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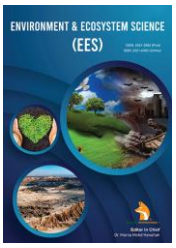

RESEARCH ARTICLE

GENETIC DIVERSITY OF NATURAL AND RESTORED API-API PUTIH (*AVICENNIA ALBA*) POPULATIONS IN THE WEST COAST OF PENINSULAR MALAYSIA

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ABSTRACT

A large tract of mangrove forest in Malaysia has been lost due to increased anthropogenic activities. Restorative practices of mangrove forest have been adopted nationwide to re-establish ecosystem services in combating coastal erosion. However, genetic considerations in local mangrove restoration practices are still far lacking despite the vast literature on their genetic diversity. To understand whether the restored mangroves can impact the genetic diversity distribution among natural populations, we used eight microsatellite markers to assess the genetic diversity of the Api-api putih (*Avicennia alba*) between the natural and restored populations along the west coast of Peninsular Malaysia. We found no difference in terms of genetic diversity between these populations. Two genetic clusters were detected among *A. alba* along the west coast based on Bayesian clustering and discriminant analysis of principal components (DAPC). The southwest monsoon current circulation that coincides the timing of seed dispersal of *A. alba* may explain such pattern of genetic differentiation. Despite the minimal genetic structure, our results suggest that seed sourcing from either population is viable for the local mangrove restoration programs in the future.

KEYWORDS

mangrove restoration, genetic evaluation, anthropization, genetic drift

1. INTRODUCTION

Mangroves are woody communities that grow in tropical and subtropical coastal intertidal zones and are periodically submerged by sea water. They are keystone ecosystems that provide many ecosystem services such as food provisioning, coastal protection and carbon sequestration (Hutchison et al., 2014; Hashim and Shahruzzaman, 2017; Lovelock and Duarte, 2019). Malaysia is one of the few Southeast Asian countries with large tracts of mangroves. However, the mangroves in Malaysia have shrunk 19.5% from 1990 to 2010, with a huge loss noted in a few states along the west coast of Peninsular Malaysia (Hamdan et al., 2010). The populations of mangroves are facing a decline mainly caused by anthropogenic stressors such as aquaculture expansion and coastal development (Ghazali, 2006).

The recognition of the importance of mangrove forests has led to widespread efforts to restore or rehabilitate deforested mangrove areas (Andradi-Brown et al., 2013). According to the Society for Ecological Restoration, restoration is defined as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed', while rehabilitation refers to 'reparation of ecosystem processes, productivity, and services' (Andradi-Brown et al., 2013). There have been significant mangrove restoration activities in Malaysia after tsunami in 2004 with the formation of national working group committee to restore Malaysia coastal zone with mangrove replanting and research activities. To ensure a successful restoration, we need to consider the reasons for the loss of mangroves, selection of seedling source, restored tree species, restored sites and the level of engagement among the local residents in the long-term management projects (Hai et al., 2020). Typical zonation of mangrove forest in Malaysia is dominated by *Avicennia* spp. or *Sonneratia* spp. on the seawards followed by *Rhizphora* spp., *Brugueira* spp. and *Xylocarpus* spp. towards the inland (Hashim and Shahruzzaman, 2017). *Avicennia alba* or locally known as Api-api putih, are a particularly common choice of replanted mangroves due to their fast growth rate, wide salinity tolerance range and relatively high regeneration rate, which facilitate initial establishment (Jayatissa and Wickramasinghe, 2006; Alura and Alura, 2016). These traits also play an important role as protective green shelterbelts and coastal bio-shields against wave surges and tsunami (Tamin et al., 2011). Prior to restoration, the modification of the eroded coastline is essential to ensure a successful restoration outcome. For instance, the placement of either rock revetments or geotubes at the restored sites are keys to the survival of the replanted mangroves (Hashim and Shahruzzaman, 2017).

In Malaysia, many mangroves restoration and rehabilitation projects were conducted either through integrated conservation and development projects or community-based natural resource management programs (Omar et al., 2020). For example, 1.5 hectares (ha) of young mangrove stands (*Rhizophora* sp. and *Avicennia* sp.) were replanted at Sungai Haji Dorani in 2009 (Singh et al., 2020). In 2017, around 6.9 ha of mangrove tree saplings consisting of *Rhizophora* sp., *Bruguiera* sp. and *Avicennia* sp. were planted at Southern Manjung by the local community (Friends of Lekir Sitiawan Mangrove Association; SHBLS). Our review of the literature indicates very few examples of studies that include genetic indicators in evaluation of restoration success for mangrove populations (Salas-Leiva et al., 2009; Granado et al., 2018). Species with high genetic diversity is likely to adapt and survive due to increased persistence, thus making them less

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prone to extinction (Frankham, 1995). The amount of genetic variation is nonetheless an indicator of functional and resilient ecosystems and hence also the long-term success of restoration activities (Thompson et al., 2010).

The genetic diversity of mangroves in Malaysia has been studied using amplified fragment length polymorphisms (AFLPs), single sequence repeats (SSR) or microsatellites, and chloroplast DNA (cpDNA) (Liao et al., 2006; Huang et al., 2008; Wee et al., 2013; Wee et al., 2015; Tsuji et al., 2016; Azman et al., 2020; Wee et al., 2020; Triest et al., 2021). Among the mangrove species studied, a strong East-West genetic division was detected in *Avicennia marina and A. alba* populations in Peninsular Malaysia based on microsatellite markers (Wee et al., 2020; Triest et al., 2021). Recent study identified two genetic clusters of *A. marina* along the Malacca strait, suggesting a genetic break at this region under the influence of oceanic current (Triest et al., 2021). However, these studies only focused on the natural populations of *Avicennia* and information on the gene flow between the natural and the adjacent restored mangroves is still lacking. Genetic pollution is a crucial issue that needs to be addressed for restoration activities, especially when the initial genetic diversity of the plants prior the restoration efforts is not well known.

In this study, we used microsatellite markers to assess the genetic diversity of *Avicennia alba* in the west coast of Peninsular Malaysia. This species is chosen because *Avicennia* represents the largest polymorphic genus of mangrove and is known to display a stronger tendency of inbreeding at their distribution range edges (Hazarika et al., 2013). A study based on the inter-simple sequence repeat (ISSR) marker had found that introduced mangrove population had lower genetic diversity compared to its adjacent remnant population (Granado et al., 2018). Thus, we hypothesized that *A. alba* at the restored sites will experience a genetic bottleneck and drift associated with a low number of transplanted individuals (as in natural founder events). The source of transplanted trees can also affect the genetic composition of restored populations. If alien populations are employed, for instance, genetic contamination of regional gene-pools may occur. To our best knowledge, the genetic effects of replanting and introduction of selected species on existing gene pools of mangroves in Malaysia remains to be investigated. The purposes of this study were to 1) assess if there are major genetic discontinuities in this region, and 2) verify if genetic diversity and composition differs between natural/ restored sites.

2. Material and Methods

2.1 Study site

Field sampling was conducted at four regions along the west coast of Peninsular Malaysia, namely Kuala Sepetang, Manjung Selatan, Sabak Bernam and Pulau Carey (Figure 1). We chose the control (hereafter, natural) locations in the proximity of their respective restored areas, to have comparable conditions within each site whenever possible; except Kuala Sepetang and Pulau Carey. Kuala Sepetang and Pulau Carey represented the reference (hereafter, control) populations from the northern and southern limit of our sampling area. At each site, leaf tissue was collected from 10–30 individuals randomly, resulting a total of 152 leaf samples. All samples were stored in silica gel until DNA extraction.

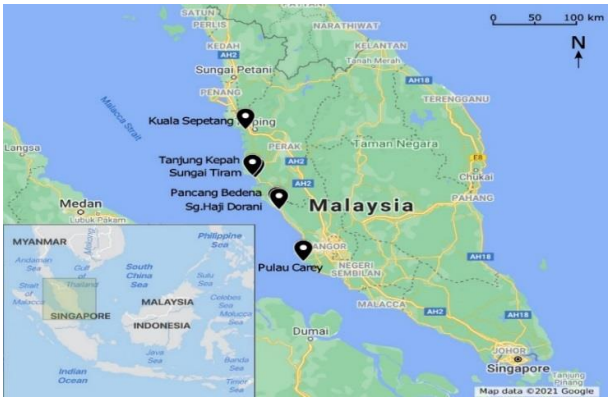

Figure 1: Sampling map of the 152 leaf samples of *Avicennia alba* along the west coast.

2.2 DNA extraction, amplification, and sequencing

Total genomic DNA were extracted using the Nucleospin® 96 Plant Kit (Macherey-Bagel Duren, Germany). After extraction, the quality and integrity of DNA were verified by electrophoresis in a 2% agarose gel prior to polymerase chain reaction (PCR). Eight microsatellites (or simple sequence repeats, SSR) markers (Table 1) were amplified and genotyped for all population samples using ABI 2720 Thermal Cycler (Applied Biosystems, Foster City, CA) in a final volume of 10 μL that consisted of 1x Go Taq® Flexi Buffer, 250μM of each dNTP, 2mM of $MgCl_2$, 0.5μM of each primer, 1 U GoTaq® G2 Flexi DNA Polymerase (Promega, U.S.A.), 20 – 50 ng of DNA template and water to adjust the volume. The PCR products were separated in an ABI PRISM capillary automated sequencer 3130XL Genetic Analyzer (Applied Biosystems, CCMAR, Portugal). The scoring of alleles was done manually in STR and (Veterinary Genetic Laboratory, University of California, Davis; http://www.vgl.ucdavis.edu/STRAnd) using the LIZ™ size standard (Applied Biosystems, California, USA).

Table 1: Microsatellite loci that used in the current study. Tm represents the annealing temperature.

Locus	Primer sequence	Tm (°C)	Reference
Aa13	F: CCGTTTCCATTTTCCTTTATTC R: GCACTCCTACTCTCATCCC	52	Texeira et al. 2003
Aa22	F: TCCCATTTGCATTACAGTCTG R: CGAGCGTGTGCTAATCTTCC	52	Texeira et al. 2003
Aa23	F: ACTGGATGATTGGTGTTTTTTA R: AGGTGCGTGGGTATGTTG	52	Texeira et al. 2003
Aa26	F: GGATTAAGAATGAAGAAAGGGG R: CCAAGTGTGGAATGTTGTATCTT	52	Texeira et al. 2003
Aa28	F: CTCGTGGACACCTCATTATCC R: TAACCACTGGCACAAACTCC	52	Texeira et al. 2003
Aa67	F: AACTCAAGAGAAGCGATGGC R: TAAGCGAAGATCCTGATTCG	52	Texeira et al. 2003
M47	F: TGACACCAAGGGAAATCAACATGCC R:GAACCTAGCGACCAATAGATCATCCTG	60	Maguire et al. 2000
M81	F:GAATGATGATCGGATGTTGCTACTCCG R: CAATCCCAAAGCCCCAAAAATAATCC	60	Maguire et al. 2000

2.3 Genetic parameters analysis

Prior to the data analysis, individuals with less than 75% amplification success rate were excluded from further analysis. The within-population indices of genetic diversity including the number of different alleles per locus, expected (HE) and observed (HO) heterozygosity and FIS were calculated using Genodive 2.0 (Meirmans and van Tienderen, 2004). We also tested departures from Hardy-Weinberg equilibrium (HWE) and genotypic linkage disequilibrium (LD) using the R package adegenet (Jombart, 2008). As expected (HE) is considered a better estimator of the genetic variability present in a population, thus we used one-way ANOVA to calculate the variances explained by this genetic diversity parameter upon the control, natural and restored populations, after checking the assumption of normality and homoscedasticity in R (Nei, 1987). We also compared the allelic richness between control, natural and restored populations using one-way ANOVA, after obtaining the values from FSTAT using the rarefaction method. To explore the population structure, a Bayesian cluster analysis was performed with STRUCTURE 2.3.4 with prior information on the geographic origin of each sample (Pritchard et al., 2000). The analyses were run under the admixture model with a burn-in of 200,000 Markov Chain Monte Carlo (MCMC) iterations, followed by 500,000 iterations for each run (Falush et al., 2003).

The number of K (putative populations) ranges from 1 to 9, and 20 replicate analyses for each value of K. The number of clusters was inferred by comparing the ln Pr (X|K) among different values of K obtained from STRUCTURE harvester online (Earl and Vonholdt, 2012). The highest ln Pr (X|K) value was selected as the most parsimonious number of populations in our sample. The ad hoc statistic ΔK was considered (Evanno et al., 2005). Structure Harvester was used to estimate the total population (K) in the samples. The graphic developed by CLUMPAK were used to illustrate the results (Kopelman et al., 2015). To cross-check the results obtained from the STRUCTURE, we performed a discriminant analysis of principle components (DAPC) implemented in RStudio using adegenet package to verify the number of genetic groups present within our data. We did a cross validation for the DAPC analysis using the function xvalDapc() with default parameters, to ensure that we selected the correct number of principal components (PCs) for the analysis (Jombart, 2008). The missing data were replaced by the mean allele frequency for each locus.

3. Results

3.1 Genetic diversity

Of the 152 leaf samples collected, 50 samples failed to attain 75% of the amplification success rate. A total of 49 alleles were detected across eight microsatellite loci. An exact test for genotypic linkage disequilibrium yielded no significant p value across the populations, and therefore an independent assortment of all loci was assumed. A summary of the basic population genetic diversity indices based on 102 leaf samples is presented in Table 2. In general, allelic diversity was very low, with mean number of alleles per locus ranging from 1.63 to 4.88. Expected heterozygosity was much higher than the observed heterozygosity in all populations, this discrepancy resulting from Hardy-Weinberg departs at one/ few/ many loci. As a result, FIS values were extremely high. There was no significant difference between the observed heterozygosity among different types of mangrove groups, as determined by one-way ANOVA (F (2,3) = 1.8316, p = 0.302) (Figure 2a). A similar pattern was observed for the comparison of allelic richness of the same groups (F (2,3) = 0.3137, p = 0.678) (Figure 2b).

Table 2: Site, region, sample size (*N*), number of alleles (N_a), observed (H_O) and expected (H_E) heterozygosity, inbreeding coefficient (F_{IS}) and allelic richness (Ar) for *Avicennia alba* based on eight microsatellite markers.

Site	Region	*N*	N_a	H_O	H_E	F_{IS}	Ar
Kuala Sepetang	Kuala Sepetang	8	1.625	0.094	0.219	0.571	1.609
Tanjung Kepah	Manjung Selatan	21	2.375	0.036	0.218	0.834	1.992
Sungai Tiram		8	1.625	0.031	0.181	0.827	1.629
Sg. Haji Dorani	Sabak Bernam	24	4.875	0.131	0.519	0.748	3.444
Pancang Bedena		17	3.375	0.165	0.482	0.659	2.934
Pulau Carey	Pulau Carey	24	2.625	0.092	0.286	0.680	2.246

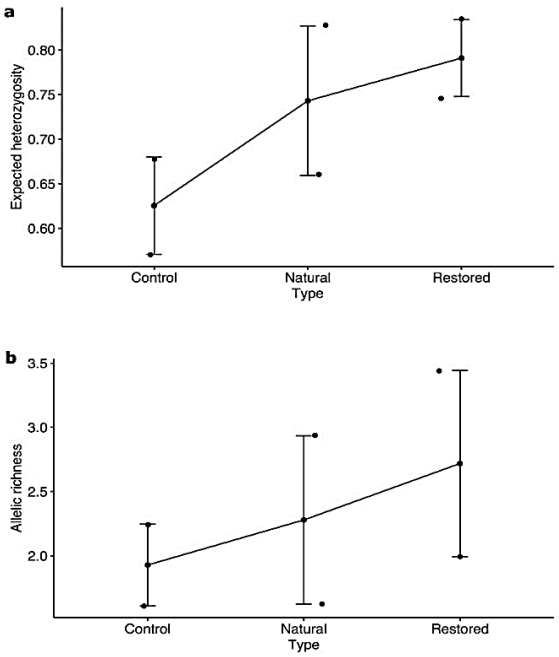

Figure 2: ANOVA plots of (a) Expected heterozygosity (H_E) and (b) allelic richness (Ar) between the control, natural and restored populations of *Avicennia alba* in the west coast of Peninsular Malaysia.

3.2 Population structure

STRUCTURE analysis suggested K = 2 genetic clusters as the most parsimonious partitioning of individuals based on the ΔK metric (ΔK = 16.276, Figure 3), roughly matching 1) orange populations and 2) blue populations, with a transition zone between Manjung Selatan – Sabak Bernam region boundary. A similar pattern was observed in the DAPC analysis, except the Kuala Sepetang cluster (Figure 4). In DAPC, sites spanning the Manjung Selatan and Sabak Bernam clusters showed a small differentiation, while the population from Pulau Carey was nested in the Sabak Bernam cluster.

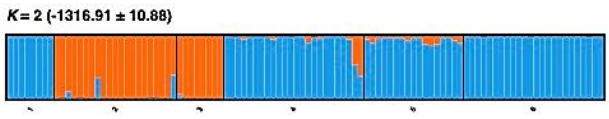

Figure 3: Results of Bayesian clustering for *Avicennia alba* populations based on 8 microsatellite loci. Results from K = 2 with mean LnP[K] SD in parentheses is presented. Site 1 – Kuala Sepetang, site 2 – Tanjung Kepah, site 3 – Sungai Tiram, site 4 – Sungai Haji Dorani, site 5 – Pancang Bedena, site 6 – Pulau Carey.

4. Discussion

Our study is one of the first to investigate the outcome of mangrove restoration on regional gene flow using a genetic approach in Peninsular Malaysia. In general, genetic diversity was low, and expected heterozygosity was also much lower than expected under a Hardy-Weinberg equilibrium. The latter can probably be attributed to a local inbreeding effect, which is reportedly common among the *Avicennia* species (Hermansen et al., 2015; De Ryck et al., 2016; Do et al., 2019). Contrary to expectations, we detected a higher genetic diversity among the restored *Avicennia alba* populations compared to their adjacent natural populations in Manjung Selatan and Sabak Bernam regions, but such differences were not significant. Our finding is consistent with a seagrass study in Barnegat Bay (New Jersey), where the authors found the restored *Zostera marina* populations were genetically more diverse than the natural populations (Campanella et al., 2013). High genetic diversity in the restored *A. alba* populations could be an early sign of a positive outcome of the restoration efforts.

However, time since transplantation has been too short for new mutations to arise and accumulate, so this increased diversity should reflect a genetically diverse source of transplants, higher gene-flow via immigration in the establishing restored populations (because of lower habitat saturation), or both. Allelic compositions between control, natural and restored populations, however, is similar, not suggesting very different source populations. In any case, increased genetic diversity has been found to extend the lifespan of the plant, promote plant density and thus enhancing ecosystem services, as reported in a seagrass restoration experiment (Reynolds et al., 2012). Our results suggest that mangrove restoration practices in the west coast of Peninsular Malaysia may hold great promise for elevating the success of ecosystem recovery in the next decades.

The STRUCTURE analysis revealed minimal genetic differentiation between the Sabak Bernam region and all locations on the west coast of Peninsular Malaysia. Our finding is consistent with a local study, where the authors detected a minor genetic barrier at Sabak Bernam region for *Avicennia marina* using the same markers (Triest et al., 2021). The genus *Avicennia* are capable of long-distance dispersal via ocean currents, ranging from a few tens of kilometers to 100 kilometers (Clarke, 1993; Binks et al., 2019). This range is close to the maximum distance (~150 km) between the northernmost and southernmost populations considered in this study. Estimated gene flow directionality along the west coast of Peninsular Malaysia is from south to north, under the influence of southwest monsoon current circulation (Daryabor et al., 2014). Such unidirectional migration route has been reported for *A. marina* on the west coast of Peninsular Malaysia (Triest et al., 2021). The monsoon season in the west coast starts from May to September, which favours the propagule dispersal of *Avicennia alba* during their fruiting seasons (Alias et al., 2020). Our analysis suggests that *Avicennia alba* tend to migrate from south to north under the stepping-stone model in the southwest monsoon current circulation scenario, which is in alignment with results from previous study.

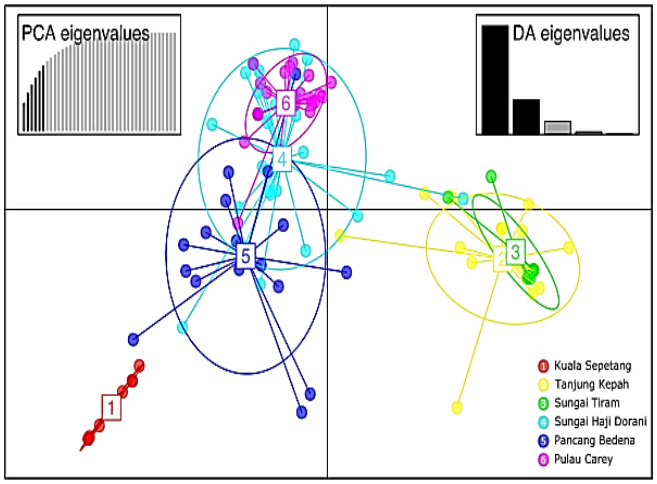

Figure 4: Scatterplot of DAPC performed on 102 *Avicennia alba* samples based on 8 microsatellite loci. Dots represent individual genotypes and ellipses represent population centroids.

In the DAPC analysis, we observed the same genetic structure as illustrated in the STRUCTURE analysis, except for the Kuala Sepetang cluster (red; Figure 4). This population most probably originated from the gene pool in the south (Sabak Bernam and Pulau Carey clusters) under the northward directed stepping-stone migration route, causing a reduction in genetic variation due to the founder effect (Triest et al., 2021). Such pattern can be explained by source-sink dynamics due to the heterogeneity of the coastal features and different levels of anthropogenic pressure among our sampling sites. Under the influence of the southwest monsoon current circulation, the estuaries (e.g. Kuala Sepetang) can act as the propagule retention hotspot compared to the exposed shoreline (e.g. remaining sites in the current study). Besides, Kuala Sepetang has been subjected to water pollution due to the human settlements in the vicinity of the Matang Mangrove Forest Reserve (Ghaderpour et al., 2014). As the change of water quality can influence the survival of *Avicennia* seedlings, we hypothesized the deteriorated water quality in this location may not favour the recruitment of fresh *Avicennia* propagules (Hastuti and Budihastuti, 2015). This was supported by the absence of young *Avicennia* seedlings and low number of maternal trees (pers. obs).

5. Conclusion

In conclusion, our results confirm that there are no major differences between the natural and restored populations of *Avicennia alba*, in terms of genetic diversity and composition. Minimal genetic differentiation was detected between the populations from Manjung Selatan and Sabak Bernam – Pulau Carey regions, suggesting more limited gene flow between these two populations. Current assessment validates both natural and restored Api-api putih (*Avicennia alba*) trees can be used as sources of planting material to assist the ecosystem recovery of coastal plant communities in the face of elevated pressures of anthropization.

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Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. The field sampling was conducted in Malaysia under the research permit no. 388125.

Author Contributions

KL collected the samples and performed the laboratory analysis with assistance from JN. The application of research permit in Malaysia was done by KL with the assistance from MN. EAS funded the laboratory work. KL took lead in writing the manuscript and all authors discussed the results and commented on the manuscript.

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