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Population genetics and ecology of Sumatran camphor (*Dryobalanops aromatica*) in natural and community-owned forests in Indonesia

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Abstract. Ritonga FN, Dwiyanti FG, Kusmana C, Siregar UJ, Siregar IZ. *2018. Population genetics and ecology of Sumatran camphor (*Dryobalanops aromatica*) in natural and community-owned forests in Indonesia. Biodiversitas 19: 2175-2182. Dryobalanops aromatica* Gaertn. f. (Sumatran camphor) is a valuable tree species that produces borneol (camphor) and good-quality timber. However, the population of this species has declined due to illegal logging and conversion of forests into plantations and has been classified as Critically Endangered by the International Union for Conservation of Nature. This study aimed to examine the genetic variation and spatial distribution of this species in a community-owned forest (Barus) and two natural forests (Singkohor and Danau Paris) in Indonesia using the Random Amplified Polymorphic DNA marker. The results of this study showed that *D. aromatica* had moderate levels of genetic variation (expected heterozygosity [He] = 0.1760 [Barus population] to 0.2134 [Singkohor population]) and genetic differentiation (Nei's Gst = 0.1257). The genetic distance was the smallest between the Singkohor and Danau Paris populations (Nei's distance = 0.0363) and greatest between the Singkohor and Barus populations (Nei's distance = 0.0534). The spatial distribution of *D. aromatica* was grouped in both Barus and Danau Paris based on Morisita's index of diversity (ip = 0.06 and 0.043, respectively). These findings indicated that genetic conservation might be performed *in situ* in combination with enrichment planting using locally propagated sources.

Keywords: Conservation, *Dryobalanops aromatica*, genetic variation, RAPD, spatial distribution

INTRODUCTION

Dryobalanops aromatica Gaertn. f. (Sumatran camphor) is a valuable tree species that produces borneol (camphor) in the form of crystals and oil, which contains bioactive compounds that have antioxidant, antifungal, and cytotoxic effects and can even counteract the spread of human immunodeficiency virus (Wibowo et al. 2011). However, populations of *D. aromatica* are declining as a result of deforestation, forest fires, and conversion of forests into oil palm (*Elaeis guineensis*) plantations (Gusmailina 2014). This species is now being considered as a rare plant in Indonesia, particularly in Central Tapanuli and Aceh Singkil Regencies and categorized as Critically Endangered by the International Union for Conservation of Nature (Dwiyanti et al. 2014; Gusmailina 2014). Consequently, it is crucial that populations of *D. aromatica* are conserved and supplemented through propagation. In Central Tapanuli, *D. aromatica* is being conserved through the development of community-owned forests. Such *ex-situ* conservation requires the population size to be sufficiently large to ensure genetic diversity within each population and reduce the chances of inbreeding, which will reduce the genetic diversity (Nguyen et al. 2014). However, only a small population is being maintained because of commercial plantations, mainly oil palm plantations, offering greater economic opportunities for the local people. In addition, there is a lack of information on the genetic diversity and structure of the species in this area, which is a fundamental requirement for the development of appropriate conservation strategy and sustainable forestry management (Tsumura 2011; Dwiyanti et al. 2015).

One of the molecular markers that can be used to determine genetic diversity within and between populations is the Random Amplified Polymorphic DNA (RAPD). The main advantages of this marker are that it produces sufficiently high levels of polymorphism, randomly samples the whole genome, and is technically relatively quick and easy to perform (Yulita and Partomihardjo 2011). The results can then be used in combination with various additional data to determine the overall status of the genetic diversity of a species (Kaur et al. 1978). Such data can include the ecological characteristics of a species such as its structure and composition, which can be determined through vegetation analysis. Therefore, this study was aimed to assess the genetic diversity and spatial distribution of *D. aromatica* in Central Tapanuli and Aceh Singkil Regencies to help formulate the most appropriate strategy for its genetic conservation. We believe that the findings of this study will help to conserve this critically

endangered plant through both *in situ* and *ex situ* conservation strategy.

MATERIALS AND METHODS

Study site

This study was conducted between October 2015 and May 2016. Leaves and field data were collected from a community-owned forest in Barus Sub-district, Central Tapanuli District, North Sumatra Province (02°04′17.9″N, 98°21′32.1″E) and two natural forests in Aceh Singkil District, Nanggroe Aceh Darussalam Province (Singkohor, 02°30′24.2″N, 97°58′23.4″E, and Danau Paris, 02°19′10.9″N, 98°08′25.7″E) (Figure 1). DNA extraction and RAPD analysis were carried out in the Laboratory of Forest Genetics and Molecular Forestry, Department of Silviculture, Faculty of Forestry, Bogor Agricultural University (IPB), Bogor, Indonesia.

Leaf morphological variation analysis

Leaves were sampled for morphological variation analysis according to the methods by Kremer et al. (2002) and Anwar (2015) with some modifications in which sinus width (SW) of the leave were not measured due to the differences in the leave form. One branch bearing at least five leaves were collected from each tree, and the following measurements were taken for each leaf: lamina length (LL), petiole length (PL), lobe width (LW), length of lamina at the widest part (WP), number of secondary veins (NSV), an angle between the primary and secondary veins (AV). The measured leaf variables were then used to calculate the leaf area (LA) and circumference of leaves (CL), aspect ratio (AR), form factor (FF) and perimeter ratio of diameter (PR) according to the methods by Wu et al. (2007) and Anwar et al. (2015). These data were then compared among populations using t-tests in Minitab version 16 (Minitab 2010).

Genetic variation analysis

About 7-30 young leaf samples were collected from each site for DNA analysis. DNA extraction was carried out using the cetyltrimethylammonium bromide (CTAB) method (Weising et al. 2005; Aritonang et al. 2007), and the quality of the extracted DNA was determined by agarose gel electrophoresis, soaking the gel in a solution of ethidium bromide for 15 min, and photographing it on a TFX-20.LM model UV transilluminator (Suharsono and Utut 2012).

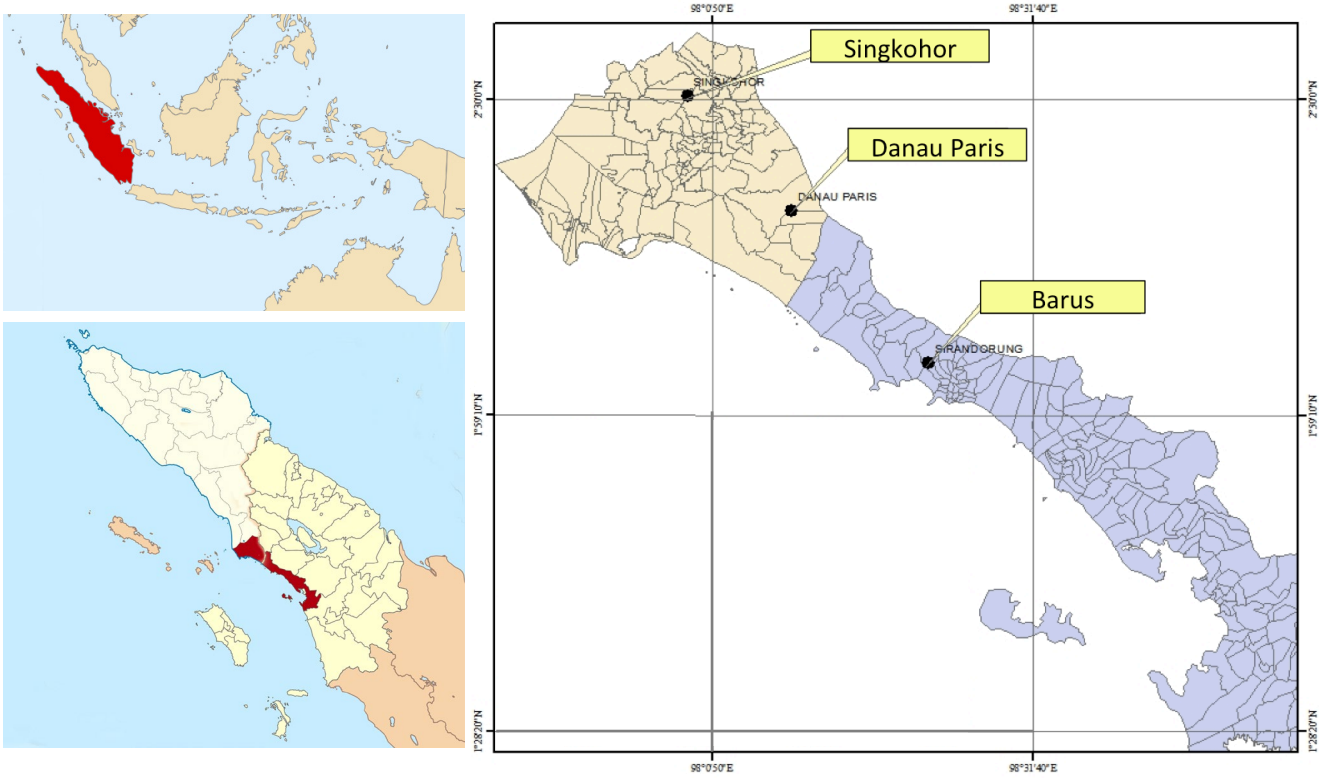

Figure 1. Location of the three *Dryobalanops aromatica* populations examined in this study

Table 1. RAPD sequence primers used in this study (Lee et al. 1999; Yulita and Partomihardjo 2011)

Locus	Sequence primer (5′-3′)	T_m (°C)	Expected size (bp)	Number of polymorphic loci
OPA-09	GGGTAACGCC	32-38	250-1100	15
OPB-08	GTCCACACGG	32-38	250-1050	12
OPB-16	TTTGCCCGGA	32-38	250-1200	13
OPB-20	GGACCCTTAC	32-38	300-1250	8
OPP-09	GTGGTCCGCA	32-38	250-1150	7
OPP-10	TCCCGCCTAC	32-38	300-1100	11
OPP-14	CCAGCCGAAC	32-38	250-900	12
OPP-15	GGAAGCCAAC	32-38	250-1000	9
OPP-19	GGGAAGGACA	32-38	200-1050	10
OPC-07	GTCCCGACGA	32-38	350-1450	11

Table 2. Morphological traits of *Dryobalanops aromatica* leaves at the Danau Paris and Barus study sites

Leaf morphological traits	Site			
	Danau Paris	CV (%)	Barus	CV (%)
LL (cm)	9.52 ± 1.55^a	6.14^L	10.59 ± 1.27^b	8.33^L
PL (cm)	0.94 ± 0.14^a	6.71^L	0.756 ± 0.23^b	3.28^L
LW (cm)	4.18 ± 0.49^a	8.53^L	4.53 ± 0.4^b	8.39^L
WP (cm)	3.76 ± 0.61^a	6.16^L	4.37 ± 0.59^b	7.40^L
NSV	73.0 ± 12.5^a	5.84^L	68.1 ± 12.6^a	5.40^L
AV (°)	74.12 ± 5.24^a	$14,15^L$	72.52 ± 3.53^a	20.54^H
LA (cm)	126.0 ± 26.5^a	4.75^L	152.5 ± 31.6^b	4.83^L
CL (cm)	43.52 ± 5.40^a	8.05^L	48.0 ± 5.20^b	9.23^L
AR	2.29 ± 0.48^a	4.77^L	2.5 ± 0.26^a	9.04^L
FF	0.83 ± 0.06^a	13.83^L	0.82 ± 0.04^a	20.5^H
PR	10.46 ± 1.30^a	8.04^L	10.64 ± 0.82^a	12.98^L

Note: Different letters indicate significant differences between the study sites (t-test, $p < 0.05$). LL = lamina length; PL = petiole length; LW = lobe width; WP = length of lamina at largest width; NSV = number of secondary veins; AV = angle between the primary and secondary veins; LA = leaf area; CL = circumference of leaves; AR = aspect ratio of leaf; FF = form factor; PR = perimeter ratio of diameter; L = low; H = high

Ten RAPD primers were selected based on the previous studies of Lee et al. (1999) and Yulita and Partomihardjo (2011) (see Table 1). The genetic diversity of *D. aromatica* populations was then assessed by interpreting the resulting DNA electropherogram and analyzing the data using POPGENE 32 version 1.31 (Yeh et al. 1999). Furthermore, NTedit version 1.07c (Jamshidi and Jamshidi 2011) and NTSYS version 2.0 (Rohlf 2008) software were used to generated dendrogram derived from UPGMA cluster analysis using Dice coefficient of similarity of RAPD marker. The number of genetically homogeneous populations (K) was estimated in STRUCTURE version 2.3.4 (Pritchard et al. 2000) using a Bayesian model-based clustering method. A burn-in of 20,000 iterations was performed followed by 100,000 Markov chain Monte Carlo iterations. Results were then collated using STRUCTURE HARVESTER (Earl and von Holdt 2012), which showed that the model was run for K values ranging from 1 to 8, with five replications for each K value.

Vegetation analysis

Vegetation was sampled using systematic sampling along transects (100 m long, 20 m wide) from random start points. Three transects were established in the natural forests at an altitude of 0-250 m above sea level (asl) or >250 m asl, whereas two transects were created in the community-owned forest. Nested plots of varying size (20 × 20 m, 10 × 10 m, 5 × 5 m, and 2 × 2 m) were established within each of the transects (Soegianto 1994). The distribution pattern of *D. aromatica* was then determined by calculating Morisita's index of dispersion (Krebs 1989).

RESULTS AND DISCUSSION

Morphological variation of the leaves

The leaves of *D. aromatica* trees growing in the community-owned forest at Barus had significantly greater lamina lengths, length of the widest leaves to the leaf base, and maximum leaf widths than those of trees growing in the natural forest at Danau Paris (Table 2), with the maximum leaf widths of trees from both locations matching the range of 3-6 cm observed by Lemmens and Bunyapraphatsara (2003). By contrast, the petiole length was significantly longer in trees in Danau Paris than that in trees in Barus. Furthermore, trees in Danau Paris had significantly more secondary veins in their leaves and a considerably greater angle between the veins than those in Barus. There were no significant differences in any of the other traits measured. Furthermore, leaves from both locations had similar form factors (FFs) of <1, indicating that they were not round (Wu et al. 2007), and leaf roundness was categorized as highly elliptical.

Diversity was assessed by calculating the coefficient of variance (CV). Based on a CV value of >20% indicating high diversity (Suhartini and Tintin 2010), only the angle between the veins and form factor of leaves in the Barus population exhibited high levels of variation (Table 2). This general lack of variation in leaf morphology is likely due to the short distance between sampling locations and the low level of genetic variation between subpopulations.

Genetic diversity within populations

There was little difference in the observed number of alleles (N_a), the effective number of alleles (N_e), percentage of loci polymorphic (PLP), expected heterozygosity (H_e), and Shannon's information index (*I*) between populations of *D. aromatica* growing in Danau Paris and Barus (Table 3). However, based on H_e, PLP, and N_a, the Barus population had the highest genetic diversity, whereas the Singkohor population had the lowest genetic diversity. These differences cannot be explained by differences in altitude because H_e is not affected by altitude and Singkohor, Danau Paris, and Barus are located at altitudes of 56, 200, and 46 m asl., respectively. Similarly, Srihari et al. (2013) found no correlation between genetic variation of *Hippophae* spp. and altitude.

Table 3. Genetic diversity parameters in populations of *Dryobalanops aromatica* at the three study sites

Population	n	PLP (%)	N_a	N_e	H_e	*I*
Singkohor	7	55.5600	1.5556	1.2973	0.1760	0.2686
Danau Paris	23	80.5600	1.8056	1.3250	0.2066	0.3271
Barus	30	88.8900	1.8889	1.3365	0.2134	0.3408
Mean	20	75.0033	1.7500	1.3196	0.1987	0.3122

Note: n = number of individual, PLP = percentage of loci polymorphic, N_a = observed number of alleles, N_e = effective number of alleles,, H_e = expected heterozygosity, *I* = Shannon's information index.

Table 4. Genetic distance based on Nei's unbiased measures and geographical distance (km)

Population	Singkohor	Paris Danau	Barus
Singkohor	*	27.8^G	64.4^G
Paris Danau	0.0363^g	*	36.3^G
Barus	0.0534^g	0.0478^g	*

Note: g = genetic distance, G = geographical distance.

The mean PLP value for *D. aromatica* was 75.00%. By contrast, other species in Dipterocarpaceae have been found to have lower PLPs, including *Vatica guangxiensis* (32.46%; Li et al. 2002), *Dipterocarpus retusus* and *D. hasseltii* (56.06% and 63.63%, respectively; Sumiyati et al. 2009), and *Parashorea chinensis* (20.80%; Li et al. 2005) using RAPD markers. Yulita and Partomiharjo (2011) argued that in RAPD analyses, the larger the number of individuals in a sample, the more alleles there will be and thus the higher the number of polymorphic loci. □

Genetic diversity between populations

Comparison of the genetic and geographical distances between the three study populations indicates that the higher the distance between locations, the higher the genetic distance (Table 4). Similarly, Schnabel and Hamrick (1990) and Alpert et al. (1993) concluded that genetic distance is positively correlated with geographic distance. Julisaniah et al. (2008) stated that cross-pollination between plants with a small genetic distance or similar relationship increases homozygosity, whereas cross-pollination between plants with a large genetic distance or distant relationship increases heterozygosity. Therefore, this information will be useful when formulating conservation strategies for *D. aromatica*, particularly for the production of high-quality seeds.

Cluster analysis showed that the individuals in each population were widely spread (Figure 2). This is presumably due to the three populations having a close relationship or low genetic diversity among them (Dst = 0.0285, Table 5). The total genetic diversity in all populations (Ht) was 0.2272, whereas the average genetic diversity within populations (Hs) was 0.1987 (Table 5). By contrast, the genetic diversity between populations (Dst) was 0.0285, which is much lower than both Ht and Hs. Genetic differentiation between the populations (Gst) was 12.57%, which is considered intermediate, whereas gene flow (Nm) between the populations was 3.4787, which reflects the mixed pollination system of *D. aromatica* that is facilitated by insects, wind, and water (Hamrick and Godt 1990). Similarly, Lee et al. (2000) using allozyme markers showed that *D. aromatica* growing in Peninsular Malaysia had an Nm of 6.6900 and pollination assisted by insects, water, and wind. This contrasts with the Nm value of 1.8424 for *Dipterocarpus littoralis*, in which pollination is only assisted by insects (Yulita and Partomihardjo 2011), indicating that insects are the primary pollinators of Dipterocarp species. Several species of bee have been identified as pollinators of *D. aromatica*, including *Apis melliphera* (Harata et al. 2012), *A. dorsata*, and *A. indica* (Appanah 1985; Ashton 1988).

Genetic structure of the populations

According to STRUCTURE HARVESTER, the genetic structure of *D. aromatica* varied considerably between the Singkohor, Danau Paris, and Barus populations (Figure 3). Analysis of the genetic patterns indicated that the highest value of ΔK was obtained when K = 2 (ΔK = 412.00). Therefore, STRUCTURE analysis divided the *D. aromatica* populations into two clusters: the natural forests (Singkohor and Danau Paris) and the community-owned forest (Barus).

Species diversity and spatial distribution

Seedlings, saplings, and trees in the natural forest at Danau Paris had high levels of species diversity (H′ > 3), whereas the poles had intermediate levels (Table 6). By contrast, all growth stages, except seedlings, had intermediate levels of species diversity (H′ = 2-3) in the community-owned forest at Barus.

Both sites had dominance (C) values of <0.5 (Table 6), indicating that no dominant species was present. C values are used to determine the concentration and distribution of dominant species, being higher when there is a higher abundance of one particular species and lower when several species are codominant. In addition, C values can be used to determine the distribution pattern of a species, with a value of <1 indicating that the population has a clumped distribution.

Table 5. The average genetic diversity of *Dryobalanops aromatica* in Sumatra, Indonesia and Peninsular Malaysia and *Dipterocarpus littoralis* in Central Java, Indonesia based on the analysis of Nei (1978)

Species	Site	Ht	Hs	Gst	Dst	Nm	Reference
Dryobalanops aromatica	Aceh Singkil and North Sumatra	0.2272	0.1987	0.1257	0.0285	3.4787	This study
D. aromatica	Peninsular Malaysia	0.5550	0.5350	0.0360	0.0385	6.6900	Lee et al. 2000
Dipterocarpus littoralis	Nusakambangan, Central Java	0.1958	0.154	0.2135	0.0418	1.8424	Yulita and Partomihardjo 2010

Note: Ht = genetic diversity in all populations, Hs = genetic diversity within the population, Gst = genetic differentiation, Dst = genetic diversity between populations;,Nm = gene flow

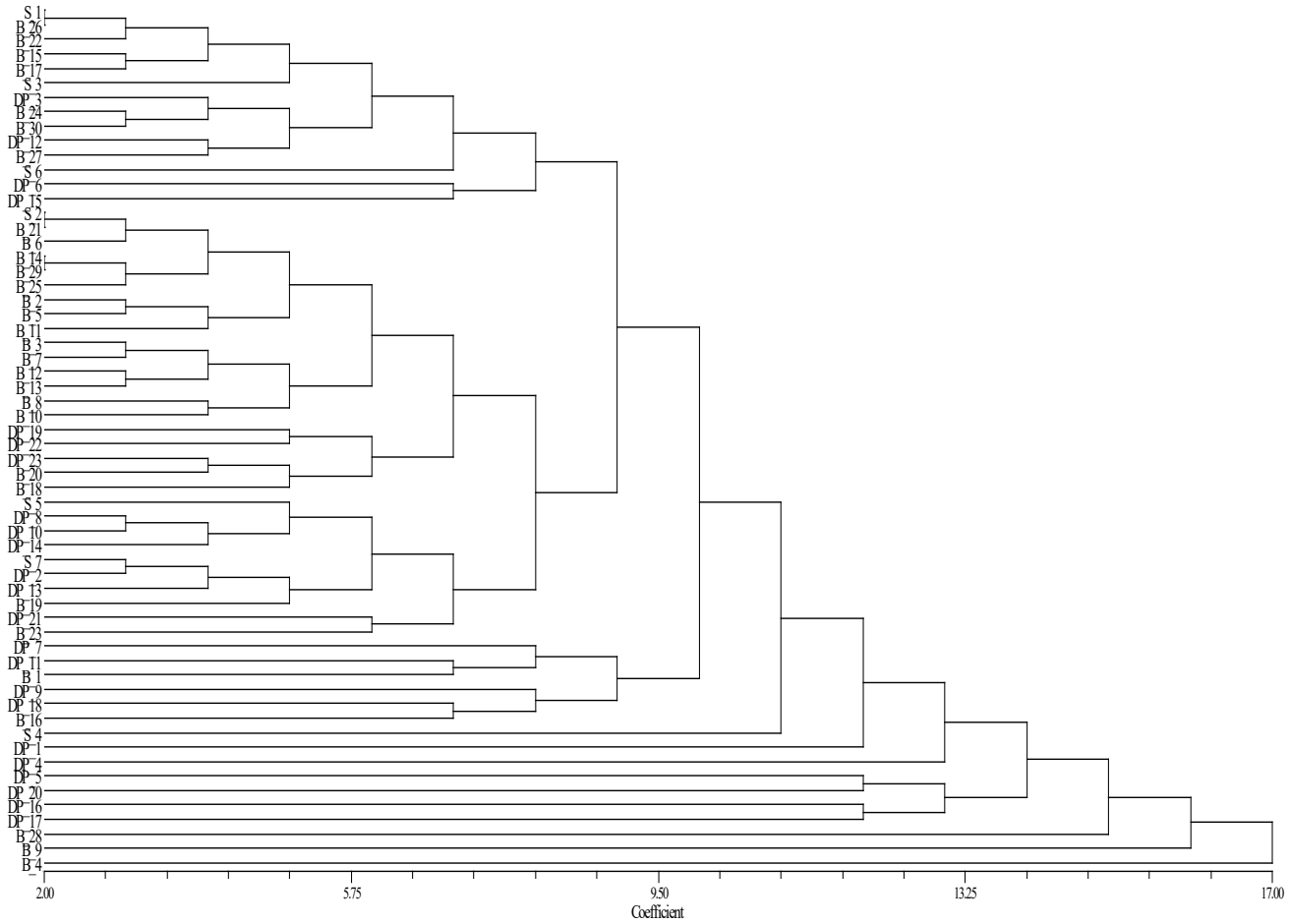

Figure 2. UPGMA dendrogram of *Dryobalanops aromatica* from the three study sites in Sumatra, Indonesia (S= Singkohor, B= Barus, DP=Danau Paris) based on RAPD profiles

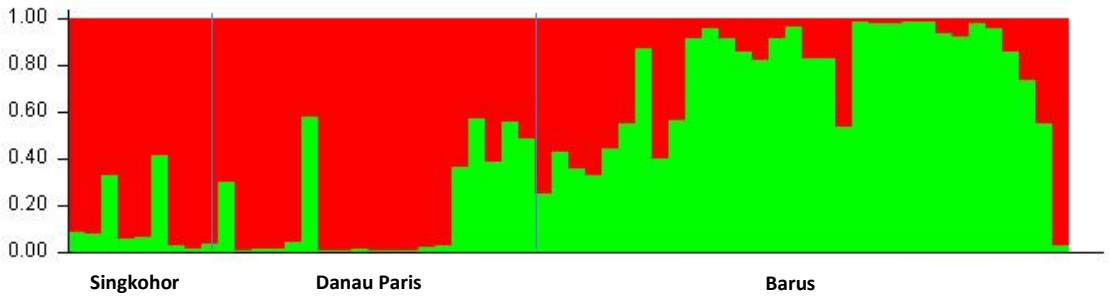

Figure 3. Population structure of *Dryobalanops aromatica* at the three study sites in Sumatra, Indonesia. The populations were separated into two clusters: Singkohor and Danau Paris (red), and Barus (green)

Table 6. Species diversity and dominance indices at Danau Paris and Barus, Sumatra, Indonesia

	Danau Paris				Barus			
	Seedlings	**Saplings**	**Poles**	**Trees**	**Seedlings**	**Saplings**	**Poles**	**Trees**
H′	3.8125	3.2049	2.8927	3.0370	3.0364	2.1292	2.8721	2.9781
C	0.0729	0.0888	0.0944	0.1197	0.1022	0.1775	0.0820	0.0850

Note: H′ = Shannon's diversity index; C = Simpson's dominance index.

Morisita's index of dispersion also indicated that the *D. aromatica* populations at both Danau Paris and Barus had clumped distributions (ip < 1; Table 7). Barbour et al. (1987) stated that plant species tend to have clumped distributions because they reproduce by seeds that fall close to the parent plant, and Sofiah et al. (2013) demonstrated that clumped distribution patterns could be generated in populations with high and low abundances. Both sites appeared to have a higher frequency and density of *D. aromatica* than other species in each growth stage, despite *D. aromatica* not having flowered in the last three years, supporting Lee (2000) argument that there is no correlation between the density of mature trees in a population and their level of flowering.

Dryobalanops aromatica was the most dominant species in the natural and community-owned forests based on the abundance of species from seedlings to trees. The importance value index (IVI) is used to describe the relative dominance of a species based on abundance, with a value of >10% indicating that a particular species is associated with other species (Sofiah et al. 2013). *D. aromatica* was associated with different species at each site in the seedling and sapling stages (Table 8) as a result of differences in altitude, microclimate, soil type, and surrounding communities between the sites. However, poles of *D. aromatica* were associated with *Shorea* spp. (meranti putih) and *Xanthophyllum excelsum* at both locations. In all growth stages (seedling to tree), the IVI of *D. aromatica* was the highest at Barus. This is likely due to this site having appropriate conditions (e.g., altitude, rainfall, and soil) for *D. aromatica* growth; Barus has clay soil texture and lies at an altitude of 46 m a.s.l., whereas Danau Paris has a dusty, clayey soil texture and is located at an average altitude of 230 m a.s.l. However, the factors that will have the most significant effect on the IVI at each site are human-related. In the community-owned forest at Barus, all species of commercial plants are well maintained until they reach maturity, resulting in *Artocarpus rigidus*, *Aporusa aurita*, *Gluta rengas*, and *Shorea* spp. being most closely associated with *D. aromatica*. By contrast, in the natural forest at Danau Paris, there is no human intervention, resulting in *D. aromatica* being the most closely associated with *Shorea* spp., *Koompassia malaccensis*, *Sterculia macrophylla*, *Sindora leiocarpa*, and *Barringtonia* sp.

Table 7. Dispersion indices of *Dryobalanops aromatica* at Danau Paris and Barus

	id	Σx	Σx^2	$(\Sigma x)^2$	M_u	M_c	ip	Pattern
Danau Paris	1.23	64.00	229.00	4096.00	0.79	1.27	0.43	Clumped
Barus	1.13	32.00	118.0	1024.00	1.13	2.09	0.06	Clumped

Note: id = Fisher's index of dispersion, Σx = sum of the number of individuals of a species in a square, Σx^2 = sum of the squares of the number of individuals of a species, M_u = uniform index, M_c = clumped index, ip = Morisita's index of dispersion

Table 8. Plants associated with *Dryobalanops aromatica* at Danau Paris and Barus

Growth stage	Danau Paris	IVI	Barus	IVI
Seedling	*Dryopteris immersa* □	15.92	*Dryobalanops aromatica*	40.95
	Aspelnium sp.	13.77	*Piper miniatum* Blume	11.28
	Nephrolepis hirsutula	19.48	*Flacourtia rukam*	16.25
Sapling	*Dryobalanops aromatica*	34.30	*Hevea brasiliensis*	36.59
	Sindora leiocarpa	25.80	*Dryobalanops aromatica*	47.72
	Barringtonia sp.	11.81	*Aporusa aurita*	21.13
			Agrostictachys sessilifolia	16.59
			Artocarpus rigidus	33.18
Pole	*Xanthophyllum excelsum*	11.61	*Shorea* spp.	17.93
	Teysmaniodendron sp.	15.43	*Dryobalanops aromatica*	51.07
	Shorea spp.	15.47	*Artocarpus rigidus*	26.61
	Barringtonia sp.	12.77	*Xanthophyllum excelsum*	28.98
	Sindora leiocarpa	14.35	*Gluta renghas*	40.17
	Sterculia macrophylla	49.54	*Artocarpus integer*	16.55
	Dryobalanops aromatica	51.06		
Tree	*Sterculia macrophylla*	10.41	*Shorea* spp.	18.33
	Shorea spp.	19.84	*Dryobalanops aromatica*	69.19
	Dryobalanops aromatica	66.09	*Artocarpus rigidus*	15.24
	Nauclea sp.	17.39	*Xanthophyllum excelsum*	28.72
	Barringtonia sp.	23.37	*Gluta renghas*	21.66
	Koompassia malaccensis	32.21		

In conclusion, *D. aromatica* had an intermediate level of genetic diversity (H_e = 0.1987), with the Barus population having the highest levels (H_e = 0.2134) and the Singkohor population having the lowest levels (He = 0.1760). *D. aromatica* also had an intermediate level of genetic differentiation (Gst = 12.57%), with no evidence of the three populations being genetically segregated. This species had clumped spatial distribution patterns at Danau Paris and Barus (ip = 0.06 and 0.43, respectively). These findings indicated that *in situ* management in combination with enrichment planting in areas with a low abundance of plants using locally sourced seeds or other plant materials would be an effective genetic conservation strategy for *D. aromatica*.

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