leprosula* in this study suggests that this species is well-suited for enrichment planting programs within the Harapan Rainforest. High genetic diversity is a favorable indicator for the management and conservation of species, as it typically correlates with increased resilience to environmental changes, pests, and diseases, as well as enhanced capacity for adaptation over time (Benítez-Benítez et al., 2022). These results suggest that incorporating both mother trees and their naturally regenerated seedlings from this region can yield a robust, genetically diverse stock for restoration initiatives. Furthermore, it is essential that the protocols for seed collection adhere to best practices, which include sourcing from multiple mother trees. For effective species conservation, it is crucial to highlight that the three species studied should be preserved, as their genetic diversity is lower compared to other populations within the country.

Additionally, the genetic structure of the tree species, as illustrated by the UPGMA dendrogram, revealed that the populations of *R. acuminata, S. guiso*, and *R. leprosula* can be clustered into three distinct groups based on species, with *R. leprosula* and *R. acuminata* forming a sister group and distinct from *S. guiso* (Figure 4). This arrangement supports the recent taxonomic revision of the tribe Shoreae, which reclassified red meranti species into the genus *Rubroshorea*. This includes *Rubroshorea leprosula* (formerly known as *Shorea leprosula*) and *Rubroshorea acuminata* (formerly known as *Shorea acuminata*), while *Shorea guiso* remains in the *Shorea* genus (Ashton & Heckenhauer, 2022). The separation between the genera *Rubroshorea* and *Shorea* was based on molecular phylogenetic trees derived from plastid and nuclear data. These trees provided evidence that divides the genus *Shorea* sensu Ashton into five groups, corresponding to Ashton's sections: *Doona, Anthoshorea, Rubroshorea, Shorea* balau (*selangan batu*), and *Richetia*. Furthermore, specific wood characteristics were observed only in the pink to red-brown inner bark and wood, which are absent in some species that exhibit yellow-brown coloration, yet present in *S. guiso* (Blanco) Blume, section *Shorea*, subsection *Shorea*.

The pattern of the UPGM dendrogram was also consistent with the STRUCTURE results, which indicated that the seedlings of the three species could be distinctly categorized into three genetically distinct groups (Figure 5). Although several individual seedlings from each species suggest a potential hybrid event, such as between *R. acuminata* and *S. guiso* and between *R. acuminata* and *R. leprosula*. It is important to note that *R. leprosula* has been reported to possess natural hybrids within its habitat (Meinata et al., 2021). A study conducted by Ng et al. (2020) confirms the occurrence of natural hybridization between *Shorea leprosula* (syn. *Rubroshorea leprosula*) and *Shorea curtisii* (syn. *Rubroshorea curtisii*) in the Pasir Panjang Forest Reserve, Negeri Sembilan, Malaysia. Furthermore, a study by Kenzo et al. (2019) has identified the extent of interspecific hybridization between *S. curtisii* (syn. *Rubroshorea curtisii*) and *S. leprosula* (syn. *Rubroshorea leprosula*), and between *S. leprosula* (syn. *Rubroshorea leprosula*) and *Shorea parvifolia* (syn. *Rubroshorea parvifolia*) in a forest fragment in Singapore. In the present study, the geographical proximity of *R. leprosula* to *S. guiso* raises the possibility of hybridization occurring within the Harapan Rainforest. Nevertheless, the present study lacks sufficient evidence to substantiate this hypothesis, thereby indicating the necessity for further research in this area.

Both genetic distance and STRUCTURE analyses indicated that *R. leprosula* and *R. acuminata* are closely related and distinct from *S. guiso*. The genetic similarity observed between *R. leprosula* and *R. acuminata* in this study likely indicates a relatively recent common evolutionary origin. This suggests that both species may have descended from a shared ancestor that evolved in close temporal proximity. Within the genus *Rubroshorea*, which is highly diverse across Southeast Asia, adaptive radiation appears plausible. This process occurs when multiple species emerge from a common ancestor in response to variations in their respective habitats. The genetic proximity between *R. leprosula* and *R. acuminata* can be attributed to several interrelated factors: a common phylogenetic origin, analogous habitats and selection pressures, potential gene flow or hybridization, speciation that occurs without complete geographic isolation, and genetic conservatism within this genus.

Conclusion

This study revealed that *R. acuminata, S. guiso*, and *R. leprosula* employ the gyration method for seed dispersal. This mechanism may account for the observed distribution pattern of seedlings surrounding the mother trees of these three species in the Harapan Rainforest, where seedling density declines with increasing distance from the putative mother tree. Despite similarities in dispersal method, seedling density varies among the three species, with *R. leprosula* showing the highest density. This phenomenon may be linked to the greater survival rate of *R. leprosula* seedlings, indicating a robust potential for natural regeneration in this species. Furthermore, the study indicated that ten previously developed microsatellite markers for *R. leprosula* and *S. curtisii* can be used to estimate genetic diversity among the three species studied. Among them, *R. leprosula* exhibits slightly greater genetic diversity in both the mother trees and the seedlings than the other species. The high genetic diversity observed in both the mother trees and the seedlings of *R. leprosula* in this study suggests that this species is recommended for enrichment planting initiatives within the Harapan Rainforest. Analyses of genetic distance and STRUCTURE indicated that *R. leprosula* and *R. acuminata* are closely related, while *S. guiso* appears more genetically distinct. This finding supports the recent taxonomic revision of the tribe Shoreae. The outcomes of the present study provide essential foundational data for formulating management strategies to conserve these ecologically and economically significant species, particularly within the Harapan Rainforest.

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