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Lack of local management and limited adaptive capacity are pushing the vulnerable seagrass (*Halophila beccarii* Aschers.) towards extinction across the Indo-Pacific

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Seagrass ecosystems worldwide are undergoing rapid decline due to intensifying anthropogenic pressures and climate change, leading to severe habitat degradation and species loss. Among these, *Halophila beccarii* Ashcers., a small intertidal seagrass species endemic to the Indo-Pacific, is particularly vulnerable. Despite its ecological importance in supporting biodiversity, sediment stabilization and carbon sequestration, the species remains understudied and its adaptive capacity (AC) to environmental change is poorly understood. Using published literature spanning 1977-2024, we systematically reviewed morphological, ecological, and genetic characteristics of *H. beccarii* across 14 countries in the Indo-Pacific bioregion. Following the current available AC framework, which considers species responses to environmental change through Persist in Place (PiP) or Shift in Space (SiS) pathways. Our synthesis revealed that *H. beccarii* exhibits generally low AC, with more than half of the assessed attributes indicating limited resilience. Although the species is reported from 13 Indo-Pacific countries, its area of occupancy is extremely restricted (312.7 ha) and populations occur as small, fragmented patches. Demographic observations from Malaysian population indicate an annual life cycle with rapid generational turnover and seasonal recruitment, suggesting short-term persistence potential. Additionally, limited dispersal ability, low genetic diversity, and narrow habitat specialization constrain large-scale range shifts. Overall, the adaptive profile of *H. beccarii* indicates a strategy dominated by PiP responses, supported by physiological tolerance and clonal growth, but limited capacity for spatial distribution. Country-specific conservation policies remain scare, with only Malaysia and the Philippines incorporating the species with national conservation and management frameworks. Without targeted conservation interventions, *H. beccarii* populations across the Indo-Pacific may experience irreversible declines. Our assessments highlight the urgent need to strengthen research on key adaptive traits, particularly population genetics, reproductive ecology and demography dynamics to refine vulnerability predictions and guide regionally coordinated conservation actions. Enhancing the AC of *H. beccarii* through integrated management, restoration and monitoring programs is critical to prevent further local extirpations and secure the resilience of Indo-Pacific seagrass ecosystems under accelerating environmental change.

KEYWORDS

climate change, conservation, costal management, *Halophila beccarii*, Indo-Pacific, resilience, seagrass, vulnerability assessment

1 Introduction

Seagrasses are foundational marine angiosperms that underpin the productivity and stability of coastal ecosystems. They provide key ecosystem services, including carbon sequestration, sediment stabilization, nutrient cycling, and habitat for diverse fauna, thereby sustaining coastal livelihoods and food security (McKenzie et al., 2021; Nordlund et al., 2016; Unsworth et al., 2018b). Despite their ecological and socioeconomic importance, global seagrass meadows are declining at an estimated rate of 7% per year with an estimated 5,602 km^2 (19.1% of surveyed meadow area) loss, primarily due to escalating anthropogenic pressures such as coastal development, eutrophication, and pollution (Bertelli et al., 2020; Dunic et al., 2021; Hastings et al., 2020; Mishra et al., 2025; Waycott et al., 2009). Such negative impacts of these stressors have been evidenced by 14% (n=15, 6 endangered and 9 vulnerable) of seagrass species currently being at risk of extinction, with members of the genus *Halophila* (i.e., *Halophila beccarii* Aschers., *Halophila baillonis*, *Halophila hawaiiana, Halophila engelmanni*, and *Halophila nipponica)* being among the most vulnerable (Dunic et al., 2021; Short et al., 2011; Turschwell et al., 2021).

Halophila beccarii, a small monoecious seagrass endemic to intertidal mudflats across the Indo-Pacific has undergone substantial habitat loss and population fragmentation (Mishra and Apte, 2021; Nguyen et al., 2021; Yu et al., 2020). Early records from India described stable estuarine populations, but subsequent assessments report meadow contraction due to coastal development, dredging, eutrophication, and sedimentation (Jagtap, 1991; Jiang et al., 2020; Thangaradjou et al., 2009). Remote sensing analyzes indicate loss and fragmentation in India and China, while estuarine instability affects Bangladesh populations of *H. beccarii* (Abu Hena et al., 2007; Umamaheswari et al., 2009). In the Philippines, possible local extirpation has been suggested (Liao and Geraldino, 2020). Additional stressors such as local pollution, reduced light availability and microplastics further compromise meadow stability (Huang et al., 2021; Premarathne et al., 2021). Additionally, this Indo-Pacific region, one of the most densely populated and economically dynamic globally, has witnessed extensive coastal alteration through reclamation, aquaculture, and urbanization [United National Department of Economic and Social Affairs, Population Division (UNDESPAD, 2022). Consequently, these modifications have led to loss and decline of *H. beccarii* meadows that are currently restricted to less than 2,000 km^2 globally and is listed as Vulnerable by the IUCN Red List (Short et al., 2011; IUCN, 2021).

In addition to direct human disturbance, *H. beccarii* is threatened by synergistic environmental changes such as eutrophication and biological invasions. Nutrient enrichment promotes macroalgal blooms (*Ulva intestinalis*, *Enteromorpha compressa*) that outcompete seagrasses for light and space, while the expansion of the invasive cordgrass *Spartina alterniflora* alters sediment biogeochemistry, leading to meadow degradation and local extinction (Cui et al., 2021; Mishra and Farooq, 2025, 2022; Su et al., 2020). The loss of *H. beccarii* meadows has implications beyond biodiversity decline, it also disrupts carbon sequestration and diminishes their role as nursery habitats and bioindicators of pollution (Geng et al., 2022; Luo et al., 2022; Mishra et al., 2025; Zhang et al., 2022).

Global climate change (e.g., ocean warming, sea-level rise, and extreme weather events) amplifies existing local stressors through multiple interacting mechanisms that constrain seagrass response to these changes (Mishra et al., 2025, 2019). Seagrass productivity and survival are strongly influenced by temperature and irradiance; many tropical species are projected to approach their upper thermal limits within the next century (Bennett et al., 2022; Marbà et al., 2022). While rising CO_2 levels may transiently enhance photosynthesis in carbon-limited systems, this benefit is often offset by thermal stress (e.g., ocean warming) and local stressor interactions (Collier et al., 2018; Ravaglioli et al., 2024). Ocean warming can also disrupt metabolic balance by increasing respiratory demand relative to photosynthetic carbon fixation, reducing growth and survival of seagrasses (Fang et al., 2020; Mishra et al., 2025). Sea-level rise and increased turbidity can reduce light availability in shallow habitats, limiting photosynthesis and sediment carbon dynamics (Jiang et al., 2020; Premarathne et al., 2021). Extreme weather events and coastal run-off can physically disturb seagrass meadows, enhance sediment instability, and increase nutrient inputs that favor macroalgae or invasive macrophytes growth, leading to competitive displacement (Huang et al., 2006; Jiang et al., 2020). Consequently, seagrass responses to climate drivers vary across spatial and temporal scales, governed by species-specific traits, population genetics, and phenotypic plasticity (Chefaoui et al., 2018; Mishra and Apte, 2021; Nguyen et al., 2021).

Understanding these mechanisms requires integrating the concept of Adaptive Capacity (AC), the intrinsic ability of a species or population to tolerate, adjust or recover from environmental change (IPCC, 2023; Thurman et al., 2020). Within climate vulnerability assessments, AC complements exposure and sensitivity metrics, providing a functional measure of resilience (Golladay et al., 2016; Thurman et al., 2020). The framework proposed by Thurman et al.

(2020) identifies 37 attributes across seven ecological complexes; distribution, movement, evolutionary potential, ecological role, abiotic niche, life history, and demography, capturing both the “Persist in Place (PiP)” and “Shift in Space (SiS)” adaptive pathways (See Supplementary Tables 1, 2). Evaluating these attributes for *H. beccarii* can elucidate how its biological and ecological traits influence persistence under accelerating climate and anthropogenic stressors.

Considering the accelerating habitat loss and limited knowledge of *H. beccarii’s* ecological and genetic diversity, this study aims to assess its “adaptive capacity (AC)” across the Indo-Pacific. Specifically, we identify key knowledge gaps in phenotypic plasticity, reproductive ecology, population dynamics, and conservation management. This synthesis provides a foundation for climate-smart strategies to enhance the long-term persistence and resilience of this vulnerable seagrass species.

2 Materials and methods

2.1 Literature search and data compilation

A systematic literature review was conducted to compile all available information the distribution, ecology and adaptive attributes of *H. beccarii* across the Indo-Pacific bioregion. Searches were performed using ‘Web of Science’, ‘SCOPUS’ and ‘Google Scholar’ up to December 2024, employing combination of keywords related to the species identify and ecological traits: (“seagrass” OR “*Halophila beccarii*”) AND (“distribution” OR “morphology” OR “reproductive features” or “ecology” OR “metals” OR “population dynamics” OR “carbon stocks” OR “anthropogenic disturbances” OR “extinction” OR “conservation” OR “management” OR “Asia”).

The search was restricted to Asia, where *H. beccarii* has been reported to be historically observed; India, Sri Lanka, Bangladesh, Brunei, Cambodia, Myanmar, Thailand, Singapore, Malaysia, Indonesia, Vietnam, Philippines, Hong Kong, and China (including Taiwan). The search included peer-reviewed journal articles including research and review articles only.

An initial pool of 225 publications was identified, which was screened for relevance and duplicates (Supplementary Table 3). Studies lacking species-specific data or quantitative ecological variables were excluded. The final dataset comprised of 112 studies that contained variables of our interest on *H. beccarii’s* distribution, phenotypic traits, reproductive ecology, molecular biology and associated environmental conditions (Supplementary Table 4). When a research article included more than one country, location or habitat type in their studies, each variable was then recorded separately for each country and counted as number of studies (frequency) throughout the review.

2.2 Data extraction and variable categorization

Data from the selected studies were systematically categorized by country and habitat type, including both monospecific and mixed assemblages with mangroves, saltmarshes, and macroalgae. The variables were classified under the following ecological themes: i) distribution and habitat characteristics (i.e., geographic coordinates, area of occupancy, and co-occurring species), ii) morphometrics (i.e., leaf length, width, petiole length and rhizome diameter, shoot density, above and below-ground biomass), iii) reproductive ecology (i.e., flowering period, fruiting, seed germination, reproductive mode (sexual vs asexual) and mating system, iv) molecular and genetic traits (i.e., genetic diversity indices, hybridization potential and molecular markers used) and v) environmental parameters (i.e., sediment type, depth range, salinity and temperature conditions). When studies encompassed multiple countries or habitats, data were separated and recorded independently for each case to ensure accurate geographic representation. All coordinates were converted to decimal degrees and mapped using ArcGIS PRO (ESRI) to visualize the current distribution of *H. beccarii*. When data were presented graphically, numerical values were extracted using Web Plot Digitizer (Ver. 2021).

2.3 Assessment of adaptive capacity

The Adaptive Capacity (AC) of *H. beccarii* was evaluated based on the framework proposed by Thurman et al. (2020) and Golladay et al. (2016), which assesses species resilience based on 37 ecological attributes grouped into seven themes i) distribution, ii) movement, iii) evolutionary potential, iv) ecological role, v) abiotic niche, vi) life history, and vii) population demography. These attributes collectively represent mechanisms through which species may either “Persist in Place (PiP)” through physiological tolerance or local adaptation or “Shift in Space (SiS)” through dispersal and migration (Supplementary Material S1).

Each attribute was assessed using information compiled from the literature review and assigned a qualitative AC score (Low, Moderate or High) following the evidence-based criteria summarized in Table 1. Specifically, High AC was assigned when multiple peer-reviewed studies reported consistent evidence supporting a strong adaptive trait or broad ecological tolerance (Supplementary Material S2). Moderate AC was assigned when information was limited to a single study, location-specific observation or when evidence suggested intermediate adaptive potential. Low AC was assigned when evidence indicated restricted ecological tolerance, limited dispersal ability, or when available studies reported inconsistent or conflicting findings. Attributes for which no information was available were classified as “Unknown” following the guidance of Thurman et al. (2020).

To improve consistency in scoring across attributes, all available references related to each adaptive trait were compiled and summarized (Supplementary Tables 2-S4). When multiple studies reported consistent ecological patterns, the AC score reflected the consensus interpretation of these findings. In cases where conflicting evidence existed among studies, the attribute was conservatively assigned a low AC category unless sufficient agreement supported higher classification. This approach ensured that the scoring reflected the strength and reliability of the available evidence rather than isolated observations.

In some cases, where a single study provided relevant information to multiple adaptive capacity attributes (e.g., physiological tolerance, reproductive traits or dispersal mechanisms) the findings

TABLE 1 Template of AC assessment and assigning values (low-moderate-high) for *H. beccarii* based on literature review.

Adaptive capacity attribute	AC assessment	Literature to support assessment	Evidence (based on which AC assessment is carried out)
Attribute	Low,	Citations	High= accepted consensus from peer reviewed literature (at least two publications in agreement) or general knowledge (e.g., taxonomically determined)
	Moderately low,		
	Moderate,		Moderate= one peer-reviewed publication (or information in support of assessment is location-or-context specific)
	Moderately high or		Low= expert best estimate/personal knowledge/opinion, unpublished data or discrepancies in available information
	High		**None=** unknown (data available and/or no best estimate) or high degree of variability/uncertainty in available information
	"NA" if not applicable		
	"Unknown" if information is unavailable and there is no best estimate		

The template is adopted from Thurman et al. (2020).

from that study were evaluated independently for each attribute and compared with other available literature describing similar ecological traits of *H. beccarii*. If multiple studies reported consistent ecological patterns across regions, the attribute was assigned a higher confidence AC score (High or Moderate). Conversely, when evidence was limited, location-specific or inconsistent among studies, the attribute was conservatively assigned a lower AC category. For example, the demographic attributes were not directly reported across the entire distribution range, therefore, information from detailed population studies was used to infer species-level characteristics. Observations from Malaysian populations describing life cycle stages, reproductive timing, and recruitment patterns were used to inform demographic attributes where comparable information from other regions was unavailable. The confidence of each AC score was determined by the consistency, geographic representation, and methodological robustness of the supporting literature, following the guidance of Thurman et al. (2020).

When direct information for a specific attribute of *H. beccarii* was unavailable, surrogate variables from ecologically analogous traits were applied following the guidance of Thurman et al. (2020). The final AC scores for each attribute were then integrated across the seven ecological themes to evaluate the overall adaptive strategy of the species and infer its relative likelihood of following PiP or SiS adaptive pathways.

2.4 Evaluation of conservation and management frameworks

Country-level policy frameworks and management initiatives related to *H. beccarii* were evaluated by reviewing national legislation, biodiversity conservation strategies, and seagrass-specific conservation plans. Each country was categorized as having either; i) species-specific protection measures, ii) broader ecosystem-based frameworks that include seagrass or iii) absence of formal policy. In addition, we identified the presence of national or regional monitoring programs and assessed their level of participation in international seagrass observation networks. This information was integrated to assess existing management gaps that may constrain AC enhancement for *H. beccarii* across the Indo-Pacific.

3 Results

3.1 Current distribution of *H. beccarii*

This review confirmed the presence of *H. beccarii* across 12 Indo-Pacific countries; India, Sri Lanka, Bangladesh, Myanmar, Thailand, Malaysia, Singapore, Vietnam, China (including Taiwan), Hong Kong, the Philippines and Brunei (Figure 1; Supplementary Material S5). Brunei represents a newly confirmed occurrence for this species; first time recorded in 2016. No verified geographical coordinates were available for reported populations in Cambodia or Indonesia (Vibol et al., 2010; Yasir and Moore, 2021).

Monospecific *H. beccarii* meadows occupy an estimated 312.7 ha across the Indo-Pacific region (Table 2), with largest documented areas in China (168.6 ha), Vietnam (80 ha) and Myanmar (39.3 ha). The vertical distribution extends from 0 to 1.7 m depth, varying with local tidal amplitude. Within this range, *H. beccarii* often co-occurs with 11 seagrass, 4 saltmarsh and 17 mangrove species in mixed intertidal assemblages (Supplementary Material S6). These data confirm a broad geographic extent of occurrence (EOO> 20,00,000 ha) but a restricted area of occupancy (AOO ≈ 317 ha), emphasizing the species fragmented distribution and vulnerability to local habitat loss.

3.2 Phenotypic and reproductive traits

Available data reveal limited intra- and inter-population variation in the phenotypic traits of *H. beccarii*. Morphological information is primarily reported from populations in India, Bangladesh, China, Brunei, Thailand, and Myanmar (Table 3). The number of

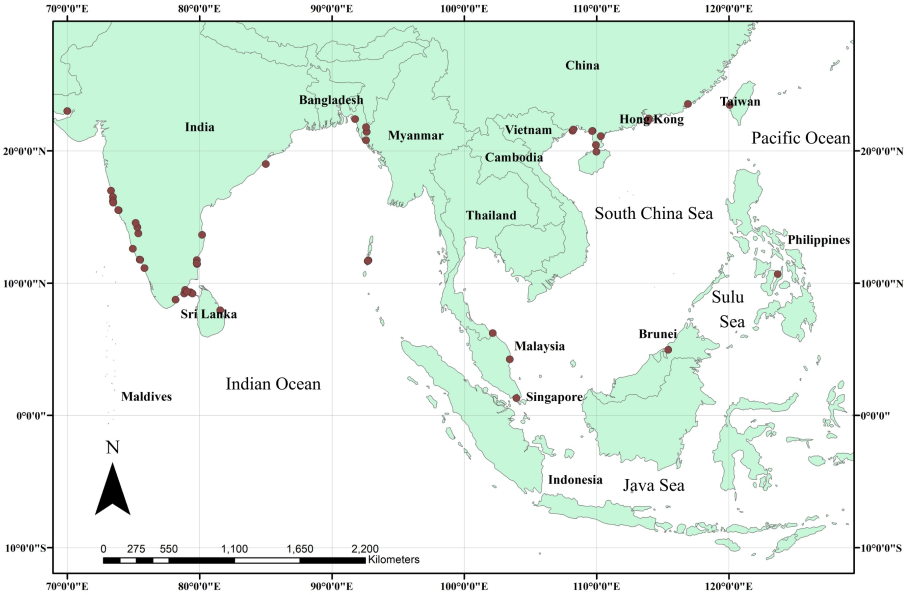

FIGURE 1
Map showing the distribution of *H. beccarii* in various countries across Asia derived through presence of geographical coordinates from literature review (See Supplementary Material S9).

leaves per shoot typically ranges between 4-8, with Brunei and Myanmar populations exhibiting higher leaf counts (4-10), but shorter leaf lengths (0.55-0.8 cm), suggesting a potential trade-off between leaf size and number. Shoot densities are highest in China (9427.07 ± 1733.61 shoots m^{-2}), followed by Bangladesh (2500 ± 76.8 shoots m^{-2}) and India (411.75± 63.15 shoots m^{-2}), consistent with greater habitat stability and productivity in these regions (Table 3).

Reproductive observations are geographically sparse, with data mainly from India and Malaysia (Supplementary Material S7). Field observations from Malaysian populations indicate that flowering and fruiting occur seasonally (February-April and August-September), with reproductive events concentrated during specific periods of the year. Seeds produced during these periods undergo a dormancy period of approximately two-three months prior to germination. In addition to sexual reproduction through flowering and seed production, vegetative propagation through rhizome extension and fragmentation contributes to meadow persistence. Such temporal plasticity may provide localized adaptive advantages but remains poorly quantified.

TABLE 2 **Area of occupancy (in hectares) derived from literature review for *H. beccarii* across its distribution limits.**

Sl.no	Country	Area (ha)	Status	Reference
1	India	14.46	Vulnerable	Abhijith et al., 2019; Jagtap, 1991; Kaladharan et al., 2011; Swapnali et al., 2022
2	Sri Lanka	1.50	Endangered	Udagedera et al., 2017
3	Bangladesh	6.84	Vulnerable	Alam and Hossain, 2020
4	Brunei	–	Vulnerable	Lamit et al., 2018
5	Vietnam	80.00	Vulnerable	Luong et al., 2014; Nguyen et al., 2021
6	Hong Kong	2.00	Vulnerable	Fong, 2022
7	Philippines	–	Extinct	Liao and Geraldino, 2020
8	China	168.57	Vulnerable	Jiang et al., 2017; Huang et al., 2006; Jiang et al., 2014; Huang et al., 2021; Lin et al., 2005; Premarathne et al., 2021
9	Myanmar	39.33	Vulnerable	Soe-Htun et al., 2001
10	Thailand		Vulnerable	Hiranphan et al., 2020
11	Malaysia	–	Vulnerable	Hossain et al., 2015
12	Singapore	–	Vulnerable	McKenzie et al., 2016
	Total	312.70		

The articles that mentioned the area individually for *H. beccarii* is mentioned here and the data from mixed meadows are not presented. The current status is kept Vulnerable as per the IUCN criterion 2010, if no local assessment is carried out. Present before but currently not available (Na).

TABLE 3 Range of morphometric variables of the seagrass *H. beccarii* across its distribution limit in various countries of Asia.

Variables	Countries						References
a. Morphometrics	India	Bangladesh	China	Brunei	Thailand	Myanmar	
No. of leaves per shoot	4.00–8.00	4.00–8.00	Na	4.00-10.00	Na	4.00–10.00	Aye and Hsan, 2014; Jagtap, 1977; Parthasarathy et al., 1988; Prabhakaran et al., 2021; Ramamurthy, 1981; Savurirajan et al., 2015; Swapnali Gole et al., 2022
Leaf length (cm)	1.60–2.91 (0.81± 0.20)	1.00–2.5	(0.87 -1.20)	0.50–0.80	1.50–4.80	0.55–0.75	Abu Hena et al., 2007; Edavilakathil, 2004; Hena et al., 2009; Htun, 2017; Jiang et al., 2020, 2017; Prabhakaran et al., 2021; Ramamurthy, 1981; Savurirajan et al., 2015
Leaf width (mm)	1.20–2.96	Na	(0.22± 0.02)	0.90–1.60	Na	1.25–2.50	Parthasarathy et al., 1988; Savurirajan et al., 2015; Edavilakathil, 2004; Savurirajan et al., 2015; Aye and Hsan, 2014; Htun, 2017; Jiang et al., 2017, 2020
Petiole length (mm)	7.94–13.92	(3.00 ± 0.21)	Na	4.00–15.00	Na	8.00–14.00	Jagtap, 1977; Ramamurthy, 1981; Edavilakathil, 2004; Savurirajan et al., 2015; Htun et al., 2017; Lamit et al., 2018
Internode length (mm)	6.40–20.04 (1.49 ± 0.24)	1.00-3.00	Na	Na	Na	1.05-2.05	Jagtap, 1977; Ramamurthy, 1981; Savurirajan et al., 2015; Swapnali et al., 2022; Prabhakaran et al., 2021; Aye and Hsan, 2014; Htun, 2017
Rhizome diameter (mm)	0.34–0.70	Na	Na	Na	Na	1.00 ± 0.10	Ramamurthy, 1981; Savurirajan et al., 2015; Aye and Hsan, 2014; Htun, 2017
Root length (cm)	0.92–3.50	Na	(1.98 ± 0.28)	Na	Na	Na	Savurirajan et al., 2015; Jiang et al., 2020
Shoot density (ind. m^{-2})	3529.00-15707.12 (411.75± 63.15)	2716–14320 (2500± 76.8)	(3465-18000-) (9427.07 ± 1733.61)	Na	Na	Na	Billah et al., 2016; Jiang et al., 2020, 2017
AGB (g DW m^{-2})	19.4–41.01	4.23–6.85 (12.67 ± 0.88)	(16.75 ± 4.81)	Na	Na	3.96–5.12	Abu-Hena et al., 2007; Billah et al., 2016; Jiang et al., 2017, 2020; Su et al., 2020; Mishra and Apte, 2021; Aye and Hsan, 2014
BGB (g DW m^{-2})	17.07–33.71	5.07–7.04 (17.33 ± 1.77)	(18.33 ± 6.58)	Na	Na	7.66–8.16	Abu-Hena et al., 2007; Billah et al., 2016; Jiang et al., 2017, 2020; Su et al., 2020; Mishra and Apte, 2021; Aye and Hsan, 2014
Total Biomass	Na	Na	Na	Na	0–204.80 (95.30)	Na	Angsupanich, 1996
b. Biochemical							
Protein (mg g^{-1})	0.70–393.12	Na	Na	Na	(1.70)	Na	Jagtap and Untawale, 1984; Pradheeba et al., 2011; Aye and Hsan, 2014
Carbohydrate (mg g^{-1})	2.93–476.18	Na	Na	Na	(3.80)	Na	Jagtap and Untawale, 1984; Pradheeba et al., 2011; Aye and Hsan, 2014
Lipid (mg g^{-1})	0.90–1.05	Na	Na	Na	(1.20)	Na	Jagtap and Untawale, 1984; Pradheeba et al., 2011; Aye and Hsan, 2014
Tanin (mg g^{-1})	1.03–1.35	Na	Na	Na	Na	Na	Jagtap and Untawale, 1984; Pradheeba et al., 2011; Aye and Hsan, 2014
Phenol (mg g^{-1})	2.1–3.75	Na	Na	Na	(3.20)	Na	Jagtap and Untawale, 1984; Pradheeba et al., 2011; Aye and Hsan, 2014
Organic carbon (%)	30.00	Na	33.00	Na	Na	Na	Jagtap and Untawale, 1984; Pradheeba et al., 2011; Su et al., 2020

Mean ± Standard deviation (SD) values are presented in brackets. Na, Not available; AGB, Above-ground biomass; BGB, Below-ground biomass.

3.3 Assessment of adaptive capacity

Of the 37 AC attributes proposed in the framework, empirical data were available for 30 (81%), while seven (19%) lacked sufficient data (Figure 2A). Among the assessed attributes, 43% were classified as low AC, highlighting limited resilience to environmental and anthropogenic stressors. Across the seven ecological themes, results revealed contrasting adaptive patterns that influence the species potential to Persist in Place (PiP) or Shift in Space (SiS) (Figure 2; Supplementary Material S2).

i. *Distribution*: Within the distribution theme, *H. beccarii* exhibits high AC for extent of occurrence (EOO>2000,000 ha) as the species is distributed across 13 Indo-Pacific countries. However, the area of occupancy (AOO) remains extremely limited, with mono-specific meadows covering approximately ≈ 317 ha, indicating low AC for geographic rarity (GR). Habitat suitability (HS) was also classified as low AC reflecting fragmented and patchy populations in shallow intertidal mudflats and estuarine environments. Similarly, commensalism with humans (CH) showed moderate AC, as some populations occur in human-modified coastal environments (Figure 2; Supplementary Material S2).

ii. *Movement*: Information for the movement theme was available for four of nine attributes that contributes towards assessing the "Shift in Space" of the population. Dispersal syndrome (DS) and migration distance (MDi) indicate high AC, reflecting the potential for vegetative fragments to disperse locally. However, seed dispersal distance (DD) and dispersal phase (DP) were assessed as low AC, as seeds are negatively buoyant constraining long-distance colonization (Figure 2; Supplementary Material S2) and the species ability to shift its distribution across larger spatial scales.

iii. *Abiotic niche*: The abiotic niche theme showed mixed responses. Physiological tolerance (PT) to salinity and desiccation was classified as high AC, reflecting the species adaptation to dynamic intertidal environments. Behavioral regulation of physiology (BRP) indicated moderate AC, suggesting some capacity for physiological adjustment under changing environmental conditions. In contrast, seasonal phenology (SP) and climatic niche breadth (CNB) were assessed as low AC, indicating sensitivity to environmental variability and a relatively narrow climatic niche (Figure 2; Supplementary Material S2). Field observations from Malaysian populations indicate that *H. beccarii* commonly occurs in shallow intertidal habitats (<1m depth), with muddy or muddy-sandy habitats and influenced by seasonal freshwater inputs.

iv. *Ecological role*: For the ecological role theme, information was available for only one attribute, Competitive ability (CA) with low AC. This indicates that *H. beccarii* has limited capacity to compete with larger seagrass species or opportunistic macroalgae or invasive species under eutrophic or disturbed conditions. Data on diversity of obligate species (DOS) and pollinator flexibility (PF) were not available (Figure 2; Supplementary Material S2).

v. *Life history*: Within the life history theme, several reproductive attributes showed low AC including reproductive phenology (RP), sex ratio (SR) and sex determination (SD), all of which appear strongly influenced by environmentally conditions such as changes in salinity and temperature., which also affects the sex ratio (SR; lower male to female ratios during seasonal changes) and sex

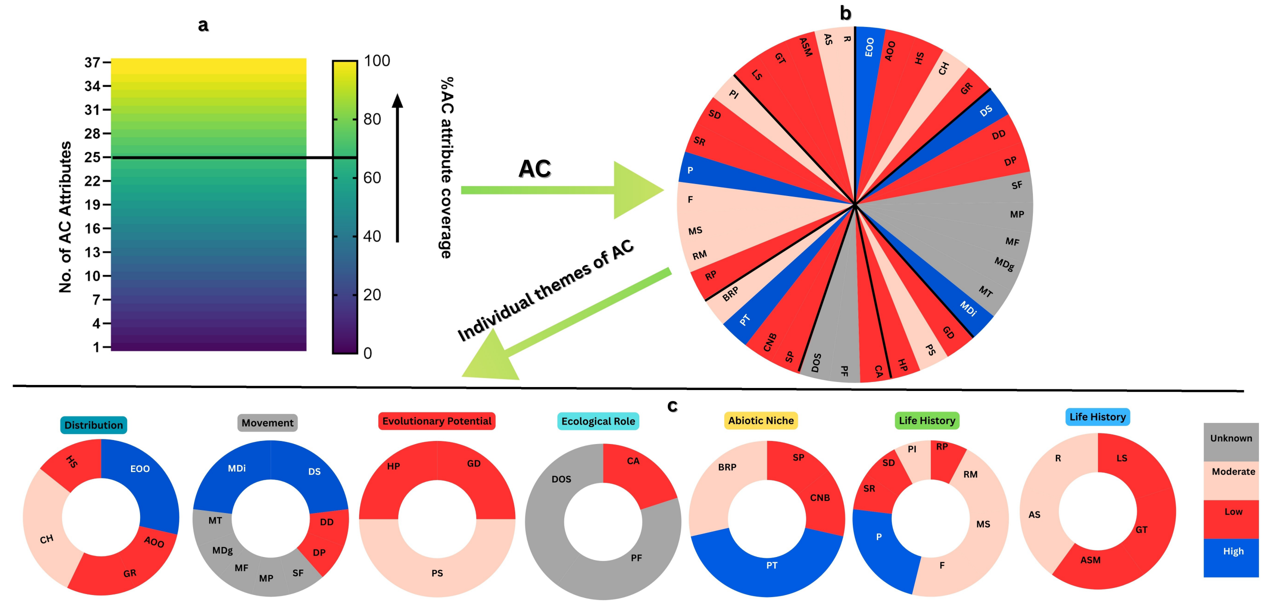

FIGURE 2
Assessment of adaptive capacity (AC) of *H. beccarii* across its distribution in Asia, where **(A)** represents the percentage coverage of known attributes of AC and the red line indicates the current known AC attributes **(B)** the AC wheel with combined 37 attributes and **(C)** the seven 'ecological themes and the individual attributes associated with these themes. Spokes in grey indicate attributes for which AC is unknown for *H. beccarii*, not applicable (NA) for this species. All attributes and their abbreviations are defined in Supplementary Material S6. EOO, Extent of Occurrence; AOO, Area of Occupancy; HS, Habitat Specialization; CH, Commensalism with Humans; GR, Geographic Rarity; DS, Dispersal Syndrome; DD, Dispersal Distance; DP, Dispersal Phase; MDi, Migration Distance; GD, Genetic Diversity; PS, Population Size; HP, Hybridization Potential; CA, Competitive Ability; SP, Seasonal Phenology; CNB, Climate Niche Breadth; PT, Physiological Tolerances; BRP, Behavior Regulation of Physiology; RP, Reproductive Phenology; RM, Reproductive Mode; MS, Mating System; F, Fecundity; P, Parity; SR, Sex Ratio; SD, Sex Determination; PI, Parental Investment.. (See Supplementary Material S2). Canva was used to generate the graphical image.

determination (SD). In contrast, reproductive mode (RM), mating system (MS) and fecundity (F) showed moderate AC, indicating limited capacity of *H. beccarii* for reproductive recovery (Figure 2; Supplementary Material S2). Parental investment (PI) was also assessed as moderate AC, as seeds exhibit a short dormancy period and develop into seedlings capable of early rhizome formation, while seed coat structures may enhance seed protection and establishment in sediments. Together, these life history traits indicate a limited but functional capacity of *H. beccarii* for reproductive recovery (Figure 2, Supplementary Material S2).

vi. *Population demography*: Empirical information was available for five attributes within the population demography theme, including life span (LS), generation time (GT), age of sexual maturity (ASM), age structure (AS) and recruitment (R). Demography information for *H. beccarii* populations indicates a short LS with a rapid turnover. Observations from Malaysian populations show that the species behaves as an annual seagrass, completing its life cycle within one year. Seed germination occurs following a dormancy period of approximately two to three months, contributing to seasonal recruitment of seedlings, juvenile shoots and flowering or fruiting plants (Figure 2; Supplementary Material S2). Density measurements reported for Malaysian populations demonstrate the occurrence of these different age classes within the same population, suggesting ongoing recruitment and seasonal cohort development, Table 3).

vii. *Evolutionary potential*: within the evolutionary potential theme, three attributes were evaluated: species genetic diversity (GD), hybridization potential (HP) and population size (PS). GD and HP showed low AC, reflecting limited genetic variability across populations and no current evidence of hybridization with other *Halophila* species (Figure 2; Supplementary Material S2). In contrast, PS was assessed as moderate AC, as some locations support relatively dense local populations despite their restricted spatial extent. Overall, the evolutionary potential of *H. beccarii* appears constrained by low genetic variability and fragmented population structure.

Overall, based on the available data from literature, it is quite evident that *H. beccarii* demonstrates greater potential to “Persist in Place (PiP)” through physiological tolerance and vegetative regeneration, while its ability to “Shift in Space (SiS)” remains limited due to depth restricted seed germination, low dispersal efficiency and low genetic connectivity across its Indo-Pacific distribution (Figure 2; Supplementary Material S2).

3.4 Current conservation and management practices

Among the 13 countries where *H. beccarii* occurs, nine possess general seagrass protection measures embedded with broader marine or coastal conservation policies (Figure 3). However, only the Philippines has implemented a species-specific conservation framework through the National Seagrass Conservation Strategy and Action Plan (Supplementary Material S8). Active national level monitoring programs are operational in China, Malayasia, and the Philippines, while Thailand and Sri Lanka contribute locally to regional or international monitoring networks. Other nations, including Brunei, and Singapore, lack targeted initiatives for this species. The absence of unified monitoring and species- specific management strategies across much of the Indo-Pacific bioregion underscores a major gap in the coordinated conservation of *H. beccarii* population and their adaptive potential under future climate scenarios.

4 Discussion

The adaptive capacity (AC) of *H. beccarii* represents its composite ability to tolerate, adjust and persist under dynamics environmental conditions. Our synthesis provides the first integrated evaluation of the AC of *H. beccarii* across its Indo-Pacific range, identifying which ecological traits support persistence within existing habitats “Persist in Place (PiP)” and which may enable migration or range shift “Shift in Space (SiS)”.

Drawing from the available literature review and the 37 attributes of the AC, the species displays a mixed adaptive strategy, combining a moderate physiological and reproductive plasticity with low dispersal and genetic variability. These findings align with Donelson et al. (2023) who emphasize that long-term persistence depends on maintaining “phenotype-environment fit”, that is the capacity of populations to express functional plasticity in pace with environmental change. Below, we interpret the adaptive capacity of *H. beccarii* through the lens of the four major global seagrass conservation challenges by Unsworth et al. (2018a), linking our literature review evidence to the relative likelihood of PiP or SiS responses.

4.1 Obtaining and maintaining information on status and conditions (challenge 2/6)

The ability of *H. beccarii* to persist in place relies on its capacity to adjust within existing microhabitats; however, limited demographic and trait-based data obscure this potential. 30 of 37 attributes were accessible, and most demographic traits such as life span (LS), recruitment (R) and age structure (AS) have data from single population (Supplementary Table 2). Populations across India, China and Vietnam exhibit local persistence despite fragmentation, suggesting stable PiP responses where habitat conditions are suitable.

Across the Indo-Pacific, *H. beccarii* exhibits a relatively large extent of occurrence (EOO> 20,00,000 ha) spanning at least 13 countries. This geographic breadth suggests high AC in terms of regional distributional potential. However, this apparent spatial range contrasts sharply with the extremely limited AOO (312.70 ha), indicating that populations are confined to small and fragmented intertidal habitats (Mishra and Apte, 2021; Nguyen et al., 2021; Huang et al., 2021). The distribution map of *H. beccarii* (Figure 1) further illustrates strong spatial clustering of populations along the coasts of India, China, Vietnam and Myanmar, while several historically reported regions lack confirmed spatial records. Similar patchy distribution patterns have been reported across Southeast Asia, where *H. beccarii* often occurs in small monospecific patches or mixed intertidal assemblages associated with mangroves and saltmarshes (Huang et al., 2006; McKenzie et al.,

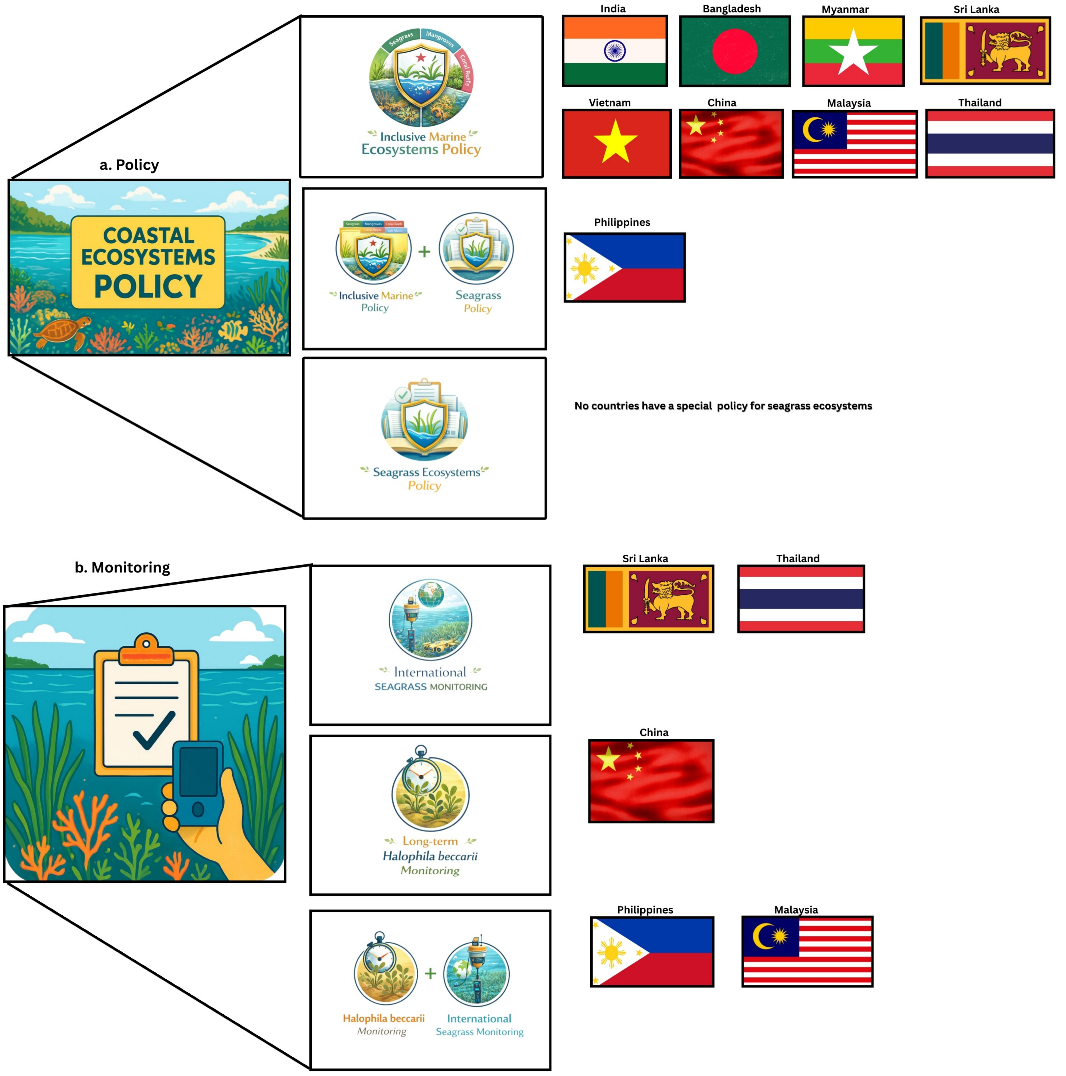

FIGURE 3
Policy **(a)** and monitoring **(b)** measures currently in place for better conservation and management of *H. beccarii* species across its distribution in Asia. Countries (i.e., Brunei, and Singapore) that have no existing policy or monitoring framework are excluded from the graph (See Supplementary Material S8). Canva was used to generate the graphical image.

2016; Nguyen et al., 2021). Such fragmented meadow structure increases vulnerability to localized disturbances and reduces connectivity among populations.

The restricted AOO therefore represents a major constraint on the AC of *H. beccarii*, despite its broad regional distribution. Habitat loss from coastal reclamation, aquaculture expansion and sediment alteration has contributed to the decline and fragmentation of many populations across Asia (Huang et al., 2006; Jiang et al., 2020; Mishra and Apte, 2021). In several areas, including the Philippines, local extirpations have already been documented (Lin et al., 2005; Liao and Geraldino, 2020), further emphasizing the vulnerability of small, isolated meadows.

Additional uncertainty in the regional distribution of *H. beccarii* arises from incomplete spatial records. Although historical reports suggest the presence of species in Cambodia and Indonesia, no verified geographic coordinates were available from the published literature (Vibol et al., 2010; Yasir and Moore, 2021). The absence of spatially explicit records limits the ability to accurately evaluate population status in these regions and highlights a key knowledge gap in the current assessment of AC. Improving standardized monitoring and georeferenced surveys across the Indo-Pacific will therefore be essential to refine estimates of habitat availability and detect early signals of population decline. Taken together, these patterns indicate the species' persistence across the Indo-Pacific is likely to depend largely on localized PiP responses with remaining suitable habitats rather than large-scale SiS redistribution.

Beyond distribution patterns, several additional AC attributes influence the status and persistence potential of *H. beccarii*. Within the abiotic niche theme, the species demonstrates relatively high physiological tolerance (PT) to intertidal stressors, including air exposure, low light and broad salinity fluctuations (Fakhrulddin, 2013; Fang et al., 2020; Premarathne et al., 2021). Such tolerance may increase adaptive plasticity through changes in physiological and morphological traits of *H. beccarii* and allow localized PiP, if environmental conditions will remain within tolerance limits. However, this capacity is constrained by a narrow climatic niche breadth (CNB) and strong habitat specialization (HS), as *H. beccarii* typically occupies shallow intertidal mudflats and sheltered estuarine environments (Geng et al., 2022; Huang et al., 2006). Therefore, changes in sediment composition, turbidity, light penetration or hydrodynamic regimes may therefore rapidly reduce HS.

Similarly, attributes associated with life history themes indicate moderate AC through a combination of sexual reproduction and clonal expansion (Parthasarathy et al., 1988; Zakaria et al., 1999). While seasonal flowering and fruiting cycles have been reported across several populations, reproductive output appears highly sensitive to environmental conditions, which may limit successful recruitment under disturbed habitats. The moderate parental investment (PI) observed in *H. beccarii*, including seed dormancy and structural adaptation of the seed coat, likely contributes to successful seedling establishment and short-term population persistence in dynamic intertidal habitats. In contrast, vegetative growth through rhizome expansion provides a mechanism for short-term persistence and local meadow recovery.

Recent, population demographic observations provide important insights into the population dynamics of *H. beccarii* (Figure 2; Supplementary Material S2). Within the AC framework, these demographic characteristics indicate moderate AC for life span (LS) and generation time (GT), as rapid recruitment and short generation time may enable population to recover quickly following localized disturbance. However, the annual life cycle also implies strong dependence on successful seasonal recruitment, making populations vulnerable to environmental disruptions that affect seed production or seedling establishment.

Taken together, the combined evidence from the distribution, abiotic niche, life history and demographic themes indicates that the AC of *H. beccarii* is primarily expressed through PiP mechanisms, where populations survive within localized habitats through physiological tolerance and clonal regeneration than through large-scale redistribution.

Many of the anthropogenic stressors identified in the introduction, including coastal development, eutrophication, and sediment alteration, ultimately will influence the distribution and habitat availability of *H. beccarii*, highlighting how environmental pressures interact with AC attributes such as GR, HS and AOO to constrain long-term persistence.

4.2 Identifying threatening activities at local scales to better target management action (challenge 3/6)

The movement theme highlights significant constraints on the AC of *H. beccarii* to shift its distribution in response to environmental change. Vegetative fragment dispersal (the “one-jump” migration described by Mishra and Apte, 2021) offers rare SiS potential but remains local (<1 km). However, seed dispersal (SD <5m) distances are generally limited and seeds are negatively buoyant, restricting long-distance migration (MDi) (Phan et al., 2017; Savurirajan et al., 2015). Consequently, natural recolonization of degraded habitats is likely to occur only over short spatial scales.

These dispersal limitations are further exacerbated by coastal habitat fragmentation driven by aquaculture expansion, land reclamation, and sediment alteration across many parts of Asia (Huang et al., 2006; Jiang et al., 2020). As suitable habitats become increasingly isolated, the ability of populations to migrate or recolonize new areas declines. As a result, the movement attributes of *H. beccarii* indicate low AC for SiS responses. Thus, while the species can regenerate and persist through clonal expansion, its capacity to shift spatially is negligible. Adaptive management should enhance PiP resilience by reducing chronic stressors that erode plasticity and maintaining intact intertidal corridors that support limited SiS. These interventions aim to preserve local phenotype-environment by sustaining the environmental window in which *H. beccarii* plastic acclimation remains effective to these changes (Donelson et al., 2023).

Local anthropogenic pressures such as aquaculture expansion, dredging, and land reclamation therefore will not only degrade habitat quality but also reduce connectivity among intertidal habitats, further limiting dispersal-related AC attributes and restricting the species ability to shift spatially in response to environmental change.

4.3 Generating scientific research to support conservation actions (challenge 5/6)

The AC of *H. beccarii* is severely under researched, particularly in its evolutionary and life-history theme. While moderate AC was observed for reproductive mode (RM) and fecundity (F), reproductive success (RS) is episodic and environmentally constrained; flowering occurs mainly in dry seasons and ceases during monsoons (Jiang et al., 2014; Zakaria et al., 1999). These limits sustained recruitment and restricted the potential for colonization (CS). Genetic studies reveal low levels of genetic diversity across several populations in the Indo-Pacific (Jiang et al., 2014; Nguyen et al., 2021). Reduced genetic variation may limit the ability of populations for adaptive evolution, particularly under increasing climate stress. These knowledge gaps limit our ability to fully evaluate key AC attributes such as genetic diversity, reproductive success, and demographic stability, which are critical for understanding whether *H. beccarii* populations can adapt to increasing environmental stressors.

However, recent molecular studies provide emerging evidence of genomic resources that may support adaptive responses in *H. beccarii* (Chen et al., 2024; Chen and Qiu, 2022). Transcriptomic analyzes have identified thousands of transcripts associated with metabolic processes, transcriptional regulation, and environmental stress responses, including transcription factor families such as MYB and NF-Y that are known to regulate plant responses to abiotic stress. These molecular datasets also reveal candidate genes involved in photosynthesis, energy metabolism, and stress tolerance pathways. Together, these findings suggest that although population-level genetic diversity may be relatively low, the species possesses molecular regulatory mechanisms that could contribute to physiological plasticity and short-term adaptation to changing environmental conditions.

Restricted dispersal among fragmented habitats may further constrain gene flow and reduce opportunities for adaptive recombination. However, Donelson et al. (2023) emphasize that *H.*

beccarii plasticity can serve as a first line of defense while genetic adaption catches up. The species' high AC in physiological tolerance (PT) offers a buffer against near term stress, yet research gaps prevent quantifying whether such plasticity is heritable or transient. Advancing research on the AC of *H. beccarii*, such as reciprocal transplant and transgenerational studies would reveal whether tolerant populations (e.g., in China and Brunei) represent genetic adaptation or phenotypic acclimation. Integrating AC metrics into restoration and conservation trials could transform *H. beccarii* from a data deficient species to a model adaptive seagrass management.

Consequently, evolutionary processes may contribute to maintaining localized persistence, but they are unlikely to facilitate significant SiS responses without external management interventions such as assisted restoration or habitat connectivity enhancement.

4.4 Conservation action in an era of climate change (challenge 6/6)

Attributes associated with the ecological role theme further illustrate the vulnerability of *H. beccarii* within changing coastal seascape and climate change scenarios. Although seagrass meadows provide important ecosystem services including sediment stabilization, carbon sequestration, and habitat provision (Nordlund et al., 2016; Su et al., 2020), *H. beccarii* itself has relatively low competitive ability (CA) compared with larger seagrass species and opportunistic macroalgae. In nutrient-enriched or disturbed environments, fast growing macroalgae and invasive plants such as *Spartina alterniflora* may rapidly dominate available substrate, reduce light availability and limit seagrass establishment (Huang et al., 2006; Premarathne et al., 2021). These competitive interactions further restrict the potential for *H. beccarii* to colonize new habitats, thereby constraining its ability to shift distribution ranges under environmental and climate change.

Consequently, climate change is likely to drive a gradual shift from PiP dominated persistence to SiS mediated range reconfiguration. Despite high AC in physiological tolerance (PT) and behavioral regulation of physiology (BRP), *H. beccarii* has low AC in climate niche breadth (CNB) and reproductive phenology (RP) (Jagtap, 1996; Prabhakaran et al., 2021), limiting long-term persistence in its current intertidal range. Sea level rise and warming will likely submerge, or desiccate existing meadows faster than populations can acclimate. Under Donelson's "phenotypic fit" model, this represents a mismatch: plasticity may maintain fitness under moderate warming but may fail under rapid or extreme events. As such, the species may depend increasingly on short-distance dispersal via fragments and assisted colonization to occupy emergent microhabitats, an anthropogenically facilitated SiS pathway. Climate driven stressors such as ocean warming, sea level rise, and increased turbidity therefore interact with multiple AC themes including abiotic niche tolerance, reproductive phenology, and ecological competitiveness ultimately determining whether populations persist locally or require spatial distribution.

Proactive conservation should integrate PiP and SiS strategies to protect thermally stable refugia (e.g., estuarine mangrove-seagrass mosaics) to sustain PiP potential. Furthermore, use of stress tolerant donor populations for restoration and translocation to new sites and finally incorporate AC and plasticity indicators (e.g., PT, BRP) into vulnerability mapping to forecast future SiS corridors.

5 Conclusions

The AC profile of *H. beccarii* reveals a predominantly "Persistent in Place (PiP)"-oriented strategy supported by short-term physiological plasticity and clonal regeneration, yet constrained by poor dispersal, limited genetic diversity, and narrow niche breadth. This imbalance renders the species demographic capability of enduring localized environmental change but highly vulnerable to large-scale habitat shifts. Enhancing resilience will require dual investment; i) reinforcing "PiP" mechanisms through habitat protection, pollution control and genetic monitoring to maintain current population cores and ii) facilitating "SiS" mechanisms through assisted migration, habitat restoration, and conservation corridors to expand the species adaptive frontier.

By explicitly linking AC attributes to PiP and SiS responses, this study provides a functional roadmap to climate-smart management of *H. beccarii*. Conservation strategies should view AC not as a fixed property but as a continuum one that can be strengthened through informed research, management, and restoration to secure the long-term survival of this vulnerable seagrass across the Indo-Pacific.

Author contributions

AM: Visualization, Validation, Conceptualization, Resources, Project administration, Formal analysis, Methodology, Writing – review & editing, Data curation, Investigation, Writing – original draft, Supervision, Software, Funding acquisition. CL: Methodology, Writing – review & editing, Data curation, Resources, Formal analysis, Validation. CP: Validation, Data curation, Writing – review & editing, Methodology, Formal analysis, Visualization, Resources. FD-G: Resources, Formal Analysis, Validation, Methodology, Writing – review & editing, Data curation. MF: Methodology, Data curation, Investigation, Writing – review & editing, Formal analysis, Validation, Resources, Visualization. MH: Methodology, Validation, Data curation, Investigation, Writing – review & editing, Resources, Formal analysis. JG-E: Conceptualization, Investigation, Writing – review & editing, Funding acquisition, Supervision, Formal analysis, Data curation, Resources, Methodology, Visualization.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2026.1734915/full#supplementary-material

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