

A comparison of the genetic diversity and population structure of four populations of *Macrobrachium sundaicum* (Heller, 1862) (Decapoda: Palaemonidae) in peat swamps on Sumatra, based on the sequence COI mt DNA gene marker

Сравнение генетического разнообразия и популяционной структуры четырех популяций *Macrobrachium sundaicum* (Heller, 1862) (Decapoda: Palaemonidae) в торфяных болотах на Суматре, основанное на последовательности ДНК-маркера COI mt

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КЛЮЧЕВЫЕ СЛОВА: кислая вода, COI, Palaemonidae, популяция пресноводных креветок.

ABSTRACT. A freshwater prawn *Macrobrachium sundaicum* (Heller, 1862) (Decapoda: Palaemonidae) is a landlocked species that can be found in peat swamps throughout the island of Sumatra, Indonesia. These peat swamp rivers are characterized by a very acidic pH value (3.3–5.0), and the water color ranges from reddish brown to dark. However, there have been no molecular studies conducted on the genetic diversity of this species in acidic environments. This study is the first attempt to explore the genetic diversity of *M. sundaicum* living in peat swamps on Riau and Jambi Province of Sumatra Island by examining the partial COI gene of the mitochondrial genome. Our study revealed that the haplotype and nucleotide diversities were low in all the river basin studied. Network analysis showed that each river had a unique haplotype, suggesting a strong population structure. This is likely due to the dispersion of ancestors during the colonization

(differences in ancient river basins), habitat fragmentation, and the landlocked life cycle of this species in peat swamps, which act as geographical barriers shaping the current distribution of this species.

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РЕЗЮМЕ. Пресноводная креветка *Macrobrachium sundaicum* (Heller, 1862) (Decapoda: Palaemonidae), вид, который можно встретить в торфяных болотах

по всему острову Суматра, Индонезия, не имеющий выхода к морю. Эти торфяные болота характеризуются очень кислым значением pH (3,3–5,0), а цвет воды варьируется от красновато-коричневого до темного. Молекулярных исследований генетического разнообразия этого вида креветок ранее не проводилось, и это исследование является первой попыткой изучить генетическое разнообразие *M. sundaicum*, обитающий в торфяных болотах в провинции Риау и Джемби на острове Суматра, изучив генный маркер COI митохондриального генома. Наше исследование показало, что разнообразие гаплотипов и нуклеотидов было низким во всех изученных речных бассейнах. Сетевой анализ показал, что креветки из каждой реки обладают уникальным гаплотипом, что свидетельствует о сложной структуре популяции. Вероятно, это связано с расселением предков во время колонизации (различия в древних речных бассейнах), фрагментацией среды обитания и жизненным циклом этого вида, не имеющего выхода к морю, в торфяных болотах, которые действуют как географические барьеры, определяющие современное распространение этого вида.

Introduction

The genus *Macrobrachium* comprises approximately 261 valid species [WoRMS, 2024] and is the largest genus within the family Palaemonidae [De Grave *et al.*, 2015]. One species of shrimp that inhabits peat swamps is the *Macrobrachium sundaicum* [Wowor, Ng, 2010]. The species *M. sundaicum* completes its life cycle only in freshwater without a pelagic larval stage [Wowor *et al.*, 2009]. In addition, the genus *Macrobrachium*, which lives in acidic water, has a larger egg size [Wowor *et al.*, 2009]. Large egg-laying species are mostly endemic to certain regions, and their abilities distribution are limited, it is thought that they have unique genes according to the river system in which they live, and stronger genetic subdivision among populations is expected to occur because it has a specific life strategy [Liu *et al.*, 2007]. Besides that, organisms that inhabit peat swamp waters have a fairly high adaptability so that morphological changes (radiation of morphological) occur which lead to cryptic species phenomena [Fahmi *et al.*, 2016]. Previously, this species was found in West Kalimantan (Kapuas Hulu; Pontianak Sekadau River; Kepadang River in Anjung; Mungan River (Sarawak); Bejit River (between Balai Ringin and Simunjan), Sumatra (Riau Archipelago (Natuna and Kundur Island); Riau Province (Bengkalis); Jambi (Arang-Arang Lake), Peninsular Malaysia (Trenghganu; Pahang; Johor State), Singapore (Neon Soon River near Seletar catchment), and southern Thailand [Wowor, Ng, 2010]. Previous studies on the genus *Macrobrachium* have generally relied on morphological characters for species identification, but this approach often yields inconclusive results [Jose *et al.*, 2016; Jurniati *et al.*, 2021]. The precision of species identification is critical to understanding biodiversity, population structure, and genetic variation, which underpin effective conservation

strategies [González-Castellano *et al.*, 2020]. So, it can be considered an interesting material to be used to reveal the genetic structure of shrimp peat swamp.

The use of molecular markers allows the detection of the genetic uniqueness of individuals, species, or populations living in a particular habitat [Maralit, Santos, 2015]. We used the mitochondrial marker cytochrome oxidase I (COI) because its sequence differences can distinguish even closely related species [Jose *et al.*, 2016] and its sequence is commonly used as a DNA barcode [Barrett, Hebert, 2005]. However, in some species, COI segments can be used for phylogeography, population and genetic diversity studies throughout *Macrobrachium* [Hurwood *et al.*, 2014; Bernays *et al.*, 2015; Thanh *et al.*, 2015; Cui *et al.*, 2018; Iketani *et al.*, 2021; Zhao *et al.*, 2021; Han *et al.*, 2022; Aliah *et al.*, 2022; Santos *et al.*, 2024]. COI genes show high levels of molecular variation within populations [Liu *et al.*, 2020].

Genetic diversity using with gen COI has been studied in several shrimps, i.e: *M. nipponense* [Li *et al.*, 2021; Xiong *et al.*, 202], *M. rosenbergii* [Khan *et al.*, 2014; Thanh *et al.*, 2015; Fei, Xilin, 2023], and *M. shokitai* [Doi *et al.*, 2024]. However, research on the genetic diversity of the *M. sundaicum* species has not been reported, especially those that prefer peat swamp habitats. Previous research on *M. sundaicum* discusses morphological characteristics [Wowor, Ng, 2010], including the existence of species shrimp in acidic waters [Wowor *et al.*, 2009] and ecology [Purnamasari *et al.*, 2024]. The discovery of *M. sundaicum* in several peat swap exchange locations in Sumatra Island can be a good model for studying population structure and genetic diversity because species with a landlocked life cycle are thought to form fragmented populations separated by rivers, with each river supporting a very small local population [Doi *et al.*, 2024]. Furthermore, this study only focuses on investigating genetic diversity of *M. sundaicum* specimens. This study aims to determine the genetic diversity of *M. sundaicum* in the peat swaps of Sumatra, Indonesia. Through this analysis, we attempt to elucidate the extent of genetic diversity in *M. sundaicum* obtained from the four peat swamp on the island of Sumatra and its potential implications for conservation strategies to conserve *M. sundaicum* populations because it is an endemic species and important role in ecology. Nonetheless, the insights gained from our genetic diversity analyses contribute significantly to the science of freshwater shrimp living in peat swamps and can serve as a foundation for future research.

Material and methods

STUDY AREA. This study is exploratory, utilizing a purposive sampling method based on information from local people regarding shrimp's presence. Sample collection was conducted in October 2022 (Table 1) in three peat swamps in Riau Province and one peat swamp in Jambi Province (Fig. 1). GPS coordinates were recorded at the collection site and were visually illustrated on a geographical map using QGIS v3.36.

SAMPLE COLLECTION. The sampling was conducted using the purposive sampling method. The selection of sampling points was based on the ease of accessibility for the researchers, with consideration for the habitat conditions that support the

Table 1. *Macrobrachium sundaicum* sampling location in this study (Fig. 1).
Таблица 1. Место отбора проб *Macrobrachium sundaicum* в данном исследовании (рис. 1).

No.	Location	Coordinates		Number of samples
		Lat. (S)	Lon. (E)	
1	Selat Panjang Island, Riau Province	0° 56'23.2"S	102°31'28.7"E	5
2	Bukit Batu, Riau Province	1° 28'08.9"S	101°55'33.4"E	3
3	Rabit, Riau Province	0° 26'30.1"S	102°43'14.7"E	6
4	Kumpeh, Jambi Province	1°39'02.0"S	103°48'40.0"E	3

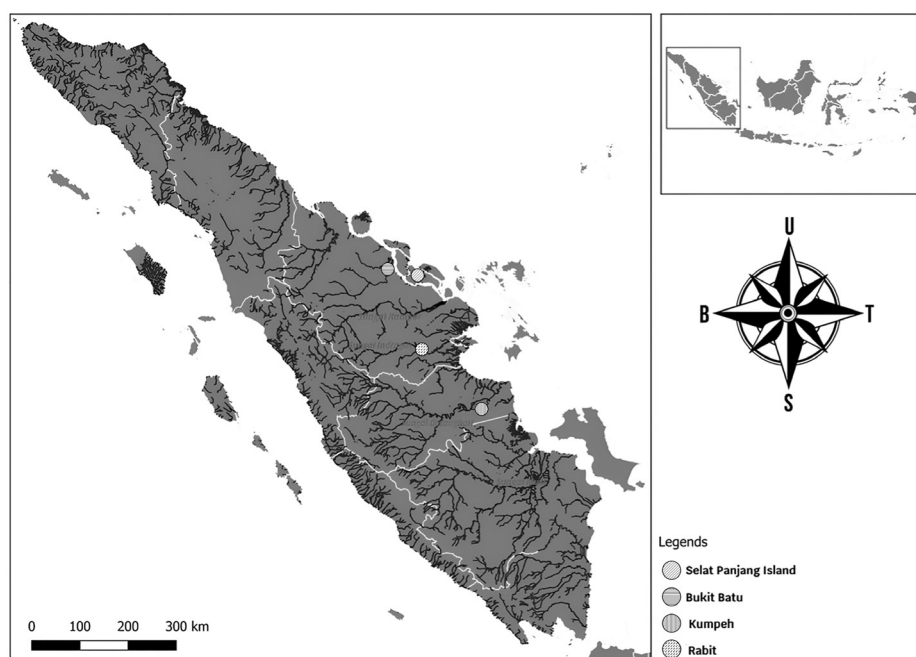


Fig. 1. Sampling location of *Macrobrachium sundaicum* in Sumatra.

Рис. 1. Место сбора образцов *Macrobrachium sundaicum* на Суматре.

presence of shrimp (i.e., substrate leaf litter). Sampling started at 05.00–11.00 pm using a hand net and trap. Sampling was carried out at reduced light because freshwater shrimp prefer to avoid light [Karpus, Harpaz, 1990] and are active at night (nocturnal) [Hongjamrassilp *et al.*, 2020] making them easier to find. The samples were preserved in 70% ethanol in the field [Ng, 2016] before being replaced with 96% ethanol for long-term preservation. In addition, we also collected habitat data such as water temperature and pH, riverine substrate, and the presence of aquatic plants in the riverine area. Water temperature and pH were measured using a thermometer and pH meter, while substrate and aquatic plant data were visually observed.

MORPHOLOGICAL IDENTIFICATION. Shrimps were identified with the help of Nikon SMZ745T (Japan) stereomicroscope using identification key by Wowor *et al.* [2004]. All studied material is deposited in Museum Zoologicum Bogoriense (MZB), Research Center for Biosystematics and Evolution, National Research and Innovation Agency (BRIN) Indonesia. Samples of the prawns were identified at the Research Center for Biosystematics and Evolution, BRIN Cibinong, in Bogor.

MOLECULAR IDENTIFICATION. The genomic DNA from abdomen muscle tissues was extracted using the DNA extraction kit Geneaid DNA Mini Kit (Tissue) provided by

Geneaid (www.geneaid.com) following the manufacturer's protocol. The Cytochrome oxidase subunit-I (COI) gene segment of the mitochondrial genome for the genus *Macrobrachium* was amplified using the forward primer AF286 (5' TCTACAAAY-CATAAAGAYATYGG 3') and the reverse primer AF287 (3' GTGGCRGANGTRAARTARGCTCG 5') [Rismawati *et al.*, 2024]. The PCR conditions included a pre-denaturation temperature of 94 °C (1 min), followed by three stages: denaturation at 94 °C (1 min), annealing at 54 °C (3 min), and elongation at 72 °C (1 min). A total of 30 cycles, followed by post-elongation at 72 °C (2 min), and a final step at 15 °C (15 min). The PCR products were separated by electrophoresis on 1% agarose gel at 80V for 55 min. The agarose gel, stained with FloroSafe dye, was observed under UV light. Amplicons with good electrophoresis results were sent to the service company 1st Base for sequencing.

DATA ANALYSIS MOLECULAR. For the molecular data, we reconstructed a phylogenetic tree to examine the relationship of *M. sundaicum* that we obtained with reference samples, *M. trompii* (De Man, 1898), and outgroup sequences, which are considered sister species for comparison: *M. malayanum* (J. Roux, 1935). The genetic distance was determined by applying the pairwise distance method with a Kimura-2 parameter model

Table 2. Sequences of *Macrobrachium sundaicum* for data analysis.
Таблица 2. Последовательности *Macrobrachium sundaicum* для анализа данных.

No	Sequence name	Accession code Gene (NCBI)	References
1	M. sundaicum Selat Panjang 1	LC852666.1	This study
2	M. sundaicum Selat Panjang 2	LC852667.1	This study
3	M. sundaicum Selat Panjang 3	LC852668.1	This study
4	M. sundaicum Selat Panjang 4	LC852669.1	This study
5	M. sundaicum Selat Panjang 5	LC852670.1	This study
6	M. sundaicum Bukit Batu 1	LC852671.1	This study
7	M. sundaicum Bukit Batu 2	LC852672.1	This study
8	M. sundaicum Bukit Batu 3	LC852673.1	This study
9	M. sundaicum Rabbit 1	LC852674.1	This study
10	M. sundaicum Rabbit 2	LC852675.1	This study
11	M. sundaicum Rabbit 3	LC852676.1	This study
12	M. sundaicum Rabbit 4	LC852677.1	This study
13	M. sundaicum Rabbit 5	LC852678.1	This study
14	M. sundaicum Rabbit 6	LC852679.1	This study
15	M. sundaicum Jambi 1	LC852663.1	This study
16	M. sundaicum Jambi 2	LC852664.1	This study
17	M. sundaicum Jambi 3	LC852665.1	This study
18	M. trompii	FM958084.1	Wowor <i>et al.</i> , 2009



Fig. 2. Shrimp *Macrobrachium sundaicum*.

Рис. 2. Креветка *Macrobrachium sundaicum*.

using MEGA 7 to determine the proximity of the haplotype and visualized used heatmap with the BOLD system. Analysis for phylogenetic trees, ML using the IQ-Tree Web Server tool with 10,000 ultrafast bootstrap (UFB) replications [Trifinopoulos *et al.*, 2016]. BI analysis was performed using MrBayes 3.1.2 software. The BI analysis used four simultaneous Metropolis combined with Monte Carlo Markov Chain (MCMC) for 10,000,000 generations, with parameter and topology sampling performed every 1000 generations. Node validity uses bootstrap values $\geq 70\%$, while node values between 50 and 70% are considered as a propensity. In BI analysis, nodes with a Bayesian posterior probability (BPP) of 95% or more were considered significant. The most suitable evolutionary model for ML was selected based on Bayesian information criteria. BI was selected based on Akaike Information Criterion using Jmodeltest software [Darriba *et al.*, 2014]. Furthermore, FigTree v1.4.3 was used to visualize the resulting ML and Bayesian trees.

GENETIC DIVERSITY AND NETWORK HAPLOTYPE. The genetic diversity in this study was calculated based on nu-

cleotide variation (π) and haplotype diversity (H_d), and analysis F_{st} by using DnaSP ver. 6 [Rozas *et al.*, 2017]. A median-joining network [Bandelt *et al.*, 1999] was constructed in Network 10.2 [www.fluxusengineering.com] based on the haplotype data (Table 2) to investigate the phylogenetic relationships among haplotypes.

Results

MORPHOLOGICAL CHARACTERISTICS OF *MACROBRACHIUM SUNDAICUM*. Based on morphological analysis by observing morphological characters the obtained specimens are very similar to the original description of *M. sundaicum* described by [Wowor, Ng, 2010]. Some of their characteristics are as follows: The specimens have short rostrum, with the tip not extending beyond the distal end of the scaphocerite but extending

Table 3. Habitat characteristics of *Macrobrachium sundaicum* at the research location.
Таблица 3. Характеристики среды обитания *Macrobrachium sundaicum* в месте проведения исследований.

Location	pH	Water temperature (°C)	Water current	Presence of aquatic plant	Substrate
Jambi	3.9	27	Fast	–	Mud, leaf litter
Selat Panjang	4.5	25	Slow	+	Mud, leaf litter, dead wood
Bukit Batu	4.7	27	Middle	+	Mud, leaf litter, dead wood
Rabit	3.6	26	Middle	+	Mud, leaf litter, fern roots, dead wood

beyond the distal end of the third segment of the antennular peduncle or the tip slightly extending beyond the distal end of the scaphocerite in young specimens. The rostrum was armed dorsally with at least 9–12 teeth (mode 11), and four teeth completely postorbital (3 or 4 in other specimens, mode 4). Ventral carina with 4–6 teeth (mode 5). Second, pereopods are dissimilar in shape, unequal in size, robust, and fingers covered by soft, dense pubescence, especially in adult specimens. The second pereopod with carpus is shorter than chela and merus subcylindrical (Fig. 2).

HABITAT. The species *M. sundaicum* species are found in peat swamp rivers with pH 3.6–4.7 and water temperature of 25–27 °C. The water is blackish brown with a slow to fast current. The substrate is mud, leaf litter, fern roots, dead wood, and the presence of aquatic plants (Table 3).

GENETIC DISTANCE AND PHYLOGENETIC. The obtained COI fragment of *M. sundaicum* was 442 bp long. The genetic distance range within the same species was 0.000–0.010 (Suppl. Table 1, Fig. 3). Therefore, the obtained *M. sundaicum* sample can be classified as one species with the *M. sundaicum* sample deposited in GenBank (NCBI) with accession number FM958084.1.

Based on the alignment results consisting of 19 sequences with 52 distinct patterns, 34 parsimony-informative, 72 single sites, and 336 constant sites. Based frequencies where adenine (A) 27.1%, cytosine (C) 28.3%, guanine (G) 18.3%, and thymine (T) 26.3%. The best evolutionary model for the phylogenetic tree was selected based on the Bayesian information criterion using the TIM2 model, the proportion of invariant sites (+I), and the discrete gamma shape parameter with four rate categories (+G4) was selected as the best evolutionary model for Maximum Likelihood (ML). BI runs were performed using the general time-reversible (GTR) + invariant sites (+I) + gamma (+G4) model selected based on the Akaike Information Criterion as the best evolutionary model. Based on the phylogenetic results, *M. sundaicum* is always in the same clade as *M. trompii* FM958084.1 (Fig. 4).

GENETIC DIVERSITY AND HAPLOTYPE NETWORK. In total, the COI mtDNA gene marker was sequenced for 17 specimens of *Macrobrachium sundaicum*, with 68 variable sites, 66 parsimony informative sites, 2 singleton variables, and a total of 11 unique haplotypes for each location (Tables 4–9). The results of genetic

diversity analysis obtained for haplotype diversity (Hd) were found to range from low to high (0.00 to 0.66) [Nei, 1987]. The highest haplotype diversity (Hd) was found in Bukit Batu (Hd= 0.80) and nucleotide diversity (π) was found in Jambi and Bukit Batu (π = 0.00454) (Table 9).

The median-joining network showed unique haplotypes for each site (Fig. 5). The values of the fixation score (Fst) showed genetic differences between populations of *M. sundaicum*, ranging from 0.56322 to 0.84615 (Table 10). Fst values close to 0 indicate no differentiation between populations, whereas values close to 1 indicate genetic differences and low gene flow between *M. sundaicum* populations of Sumatran origin.

Discussion

MOLECULAR CONFIRMATION OF *MACROBRACHIUM SUNDAICUM*. In total, 17 shrimp individuals from four locations in Sumatra, based on results of morphological identification of coverage with molecular identification, i.e., *Macrobrachium sundaicum* because based on the genetic distance (0.00–0.10), and phylogenetic results, *M. sundaicum* is in the same clade as *M. trompii*, which is a species whose name was revised to *M. sundaicum*, so we justify that the sample we studied was *M. sundaicum* [Wowor, Ng, 2010]. The phylogenetic analysis revealed that *M. sundaicum* specimens were separated into two distinct clades (Fig. 4). There of one clade is *M. sundaicum* from Selat Panjang and Bukit Batu and two clades are *M. sundaicum* from Rabit and Jambi.

The Selat Panjang and Bukit Batu populations are connected by the Siam River system, which includes the Sungai Kampar (Riau Province), which flows north through the Singapore Strait, joins the Johore River, and then flows north over a large area of the Sunda Shelf [Voriss, 2000]. The river was probably connected to its branches from the Gulf of Thailand when the sea level was 120 m BPL [Voriss, 2000]. The Rabit and Jambi populations are connected by the North Sunda River system, which flows northwards from the northeast coast of Sumatra (Sungai Indragiri, Sungai Hari, and Sungai Musi) to join the great Kapuas River from Kalimantan before entering the northeast sea of Natuna Island [Voriss, 2000]. At sea level, at or below 75 m BPL it joins many rivers in Kalimantan and Sumatra and has a major influence on the distribution of freshwater fish [Voriss, 2000]. Spatially disconnected river systems impose unique phylogeographic constraints on

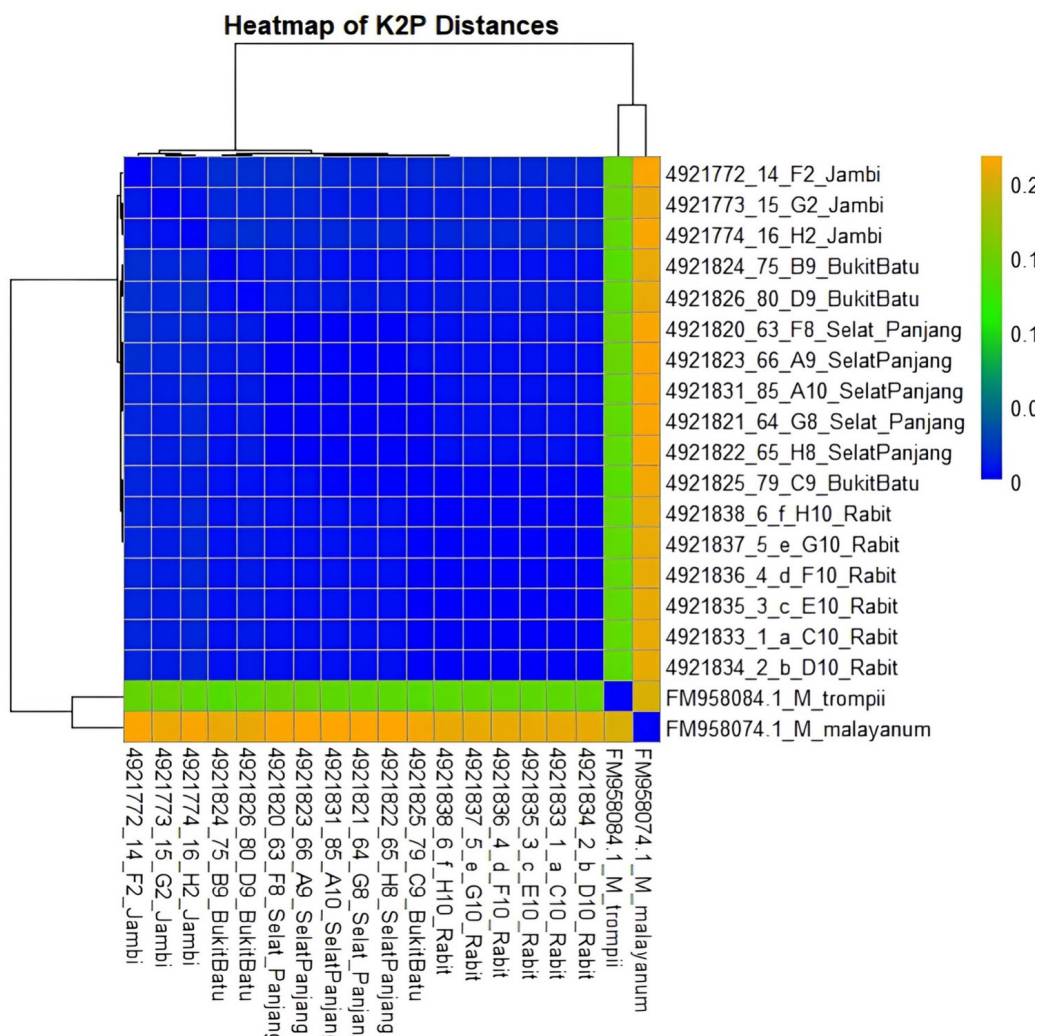


Fig. 3. Heatmap of Kimura-2-parameters (K2P) distances between sequences of *Macrobrachium sondaicum* available on BOLD Systems.

Рис. 3. Тепловая карта расстояний между последовательностями *Macrobrachium sondaicum* с параметрами Kimura-2 (K2P), доступная на BOLD Systems.

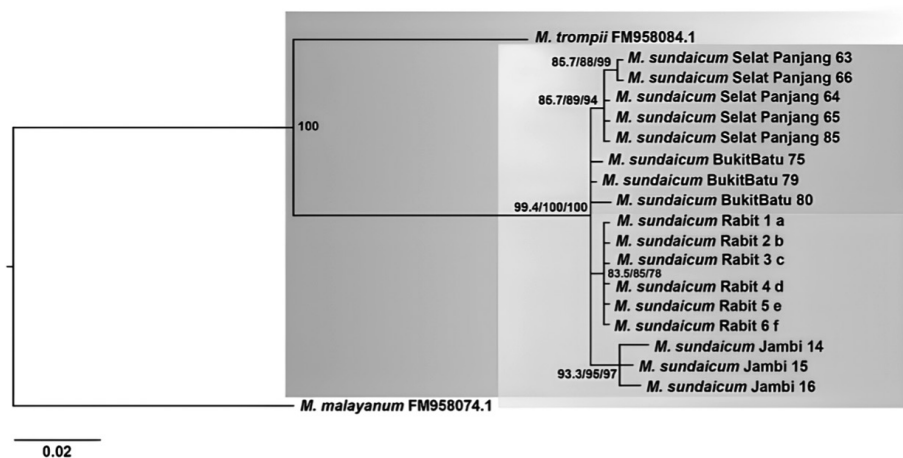


Fig. 4. Bayesian inference phylogenetics. Numbers on branches indicate: Bayesian posterior probability (BPP) bootstrap value and maximum Likelihood (ML).

Рис. 4. Филогенетический байесовский вывод. Цифры на ветвях указывают на начальное значение байесовской апостериорной вероятности (BPP) и максимальное правдоподобие (ML).

Table 4. Haplotype *Macrobrachium sundaicum*.
Таблица 4. Гаплотип *Macrobrachium sundaicum*.

Haplotype	Individuals
H-1	<i>M. sundaicum</i> Jambi 1
H-2	<i>M. sundaicum</i> Jambi 2
H-3	<i>M. sundaicum</i> Jambi 3
H-4	<i>M. sundaicum</i> Selat Panjang 1; <i>M. sundaicum</i> Selat Panjang 4
H-5	<i>M. sundaicum</i> Selat Panjang 2; <i>M. sundaicum</i> Selat Panjang 3; <i>M. sundaicum</i> Selat Panjang 5
H-6	<i>M. sundaicum</i> Bukit Batu 1
H-7	<i>M. sundaicum</i> Bukit Batu 2
H-8	<i>M. sundaicum</i> Bukit Batu 3
H-9	<i>M. sundaicum</i> Rabbit 1; <i>M. sundaicum</i> Rabbit 2; <i>M. sundaicum</i> Rabbit 3; <i>M. sundaicum</i> Rabbit 4; <i>M. sundaicum</i> Rabbit 5; <i>M. sundaicum</i> Rabbit 6
H-10	<i>M. trompii</i> *
H-11	<i>M. trompii</i> *

*references NCBI

Table 5. Nucleotide variation of *Macrobrachium sundaicum* haplotype.
Таблица 5. Нуклеотидная вариабельность гаплотипа *Macrobrachium sundaicum*.

[illegible]

Table 6. Nucleotide variation of *Macrobrachium sundaicum* haplotype (continued).
Таблица 6. Нуклеотидная вариабельность гаплотипа *Macrobrachium sundaicum* (продолжение).

[illegible]

Table 7. Nucleotide variation of *Macrobrachium sundaicum* haplotype (continued).
Таблица 7. Нуклеотидная варибельность гаплотипа *Macrobrachium sundaicum* (продолжение).

ID	Haplo-type	Position of nucleotide variants																
		237	240	243	246	249	258	261	264	267	270	273	279	285	288	291	309	330
1	H-1	C	A	A	C	C	T	A	A	T	A	A	T	T	C	C	A	G
2	H-2	–	–	–	–	–	C	–	–	–	–	–	–	–	–	–	–	–
3	H-3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	H-4	–	–	–	–	–	–	–	–	–	–	–	–	–	T	–	–	–
5	H-5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6	H-6	–	–	–	–	–	–	G	–	–	–	–	–	–	–	–	–	–
7	H-7	–	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–	–
8	H-8	–	–	–	–	–	–	G	–	–	–	–	–	–	–	–	–	–
9	H-9	–	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–	–
10	H-10	T	G	G	T	T	–	–	C	A	C	C	C	–	–	T	G	A
11	H-11	–	–	–	–	–	–	–	–	–	–	–	–	A	–	–	–	–

Table 8. Nucleotide variation of *Macrobrachium sundaicum* haplotype (continued).
Таблица 8. Нуклеотидная варибельность гаплотипа *Macrobrachium sundaicum* (продолжение).

ID	Haplo-type	Position of nucleotide variants																
		336	348	354	357	360	369	372	384	387	390	394	408	414	417	420	435	441
1	H-1	G	C	A	C	C	C	T	C	A	C	C	A	A	A	T	A	C
2	H-2	–	–	–	T	–	–	–	–	–	–	–	–	–	–	–	–	–
3	H-3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	H-4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	H-5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6	H-6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7	H-7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	H-8	–	–	C	–	–	–	–	–	–	–	–	T	–	–	–	–	–
9	H-9	–	–	–	–	–	–	–	–	–	–	–	A	–	–	–	–	–
10	H-10	A	T	–	–	T	A	C	T	T	T	T	T	G	G	C	T	T
11	H-11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	T	–	–

Table 9. The genetic diversity of populations of *Macrobrachium sundaicum* in Sumatra.
Таблица 9. Генетическое разнообразие популяций *Macrobrachium sundaicum* на Суматре.

Location	Number of samples (n)	Number of haplotypes (Hn)	Haplotype diversity (Hd)	Nucleotide diversity (π)
Jambi	3	2	0.66	0.00454
Selat Panjang	5	2	0.53	0.00121
Bukit Batu	3	2	0.80	0.00454
Rabit	6	1	0.00	0.00000
Total	17	7	0.852	0.00663

freshwater fauna [Avisé, 2000]. Typically, the dispersal of freshwater species among river basins is highly restricted, facilitated by factors such as reconfiguration of drainage pathways, transient connections between basins, and fluctuations in sea levels [Carvajal-Quintero *et al.*, 2019; Taniguchi *et al.*, 2021].

CHARACTERISTIC HABITAT. The discovery of *M. sundaicum* in Eastern Sumatra, especially in Riau Province (Selat Panjang Island, Bukit Batu, and Rabit Rivers) and Jambi Province (Kumpeh River) adds to the distribution location as a new record of existence. The species *M. sundaicum* can be found in peat waters with a

substrate of leaf litter and dead wood. Substrates of leaf litter and dead wood are preferable to shrimp because wood fragments also contain small cracks that serve as hiding places [Nogueira *et al.*, 2018], and leaf litter not only provides a food source but also serves as a hiding place for the prawns [Purnamasari *et al.*, 2024]. Meanwhile, mud substrate and fern roots are not suitable for the life of that species. Because mud substrate does not provide hiding places for shrimp. In addition, the hard roots of ferns do not provide adequate hiding places, and these roots are also difficult for *Macrobrachium* spp. to walk through or penetrate, especially when the shrimp try to rise above the water's surface. Annawaty *et al.*, [2016] state that the hard and sparse root characteristics of aquatic plants are unsuitable for *Caridina* spp. to attach to, making the shrimp unfavorable towards such habitats. The choice of substrate and specific microhabitats by an organism can be directly linked to its life cycle, serving as a source of food and a place of refuge [Nogueira *et al.*, 2018].

Peat swamps are a very important habitat, for instance, pristine peat swamp forests are the most important remaining habitat for the iconic orangutan [Erb *et al.*, 2018]. There are also likely to be other animal species that are partially or fully dependent on peat swamp forest habitats; for example, very little is known about their invertebrate and below-ground biota [Mishara *et al.*, 2021]. The biggest threat to peat swamps is habitat fragmentation into bare and degraded peatlands or plantations and smallholder agriculture has posed a threat to the ecosystem [Mishara *et al.*, 2021]. By 2015, only 6.4% of peat swamp forests in peninsular Malaysia, Sumatra and Borneo remained in a pristine condition [Miettinen *et al.*, 2016], placing several obligate peat forest species under threat of extinction [Giesen *et al.*, 2018; Thornton *et al.*, 2018]. In addition, the habitat quality of remaining areas of forested peatland is being reduced by habitat fragmentation, drainage impacts, fire from the surrounding landscape, and unsustainable (and often illegal) timber extraction [Miettinen *et al.*, 2016]. Therefore, the degradation and conversion of peatlands has led to the disruption of natural hydrological functions [Evers *et al.*, 2017], thereby increasing drought severity [Taufik *et al.*, 2020] and fire hazards [Taufik *et al.*, 2019]. Which results in the loss of biodiversity, including shrimp.

GENETIC VARIATION AND HAPLOTYPE NETWORK. The analysis of genetic variation within *M. sundaicum* was made in only four populations (11 haplotypes). For the whole population of *M. sundaicum* except for Rabbit, the haplotype diversity was found from moderate to high (0.53 to 0.80). Furthermore, low to high nucleotide diversity was also observed among the population (0.00121 to 0.00454). Pairwise *Fst* values ranged from 0.56522 to 0.97793 between *M. sundaicum* populations (Table 10). *Fst* values approaching 0 indicate no differentiation between populations, while values approaching 1 indicate total differentiation [Bird *et al.*, 2017]. Almost, every haplotype was specific to a particular river, suggesting a strong population structure in each river at small geographical scales [Doi *et al.*,

2024]. Research on the genetic structure and diversity of the island's endemic freshwater shrimp *M. shokitai* also showed that haplotype and nucleotide diversity were very low in each river on the island. Almost all haplotypes were only found in certain rivers, confirming the existence of differences in population structure among rivers at a small geographical scale [Doi *et al.*, 2024]. Research on the phylogeography and genetic structure of *M. nipponense* in East Asia shows that the high level of genetic structure among the oriental river prawn populations in East Asia was influenced by land bridges during Pleistocene glacial maxima and by human colonization. This indicates that the dispersal ability of *M. sundaicum*, a species dependent on acidic peat swamp habitats, is limited. Although freshwater shrimps have been reported to have well-defined population structures [Imai *et al.*, 2014], population structures at small scales among multiple watersheds are very rare. Some caridean shrimp species are known to undertake terrestrial migrations upstream, i.e., *Macrobrachium lanchesteri* (De Man, 1911), *M. dienbienphuense* Dang et Ngyuen, 1972, *M. australiense* Holthius, 1950 [Hongjamrassilp *et al.*, 2021; Torkkola, Hemsley, 2019]. However, the unique characteristics of peat swamp rivers make it impossible for the obligate species of shrimp *M. sundaicum* to traverse out of the drainage by walking on land. Thus, gene flow through land dispersal is thought to be very low in this species [Torkkola, Hemsley, 2019].

The results of the haplotype network analysis show that the distribution of *M. sundaicum* lineages reflects geographical boundaries at both large and small scales. In the large group, namely the Rabbit, Bukit Batu, and Selat Panjang groups become one group, while Jambi clusters itself by a large number of mutation steps (Fig. 5). Nonetheless, the phylogenetic analysis suggests the monophyly, which means derived from a common ancestor. By this, a dispersal scenario might take place during the colonization of the new area. It was further supported by the sea level during the Pliocene [Voris, 2000]. A similar pattern was also found in *M. nipponense* from Huaihe River, which phylogeographic pattern or significant divergence between upstream and midstream populations where expansion occurs time populations that show evidence of expansion in the past is estimated to be 85,500 years before the present [Cui *et al.*, 2018].

In addition, this could be attributed to the landlocked nature of *M. sundaicum*, which limits the extent of larval dispersal. Although all samples were *M. sundaicum*, the genetic variation observed indicated the presence of unique, genetically segregated haplotypes. This is consistent with the landlocked nature of *M. sundaicum*, which spends its entire life cycle in freshwaters, resulting in genetic uniqueness among geographically separated populations. The landlocked life history, they spend their entire life cycle in freshwater and have eggs that are of intermediate size (egg size value 0.027–0.059) eggs with considerable amounts of yolk needed to better adapt to limited food conditions while developing their large body size an adaptation to maintain habitat position in river flows [Hamasaki *et al.*, 2020]. These produce morphologically advanced non-feeding or facultatively lecithotrophic

Table 10. Population structure analysis (Fst) at the four sites.
Таблица 10. Анализ структуры населения (Fst) на четырех участках.

Location	Jambi	Selat Panjang	Bukit Batu
Jambi	—	—	—
Selat Panjang	0.81643	—	—
Bukit Batu	0.71429	0.56322	—
Rabit	0.84615	0.88889	0.60000

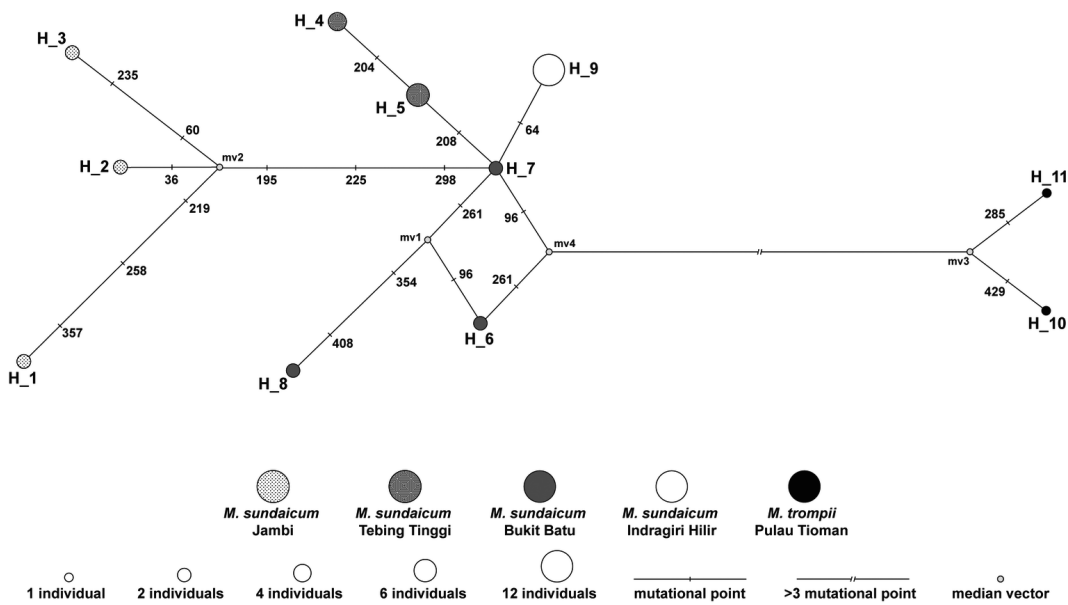


Fig. 5. Haplotype network of populations of *Macrobrachium sundaicum*.
Рис. 5. Сеть гаплотипов популяций *Macrobrachium sundaicum*.

larvae, resulting in a shortened larval developmental period before molting into the juvenile stage [Møller *et al.*, 2020], or directly producing juveniles [Bauer, 2013]. It has been argued that, in landlocked shrimps, non-feeding or facultative lecithotrophy of larvae are adaptations to limited food conditions in freshwater environments [Bauer, 2013; Hamasaki *et al.*, 2020] and faster development and settlement behaviors that large larvae exhibit are adaptations that allow the larvae to stay in or near parental habitats in flowing waters [Hamasaki *et al.*, 2020]. Food availability for shrimp in acidic waters is dominated by phytoplankton from the Bacillariophyceae class [Helmizuryani, 2021].

In conclusion, genetic diversity in *M. sundaicum* is the first time that this study has been reported and confirmed through morphological and molecular data. Based on morphology, the study revealed that there was no variation in morphology among the four sites. This was supported by molecular analysis of the phylogenetic tree, our samples clustered with *M. sundaicum* samples described by [Wowor *et al.*, 2004]. The results of haplotype network analysis show that *M. sundaicum* has unique haplotypes for certain rivers, which confirms that it has a different population structure at each study

location. This is because *M. sundaicum* entered the peat swamp due to river drainage when sea levels rose during the Pleistocene epoch and the limited distribution of this species due to its landlocked life cycle. Thus, the release of individuals from different rivers with different clades should be avoided to avoid genetic disruption, even during conservation efforts if the goal is to restore the depleted population in the river [Doi *et al.*, 2024].

Supplementary data. The following Table is available online.

Supplementary Table 1. Uncorrected genetic distances (p-distances) of the species of the *Macrobrachium sundaicum*-complex and outgroup species.

Compliance with ethical standards

CONFLICT OF INTEREST: In this research there is no conflict of interest.

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