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Presenting identification keys and future study on seagrass *Halophila major* in Indonesia

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ABSTRACT

Halophila major is a new species with a wide distribution across various regions in Indonesia. The species was identified in 2020 through a combination of morphology and molecular approaches. Several studies have shown that it has a similar morphology to *H. ovalis*, which causes significant confusion during identification. Therefore, this study aims to describe the key identification and habitat of *H. major* and summarize seagrasses study opportunities based on the trend of published articles. A bibliometric analysis was used to summarize the habitat, morphometrics, molecular confirmation, and trend of seagrass topics in Indonesia. Based on the scientific articles, *H. major* has bigger morphometrics than *H. ovalis*. In addition, the number of paired and branching cross veins was reported to be an identification key of *H. major*. The species was also considered a deep ovalis found in 2-4 m depth. Genetically, the Internal Transcribed Spacer (ITS) gene marker was appropriate to show its phylogenetic tree. *H. major* was also classified into different clades with *H. ovalis* due to various factors. The results showed that genetics, tourism, and restoration were topics with the potential to be explored in the future. This study recommended collaborating in multi-institution to transfer knowledge, technologies, and project arrangements for seagrass exploration.

Introduction

Seagrasses are marine angiosperms, existing in saline waters, which are widely distributed across tropical, subtropical, and temperate coasts worldwide (den Hartog, 1970; Phillips and Menez, 1988). These plants are classified into 6 families, namely Zosteraceae, Cymodoceaceae, Posidoniaceae, Ruppiaceae, Zannichelliaceae, and Hydrocharitaceae (Les *et al.*, 1997; den Hartog and Kuo, 2006). Several studies have shown that Zosteraceae has 3 genera (*Zostera*, *Heterozostera*, and *Phyllospadix*), while Ruppiaceae, Posidoniaceae, and Zannichelliaceae have a genus. In addition, *Ruppia*, *Posidonia,* and *Lapilaena* Cymodoceaceae have 5 genera (*Halodule*, *Cymodocea*, *Syringodium*, *Thalassodendron*, and *Amphibolis*). A previous study also reported that Hydrocharitaceae has 17 genera, but only 3 live in marine waters (*Thalassia*, *Halophila*, and *Enhalus*) (den Hartog and Kuo, 2006).

Among these Hydrocharitaceae families, the genus *Halophila* stands out due to its complex taxonomy, broad distribution, and ecological significance (Waycott *et al.*, 2002; Kuo *et al.*, 2006). This genus spread from the western Indo-Pacific to northwest Africa and southern Australia (den Hartog, 1970; Waycott *et al.*, 2002), and its taxonomic classification has experienced multiple revisions. Den Hartog (1970) initially recognized 13 species, which expanded to 15 species and 3 subspecies by Kuo *et al.* (2006). Singh *et al.* (2019) further proposed a classification system comprising 5 sections and 21 species, while the most recent revision by Kou (2020) identified 24 species across 8 sections. (Kuo, 2020). These

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continuous updates emphasize the ongoing challenges in classifying *Halophila* species and the likelihood of further discoveries (Kuo and den Hartog, 2001; den Hartog and Kuo, 2006).

A total of 17 species of seagrasses have been identified in Indonesia, including *Enhalus acoroides* (Linnaeus f.) Royle, *Thalassia hemprichii* (Ehrenberg) Ascherson, *Halophila beccarii* Ascherson, *H. decipiens* Ostenfeld, *H. major* (Zollinger) Miquel, *H. minor* (Zollinger) Hartog, *H. ovalis* (R. Brown) J.D. Hooker, *H. spinulosa* (R. Brown) Ascherson, *H. sulawesii* J. Kuo, *Cymodocea rotundata* Ascherson and Schweinfurth, *C. serrulata* (R. Brown) Ascherson and Magnus, *Halodule pinifolia* (Miki) Hartog, *H. uninervis* (Forsskal) Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, *Thalassodendron ciliatum* (Forsskal) Hartog, *Ruppia brevipedunculata,* and R. *maritima* Linnaeus (Kurniawan *et al.*, 2024; Fortes *et al.*, 2018). Sjafrie *et al.* (2018) reported 15 species in the field, such as *H. beccarii* and *Ruppia maritima*, which were preserved in the Herbarium Bogoriense Museum (Spalding *et al.*, 2003; Kiswara, 2011). Among *Halophila* species found in the country, 6 have been confirmed in Indonesian waters, with *Halophila sulawesi* recently recorded as a monoecious species from the Spermonde Archipelago, Southern Sulawesi (Kuo, 2007).

H. major, a seagrass species found in Indonesia, is significant for its taxonomic ambiguity and poorly understood distribution, which hinder accurate identification. Zollinger initially described *H. major* in 1847 as *Lemnopsis major*, but it was transferred to the genus *Halophila* by Miquel in 1855. The specimen was collected from Kambing Island, Bima Bay, Sumbawa, West Nusa Tenggara Province. Recently, Kurniawan *et al.* (2020) and Uchimura *et al.* (2008) reported the presence of *H. major* with wide distribution in Indonesia. Visually, *H. major* exhibited a morphological similarity to *H. ovalis*. Misidentification is one of the reasons for the lack of information about this species. The presence of the species was also unrecorded by the scientific authority in Indonesia. Although Fortes *et al.* (2018) reported its presence, the book of Indonesian seagrass meadow status 2018 did not list the species. In addition, the Indonesian seagrass meadow status 2021 does not provide adequate regarding its distribution, morphological, and molecular traits (Rahmawati *et al.*, 2022).

The absence of clear taxonomic data and standardized identification guidelines has contributed to inconsistencies in documenting the distribution of *H. major* in Indonesia. Misidentification with morphologically similar species, such as *H. ovalis*, further complicates its classification, leading to underreporting or inaccurate records. Without a reliable framework for identification, the true extent of *H. major's* presence in Indonesian waters is uncertain.

Despite reports of *H. major* in Indonesia, inconsistencies in its documentation show the urgent need for a standardized identification framework. Species' morphological similarity to *H. ovalis* has led to frequent misidentification, while the absence of detailed habitat descriptions further complicates its recognition in the field. Establishing clear identification keys and habitat characterizations is essential to accurately assess distribution, ecological role, and conservation status. Therefore, this study aims to describe the key identification and habitat of *H. major* and summarize seagrass study opportunities based on the trend of published papers.

Materials and Methods

Data was obtained from study articles, manuscripts, and proceedings. The search used the keyword "*Halophila* Indonesia", "Seagrass Indonesia", "*Halophila major*", "*Lamun* Indonesia", and "*Padang Lamun*" in the database. Google Scholar (http://scholar.google.com), PubMed (http://pubmed.ncbi.nlm.nih.gov/), ScienceDirect (http://www.sciencedirect.com), and ResearchGate (http://www.researchgate.net) were also used in this study. This study was conducted from 2016 to 2024 for the trend of seagrass studies in Indonesia. Meanwhile, the data range was set from 2000 to 2024 for relevant publications of *H. major*. To ensure a substantial number of publications for analysis, a broad date range was used when searching for studies on species, as publications from 2016 to 2024 were limited. In total, 510 publications were obtained from 2016 to 2024 on the trend of seagrass studies in Indonesia. Moreover, 15 papers related to *H. major* studies were collected to present the results of species based on ecological and taxonomical evidence.

A total of 375 papers were divided into 365 articles in Indonesian for seagrass studies and 10 papers focusing on extracting morphological data of *H. major*. This study eliminated 135 unrelated papers, which focused on different areas outside of Indonesian seagrass from all databases. The study of these species studies was limited to those published in international journals that were affiliated with Elsevier and indexed by Scopus. Therefore, 70% of

seagrass articles were written in the Indonesian language. Google Scholar database was the most dominant retrieval of seagrass papers. EndNote X9 was used to validate data accuracy and executed a deduplication process.

The annual number of downloaded articles was calculated by year as well as the contribution of journals, topics, and authors to seagrass studies in Indonesia. This trend was analyzed using Microsoft Excel. The term co-occurrence selected the title, abstract, and author as the analysis target. All term co-occurrences were performed using VOSviewer software (Van Eck and Waltman, 2017). The minimum number of occurrences of a term was 8 of the 2030 terms, and 28 met the threshold. A total of 28 terms were selected as relevant to seagrass studies in Indonesia. Furthermore, a bibliometric map based on term occurrence analysis was presented. The relationship between study topics and time was visualized and explained.

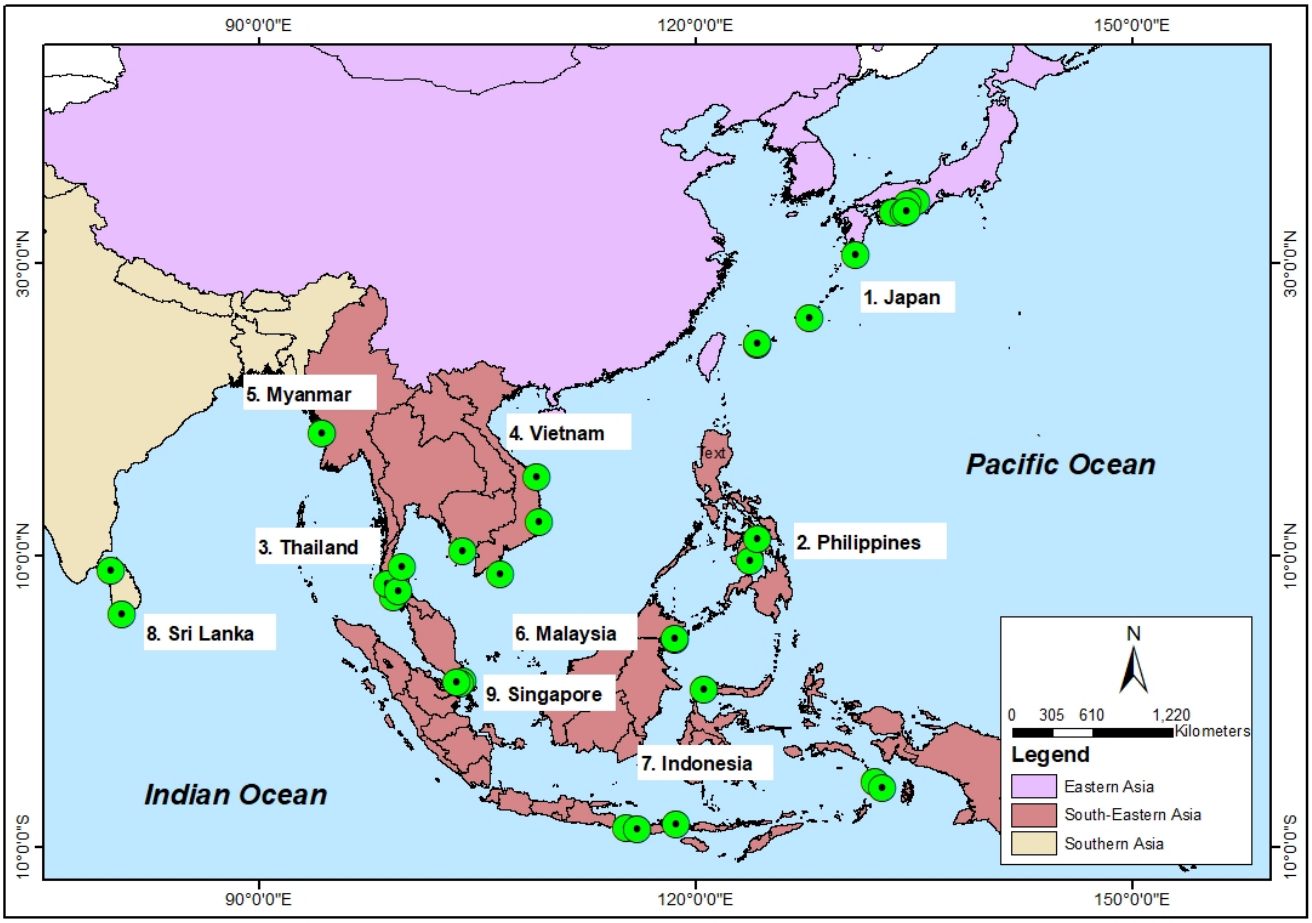

Figure 1. Distribution of *Halophila major* in Asia. **Japan:** Wakayama, Tokushima, Kochi, Tanegashima, Shishikui, Mugi-Ooshima, Nakagusuku Bay, and Ishigaki Island (Kuo *et al.*, 2006; Uchimura *et al.*, 2008; Shimada *et al.*, 2012); **Philippines:** Panglao and Kalanggaman Island (Kolatkova *et al.*, 2020); **Thailand:** Trang (Leam Yong Luam, Koh Libong, Koh Muk, Ko Lao Liang, Ao Nang), and Kanom (Uchimura *et al.*, 2008; Nguyen *et al.*, 2014; Tuntiprapas *et al.*, 2015); **Vietnam:** Nha Trang Bay, Ly Son Islands, Con Dao Islands, and Phu Quoac Islands (Nguyen *et al.*, 2013b; Nguyen *et al.*, 2021b); **Myanmar:** Gyeiktaw (Nguyen *et al.*, 2014); **Malaysia:** Mabul Island, Gusungan Island, and Tanjung Adang Laut Johor (Che Alias *et al.*, 2024; Nguyen *et al.*, 2014); **Indonesia:** Kambing Island-Bima, Sindhu Beach-Bali, Tayando Island-Tual, Weduar Beach-Kei Besar, Malala Bay-Tolitoli, and Sekotong Beach-Lombok (Uchimura *et al.*, 2008; Kurniawan *et al.*, 2020); **Sri Lanka:** Matara and Mannar (Liu *et al.*, 2020); **Singapore:** Chek Jawa and SFA Jetty St. John's Island (Kwan *et al.*, 2023).

Results and Discussion

Distribution of *H. major* in Asia

H. major was distributed in the western Pacific, including Japan, the Philippines, Thailand, Malaysia, Singapore, Indonesia, Vietnam, and the northern Indian Ocean, such as Sri Lanka (Figure 1). In these regions, its distribution was influenced by variations

in water temperature, nutrient availability, and depth. Nguyen *et al.* (2013b) reported that *H. major* was first found in Vietnam, precisely on Tre Island, Nha Trang Bay, at 4 to 6 m depth. Nguyen *et al.* (2014) conducted morphological and genetic identification on *H. ovalis* samples (initial identification) from Mabul Island, Gusungan Island (Malaysia), and Gyeiktaw (Myanmar). Using phylogenetic analysis based on chloroplast DNA sequences, it was observed that *H. major* formed a distinct cluster separate from *H. ovalis*. This led to the first confirmed record of *H. major* in Malaysia and Myanmar. However, challenges in distinguishing between these species were based solely on morphology emphasizing the importance of molecular. A survey conducted by Tuntiprapas *et al.* (2015) on the genus *Halophila* obtained samples similar to *H. ovalis* but with a larger leaf size. The result showed that the *H. major* species was identified using phylogenetic analysis.

For all seagrass species, distribution resulted from a combination of plant sexual reproduction and self-propagation, which were influenced by distribution limitations and the environment (Spalding *et al.*, 2003). Recently, species distribution changes occurred due to human alteration of the physical environment or the transport of species from their endemic locations (Short *et al.*, 2007). This species distribution caused the expansion of species into a new community and was considered invasive (Alfaro *et al.*, 2012; Thompson and Ziska, 2014; Cassey *et al.*, 2018). The impact of invasive species affected the loss of endogenic species (Clavero and Garcia-Berthou, 2005). Furthermore, 1 or 2 species of the genus *Halophila* could be invasive, although several species were endemic and had limited distributions due to unresolved taxonomic issues (Short *et al.*, 2007). Seagrasses that responded well to environmental changes persisted in the community.

Distribution of *H. major* in Indonesia

Environmental gradients affected the vertical distribution pattern of seagrass in Indonesia. From the last report, eastern Indonesia was the one geographical distribution of *H. major*, such as Malala Bay (Tolitoli Regency), Sekotong Beach (Lombok Regency), Tayando Island (Tual Regency), Weduar Coast (Kei Island), and Sindhu Beach (Bali) (Uchimura *et al.*, 2008; Kurniawan *et al.*, 2020).

The waters in eastern Indonesia had the right kind of environment for seagrass to grow, like clear water, steady temperatures, enough nutrients, and the right depth. But sometimes, too much light and changes in temperature could cause stress to the seagrass. This stress could make the seagrass change how it looks. For example, if the temperature stayed high for a long time, the leaves would get thinner, and the

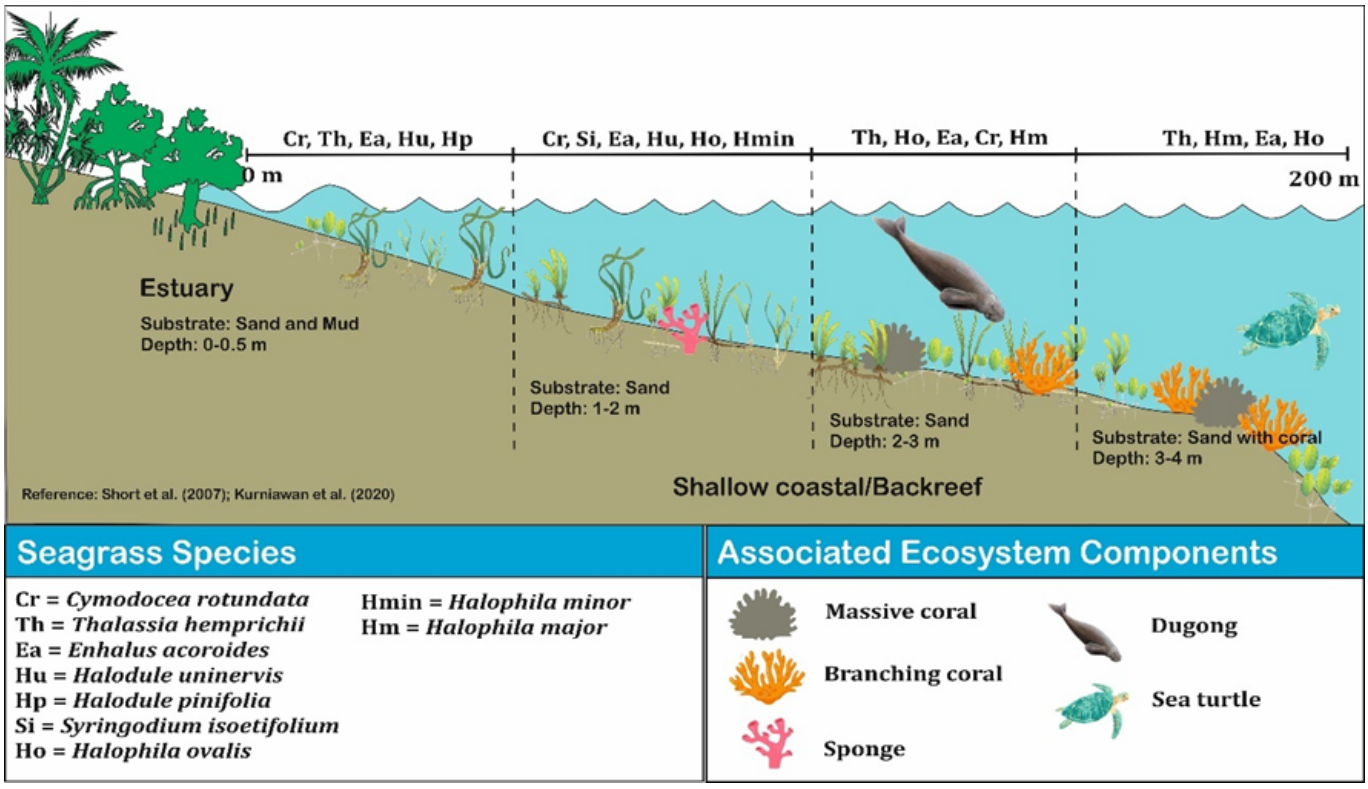

Figure 2. Vertical distribution of *H. major* in Indonesia. This image was modified by Short *et al.* (2007) and Kurniawan *et al.* (2020).

seagrass wouldn't grow as fast because its body had to work harder (Cussioli *et al.*, 2019).

H. major was found growing together with other seagrasses such as *T. hemprichii* and *C. serrulata* in Thailand (Tuntiprapas *et al.*, 2015); *H. uninervis*, *H. pinifolia*, and *S. isoetifolium* in Vietnam (Nguyen *et al.*, 2013b); and *E. acoroides*, *T. hemprichii*, and *H. ovalis* in Indonesia (Kurniawan *et al.*, 2020). Furthermore, *H. major* was also found adjacent to live coral patches. The presence of seagrass near coral reefs played an important role as a filter for pollutants and excess nutrients, which could damage coral reefs (Chhaba *et al.*, 2024). Moreover, seagrass also absorbed excess nutrients from the water, reducing the risk of eutrophication, which damaged coral reefs (Hashim, 2021).

The types of seagrass found with others were different in some regions because things like the kind of ground, how deep the water was, and how water moved were not the same. In Indonesia, *H. major* and bigger seagrass types like E. acoroides being together might mean they are trying to take the same space and light. Short *et al.* (2007) talked about how seagrass grows in layers in the Indo-Pacific. Most kinds of seagrass were in places less than 10 m deep. The Halophila genus, where H. major is included, was able to live in estuaries and also deeper waters. In Indonesia, *H. major* was seen in water 2 to 4 m deep, so it might only live in shallow places where there's enough light. But nobody knows for sure if it could also grow in deeper places. For example, *H. decipiens* was found 58 m deep in the Great Barrier Reef (Lee Long *et al.*, 1996). Also, H. spinulosa, H. ovalis, H. tricostata, and H. capricorni were in water 35 m deep (Coles *et al.*, 2000). *H. stipulacea* was found as deep as 70 m in the Red Sea. (Short *et al.*, 2007).

How seagrass was spread out up and down depended a lot on the shape of the island because the type of ground helped decide where they could grow. H. major was seen in places where there was sandy mud and the tide sometimes went out, so it was left in the sunlight. H. major didn't seem to like the same places as H. ovalis, which liked softer mud with more clay in it (Lamit and Tanaka, 2019). Instead, H. major seemed to do better in rougher sand that drained water better. This kind of ground, plus how water moved around, probably changed where H. major could live along the coast. The shape of the islands also made the ocean currents and waves different, especially on coasts and small islands in Indonesia. Because of this, H. major was found in places where there was muddy sand and it got sunlight at low tide. But in this study, H. major wasn't seen in muddy sand like H. ovalis, which liked mud with just a little bit of clay or silt (Lamit and Tanaka, 2019).

Morphometric Traits

The way *H. major* looked was affected by things like the environment and how the islands were shaped. These things changed stuff like how long the leaves were, how wide the leaves were, the angle between the veins that branched out and the main veins in the leaf, how many vein pairs there were, and how many branching veins there were. There were also other things, like the space between the veins in the leaf, the space from the veins to the edge of the leaf, the space from the veins to the edge at the tip of the leaf, and the ratio of how long the leaves were to how wide they were (Table 1).

Table 1. Comparison of morphometrics between *H. ovalis* and *H. major*.

Characters	*H. ovalis**	*H. major***
Leaf length (mm)	6-28	10-42.30
Leaf width (mm)	1.2-11	5-22.03
Paired cross veins (number)	7-17	11-22
Paired branching cross veins (number)	0-3	1-8
Distance between intra-marginal veins and lamina margin (mm)	0.16-0.6	0.1-0.72

* Uchimura *et al.* (2006); Kuo *et al.* (2006); Nguyen *et al.* (2013a); Tuntiprapas *et al.* (2015); Amale *et al.* (2016); Kwan *et al.* (2023); and Che Alias *et al.* (2024).

** Uchimura *et al.* (2006); Nguyen *et al.* (2013a); Tuntiprapas *et al.* (2015); Kurniawan *et al.* (2020); Kwan *et al.* (2023); and Che Alias *et al.* (2024).

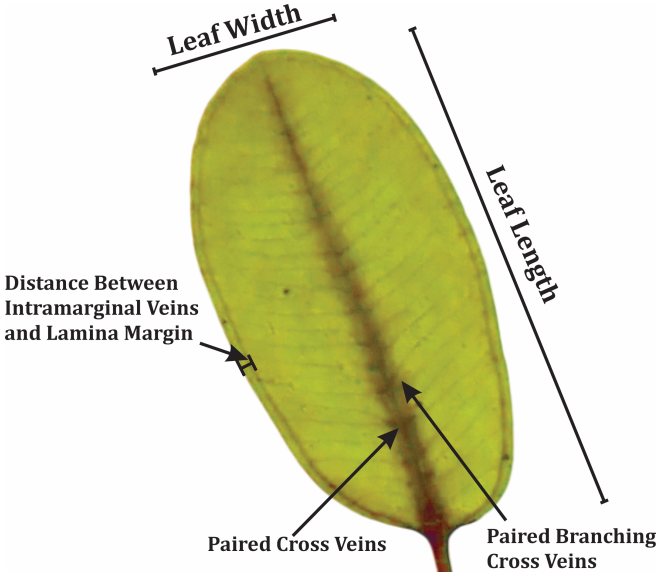

Figure 3. Morphometric characters of *H. major* as identification key.

Morphologically, *H. major* and *H. ovalis* exhibited ad a broadly similar leaf shape, characterized by elliptical to oblong outlines. However, *H. major* exhibited significantly larger leafs with a more complex venation pattern, featuring a greater number of branching veins and distinct paired cross-veins. Ecologically, this increased leaf surface area in *H. major* was likely an adaptive strategy to optimize light capture for photosynthesis in its specific habitat. A crucial distinguishing feature for field identification was the bathymetric distribution. *H. ovalis* was rarely observed in deeper waters, while *H. major* were found at greater depths. Furthermore, the number of branching veins served as a reliable diagnostic character for differentiating these 2 species (Figure 3). These morphological characteristics, particularly the larger leaf size and complex venation, represented a significant divergence within the genus *Halophila* (Kuo and den Hartog, 2006; Kuo, 2020), and could be effectively used as key identification.

The reproductive phenology of *H. major*, particularly in tropical ecosystems, remained largely undocumented due to the inherent difficulties in observing and characterizing its reproductive cycle. Seagrass phenological events were intrinsically complex, governed by a multitude of interacting environmental variables, including temperature, salinity, light availability, and nutrient concentrations, making it challenging to isolate the specific drivers (Wong and Dowd, 2023). Moreover, the variability in environmental conditions, such as fluctuating nutrient levels and water turbidity, could confound the effects of individual factors on phenological expression (Guerrero-Meseguer *et al.*, 2022). The sporadic nature of flowering, fruiting, and leaf turnover, coupled with the small, inconspicuous flowers as well as the submerged nature of pollination and seed dispersal, further complicated direct observation. Consequently, long-term monitoring, requiring substantial and sustained resources, was crucial for explaining phenological shifts (Qin *et al.*, 2020). Existing phenological data for tropical *Halophila* species majorly pertain to *H. ovalis*, with reports of year-round reproduction (den Hartog, 1970) and seasonal flowering from August to December in South Sulawesi (Verheij and Erftemeijer, 1993). The high oceanographic dynamics, minute flower size, and potential for sediment burial in tropical environments presented significant obstacles to phenological studies of *Halophila* species. As a result, the reproductive characteristics of *H. major* in these regions represented a critical knowledge gap. While Kuo *et al.* (2006) provided valuable insights into the reproductive biology of *H. major* based on specimens from Japan, concluding these results to tropical populations needed further investigation due to potential regional variations. Therefore, focused study efforts were required to understand the reproductive phenology of *H. major* in tropical waters, which contributed to a more comprehensive understanding of seagrass ecology and conservation.

Table 2. *H. major's* sequence in GenBank.

Countries	Number of sequences			References
	ITS	rbcl	matK	
Indonesia	6	-	-	Uchimura *et al.* (2008) and Kurniawan *et al.* (2020)
Thailand	12	-	-	Uchimura *et al.* (2008) and Nguyen *et al.* (2014)
Vietnam	4	1	1	Nguyen *et al.* (2013a), Nguyen *et al.* (2013b), and Nguyen *et al.* (2021b)
Sri Lanka	46	45	-	Liu *et al.* (2020)
Malaysia	5	-	-	Nguyen *et al.* (2014) and Alias *et al.* (2024)
Philippines	2	-	-	Kolatkova *et al.* (2020)
Japan	1	-	-	Uchimura *et al.* (2008)
Myanmar	1	-	-	Uchimura *et al.* (2008)
Singapore	5	-	8	Kwan et al (2023)
China	2	-	4	Shuo et al (2023) and Yu et al. (2023) *unpublished*
Total	**84**	**46**	**13**	

Molecular Traits

The molecular data for *H. major* deposited in GenBank exhibited a notable disparity in sequence representation across different genetic markers. These included Internal Transcribed Spacer (ITS) with 84 sequences, ribulose-bisphosphate carboxylase large chain (rbcL) with 46 sequences, and maturase K (matK) with 13 sequences, originating from Japan, Southeast Asia, and Sri Lanka (Table 2).

In this study, this disproportionate distribution emphasized the prevalent use of ITS for species identification, while rbcL and matK remained comparatively underutilized. This disparity showed a significant study gap in gene exploration for phylogenetic analysis, as supplementary sequencing of rbcL and matK contributed to a more comprehensive explanation of the evolutionary relationships within *H. major*. Factors, such as the discovery of H. major in field surveys and the advancement of genetic-based identification technologies, influenced the variation in sequence deposition within GenBank. The inherent challenges in seagrass species identification, particularly within the genus *Halophila*, introduced inaccuracies and inconsistencies in data collection and submission. Therefore, the limited sequence availability negatively impacted the resolution and accuracy of phylogenetic analyses, potentially resulting in phylogenetic trees with reduced robustness and a lack of support for interspecific relationships.

The utilization of alternative genetic markers in phylogenetic analyses showed positional or clustering variations within the resulting topologies. While chloroplast genes remained viable for exploration, microsatellite DNA was strongly recommended for elucidating interspecific relationships in seagrasses. Microsatellites, characterized by their high allelic variability, offered superior discriminatory power, enabling precise differentiation among seagrass species, populations, and individuals (Jeffery *et al.*, 2024). Furthermore, their enhanced sensitivity aided the detection of subtle genetic divergences among individuals and populations (Waycott *et al.*, 2021). Although the ITS region had been widely used in addressing taxonomic ambiguities within the genus *Halophila*, the Consortium for the Barcoding of Life (CBOL) advocated for the broader application of rbcL and maturase K (matK) genes. Lucas *et al.* (2012) showed that the matK gene possessed the resolution to distinguish species and ecological types (ecotypes) within certain plant taxa, suggesting its potential utility in resolving fine-scale taxonomic and ecological distinctions in seagrasses.

The use of different genes impacted the consistency of the results of the relationship tree, so a consistency test was needed on the phylogenetic tree. For instance, the phylogenetic reconstruction of *Halophila ovalis* and its subspecies, *H. ovalis* subsp. *bullosa* showed divergent topologies depending on the outgroup selection. When *H. pinifolia* was used as the outgroup, a distinct clustering of the *H. ovalis* taxa was observed. Meanwhile, using *S. isoetifolium* as the outgroup, a strategy feasible only with trnH-psbA and matK sequence data, resulted in the grouping of both *Halodule* taxa into a parallel branch, separate from the *H. ovalis*/*ovalis* subsp. *bullosa* clade (Singh *et al.*, 2019). This discrepancy emphasized the sensitivity of phylogenetic inferences to outgroup selection, particularly when using different genetic markers, which showed the potential for alternative outgroup choices to show contrasting evolutionary relationships.

Phylogenetic trees distinguished between *H. major* and *H. ovalis* clearly (Kurniawan *et al.*, 2020; Nguyen *et al.*, 2021a; Nguyen *et al.*, 2021b; Kwan *et al.*, 2023; Che Alias *et al.*, 2024). Nguyen *et al.* (2021b) showed that the phylogenetic tree of *H. major* from Indonesia, Thailand, and Malaysia was in one cluster. Haplotype analysis strengthened their closeness, as observed in the region with samples from Thailand as its center. *H. major* from Indonesia, Malaysia, and Thailand were geographically close and had the same environmental conditions. Nguyen *et al.* (2021b) showed that the Wallacea region (including Indonesia) had a high level of nucleotide and haplotype diversity. Furthermore, there were no significant differences between regions but significant differences within the population. As a result, haplotype connectivity studies were needed to answer the phylogeography of *H. major* in Indonesia. Haplotype connectivity studies facilitated the characterization of population structure and gene flow, thereby enabling the reconstruction of historical distribution patterns and the elucidation of the evolutionary history of *H. major* (Nguyen *et al.*, 2014). Consequently, the identification and spatial distribution of haplotypes across disparate geographic regions provided insights into the influence of historical and contemporary geographic barriers in shaping the observed distribution of this species. *H. major* had variants or subspecies such as its relative, *H. ovalis* subsp. *bullosa* (Singh *et al.*, 2019, 2020). Species delimitation method allowed for phylogenetic analysis of *H. major* in Indonesia with this wide geographical distribution.

Seagrass Future Study

Analysis of Indonesian seagrass study publications showed an upward trend from 2016 to 2017 (Figure 4). However, there was a subsequent decline in publication output from 2021 to 2024, despite a plateau in 2023 coinciding with 2021 levels. Publications in 2020 typically reflected those conducted in 2019. The period spanning 2019 to 2022 was significantly impacted by the COVID-19 pandemic, resulting in the curtailment of field and laboratory activities. In response to these constraints, previous studies exhibited adaptability

by adopting online methodologies, including surveys, interviews, and virtual experiments, while concurrently increasing their utilization of pre-existing datasets and computational modeling techniques, such as machine learning. Consequently, a reduction in primary study publications occurred, accompanied by an increased reliance on literature synthesis through meta-analysis and bibliometric analysis. However, access to paid database resources remained a significant limitation for some Indonesian study teams, thereby impeding their productivity in conducting comprehensive seagrass studies.

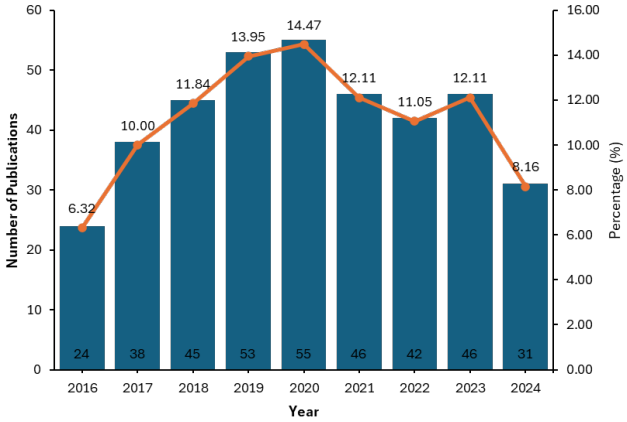

Figure 4. Indonesian seagrass publication in Google, PubMed, ScienceDirect, and Researchgate from 2016-2024.

Journals related to seagrass were evaluated using the number of published documents. From 2016 to 2024, there were 10 publishers related to seagrass (Figure 5). IOP Conference Series, namely Earth and Environmental Science was the conference proceeding with the highest percentage (10.79%) around 41 articles. Biodiversitas Journal of Biological Diversity was the journal that published the most seagrass studies (5.53%), around 21 articles, while the lowest was Jurnal Biologi Tropis (1.32%), around 5 articles. However, a reduction in the number of journals specifically dedicated to seagrass had been observed in 2024. This decline could be attributed to a confluence of factors, including limitations in study funding, evolving priorities, and challenges in fostering collaborative initiatives. Furthermore, local study teams often face impediments in publishing in reputable, Scopus-indexed journals, primarily due to language barriers and limitations in English scientific writing proficiency. As a result, there was a tendency to disseminate results through conference proceedings. These journals served as critical platforms to disseminate cutting-edge results and contributed to the advancement of scientific sustainability. Their role was paramount in promoting study collaboration, facilitating knowledge dissemination, and informing evidence-based policy formulation within the field of seagrass ecology and conservation.

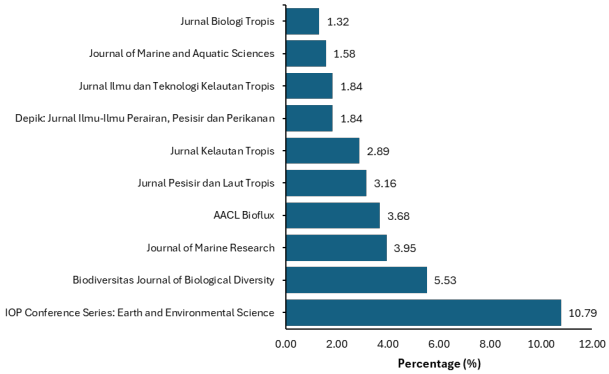

Figure 5. Percentage of documents of the top 10 journals in Indonesian seagrass study.

This study analyzed the collaboration network of authors. Nugraha, A.H. had the most documents, with 12 papers. Ambo-Rappe, R, was the second author with 9 papers, and Rahmawati, S, was the third author with 8 papers. These were authors with seagrass studies on several topics, such as morphometric, physiological, restoration, biomass, and carbon studies. Nugraha, A.H. from Raja Ali Haji Maritime University mapped seagrass (Putra *et al.*, 2023), evaluated morphometric characters and growth of seagrass seeds on different substrates (Nugraha *et al.*, 2021), and described seagrass as a marine debris trap (Nugraha *et al.*, 2024). Ambo-Rappe, R. from Makassar University conducted a study on seagrass restoration (Ambo-Rappe, 2022) and described seagrass management strategies in Indonesia (Rifai *et al.*, 2022; Sjafrie *et al.*, 2023; Salim *et al.*, 2024). Rahmawati, S. from the Oceanographic Study Center, National Study and Innovation Agency measured biomass and carbon stocks in seagrass (Rahmawati *et al.*, 2019; Nugraha *et al.*, 2020; Wahyudi *et al.*, 2020; Sakmiana *et al.*, 2023; Ambomasse *et al.*, 2024).

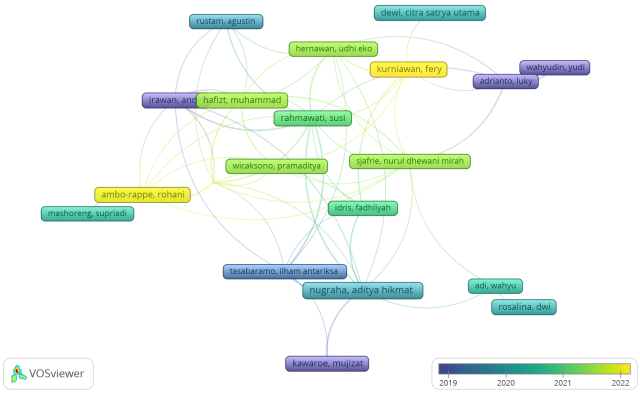

Figure 6. Author collaboration diagram.

Figure 6 showed the strength of the network among the authors using VOSviewer. The strongest collaborator was Rahmawati, S. This author closely related to Rustam, A., Irwan, A., Hernawan, UE., and Idris, F. The second collaborator was Nugraha, AH, who collaborated with Tasabarmo, IA., Kawaroe, M., Adi, W., Idris, F., and Sjafrie, NDM. This network showed a typical homogeneity, strongly collaborating with the same institution. The development of multi-institutional cooperation was very needed to strengthen the development of seagrass studies in the future. Furthermore, the limited extent of cross-agency collaboration in seagrass study could be attributed to a confluence of factors, using divergent institutional goals and priorities, communication limitations, equipment resource constraints, bureaucratic impediments, and a deficit of inter-institutional trust. Strategic interventions were required to foster improved collaborative initiatives. These included augmenting access to data and information repositories, securing increased funding allocations for collaborative projects, streamlining bureaucratic processes, and leveraging technological advancements and innovative methodologies. Multi-institutions shared experiences, technological advances, and the strength of cooperation in Indonesia's seagrass projects for sustainable seagrass management.

A total of 28 most relevant terms were collected from the publication titles and abstracts. These terms were visualized for their co-occurrence network. Figure 7A showed 3 term clusters. Cluster I was Indonesia, area, seagrass, *Enhalus acoroides*, study, species, analysis, data, stakeholder, diversity, North Sulawesi, water, seagrass bed, and coastal water. Cluster II was seagrass ecosystem, carbon stock, site, case study, seagrass species, small island, community structure, *Enhalus acoroides*, seagrass ecosystem, and density. Cluster III included seagrass meadow, conservation, ecosystem, region, and potential. Based on the occurrence, the term "Indonesia" appeared the most, with 162 papers, the second was "seagrass," with 88 papers, and the third was "seagrass meadow", with 46 papers. Subsequently, the most relevant term was stakeholder with a value of 3.44, followed by case study (2.16) and community structure (1.95). In general, all of these terms were the most frequently occurring and relevant terms commonly used by authors for titles and abstracts.

Carbon stock, site, species, data, and stakeholders with yellow clusters appeared in the period 2023 to today. Terms with green clusters were analysis, study, area, seagrass ecosystem, diversity, ecosystem, conservation, region, potential, case study, seagrass species, and small island, appearing between 2021 and 2022. Blue terms appeared in the period before 2021. Global issues on climate change mitigation affected the amount of carbon stock study in seagrass (Sakmiana *et al.*, 2023; Stankovic *et al.*, 2023; Ambomasse *et al.*, 2024; Dewi *et al.*, 2024a; Dewi *et al.*, 2024b). Moreover, seagrass was part of the blue carbon ecosystem that absorbed more CO2 than terrestrial vegetation (Wahyudi *et al.*, 2020; Wahyudi *et al.*, 2022). Currently, seagrass carbon study developed rapidly in Indonesia.

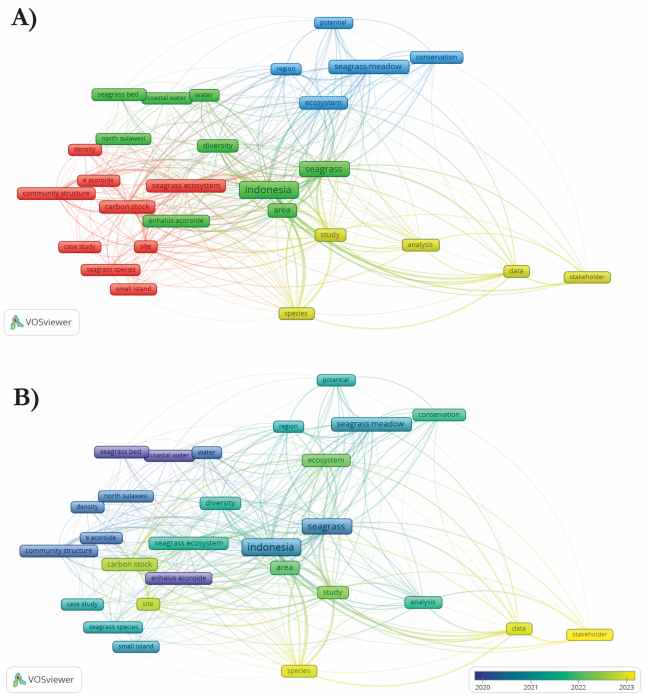

Figure 7. Co-occurrence network map based on title and abstract. (A) Diagram of title and abstract sharing. (B). Graph of co-occurrence title and abstract for time.

This study adopted and modified the grouping of seagrass study topic trends from Fortes *et al.* (2018). The highest trend was Biodiversity and Community Structure from 2016 to 2024, with 22.37% (Figure 8). The second was the Ecology and Environment topic, with 18.95%, while the third was Climate Change and Blue Carbon, with 13.68%. Genetics, tourism, and restoration were the least explored topics in seagrass study from 2016 to 2024. The limited focus on seagrass genetics was due to the high cost of molecular analysis and the lack of well-equipped laboratories. Meanwhile, seagrass tourism had gained attention because marine tourism in Indonesia tended to focus on coral reefs and mangroves. Seagrass restoration was often considered challenging due to environmental pressures such as

pollution and coastal development. To address these gaps, investments in genetic study infrastructure could stimulate further study in these areas. These also included the promotion of seagrass as an ecotourism asset (e.g., through dugong conservation), and the refinement of restoration techniques tailored to Indonesian coastal conditions. Seagrass genetic studies described the kinship and connectivity between populations in several regions (Hernawan *et al.*, 2017; Putra *et al.*, 2018; Hernawan *et al.*, 2023). Seagrass species discovery studies used genetics to confirm morphological character suspicion (Kurniawan *et al.*, 2020; Kurniawan *et al.*, 2024). The small number of publications on genetic studies of seagrass was influenced by laboratory equipment that had not been established and quite expensive materials. Seagrass studies had few enthusiasts because the issues were not as interesting as the topics of tourism and restoration. The problem with the topic of tourism was the absence of tourist attractions in seagrass. Tourists preferred recreational activities on coral reefs and mangroves. Seagrass restoration was considered impossible due to high environmental pressure in Indonesia. The best methods and seagrass species restoration were developed (Asriani *et al.*, 2018; Ambo-Rappe, 2022; Darus *et al.*, 2023; Rifai *et al.*, 2023). Therefore, seagrass restoration had a high opportunity to increase quantity and quality.

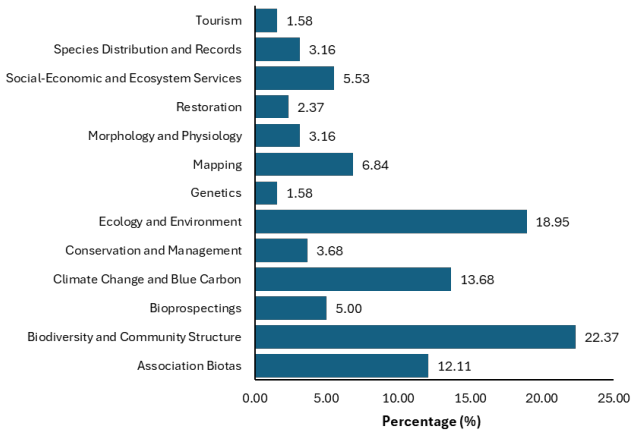

Figure 8. Trending study topic for the past 9 years in Indonesia.

The underrepresentation of seagrass topics presented an opportunity for further studies on *H. major*, a rediscovered species with significant ecological and evolutionary importance. Future study directions included (1) genetic analysis to understand the adaptive mechanisms of *H. major* across different habitats, (2) its role in seagrass restoration projects as a pioneer species, (3) its ecological function as a major food source for dugongs, and (4) the potential for seagrass-based ecotourism. Furthermore, due to the limited conservation policies targeting *H. major*, the establishment of seagrass nurseries and habitat protection initiatives must be explored to ensure its long-term sustainability.

As a pioneer and colonizing species, *H. major* adapted to the environment, which affected its genetic evolution (Kilminster *et al.*, 2008; Nguyen *et al.*, 2021b). In direct connectivity, *H. major*, as a member of the genus *Halophila*, became dugong food, which had the potential as a tourist attraction. The relationship between dugong, *H. major*, and tourism was an interesting topic to evaluate. Furthermore, with the limited distribution of *H. major* and the absence of species conservation policy, the development of *H. major* seagrass nurseries was a potential target. According to previous studies, the life cycle and phenology of *H. major* were studied to be described comprehensively. Other topics for the *H. major* in Figure 8 were very interesting, but collaboration was key to the sustainability of science in this seagrass field.

Conclusion

In conclusion, this study provided identification keys, distribution patterns, molecular evidence, and future study of *H. major*. The distribution of *H. major* suggested that it could also be present on the other islands within the same or a different ecoregion. Furthermore, field surveys showed other species from the complex genus *Halophila*. The integration of morphological and molecular approaches allowed for the continued rediscovery of new species in modern taxonomy. This study also contributed to identifying *H. major* in the field and showed opportunities in seagrass studies. Genetics, tourism, and restoration remained underrepresented, presenting opportunities for future studies, which must focus on underexplored topics. These included genetics, particularly in understanding species relationships, connectivity, gene expression, and genetic conservation. Furthermore, these areas posed challenges due to limited molecular data, the complexity of genetic differentiation, and the need for advanced sequencing technologies. Multi-institutional collaboration was crucial for advancing distribution studies, species exploration, and seagrass management. Such collaborations facilitated the sharing of expertise, and technological advancements, and coordinated policy development for sustainable seagrass conservation.

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