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RESEARCH

Mangrove Community Structure Following Dieback Events in the Maldives: Special Emphasis on the Genus *Bruguiera*

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Abstract

Climate change is driving significant transformations in coastal and wetland ecosystems. A large-scale dieback event of *Bruguiera cylindrica* was observed in the northern islands of Maldives, attributed to extreme climatic conditions, sea level rise, and increasing salinity. This study investigates mangrove species distribution, structural composition, and zonation patterns across seven dieback-affected islands and one non-dieback (control) island, with a particular focus on the genus *Bruguiera*. A total of nine true mangrove species were identified, with Neykurendhoo and Kulhudhuffushi exhibiting the highest diversity, at six species each, while Keylakunnu recorded the lowest diversity, with three species. The structural analysis revealed significant variation in species dominance, with mangrove density ranging from 244 to 28,000 trees/ha and basal area from 17.8 to 13,361.4 m²/ha. Zonation patterns differed distinctly between basin and pond-based mangroves, influenced primarily by tidal amplitude and frequency. *Lumnitzera racemosa* was confined to low intertidal zones in pond-based mangroves, while high regeneration or migration towards the mid-intertidal/dieback zones was observed in basin mangroves. A detailed assessment of *B. hainesii* showed healthy populations on Kelaa Island but declining numbers on Kulhudhuffushi, emphasizing its vulnerability. Molecular analyses using CesA, UNK, and trnS-trnG gene sequences revealed haplotype diversity within the *Bruguiera* genus, suggesting potential hybridization and evolutionary adaptation in *B. hainesii.* These findings highlight the urgent need for in-situ and ex-situ conservation strategies like mass propagation of *B. hainesii*, legal protection of mangrove habitats, and the establishment of a nationwide ecological monitoring system, which are crucial for biodiversity, coastal resilience, and climate change mitigation.

Keywords Hybrid · Mangroves · Molecular markers · Climate change · Die-back

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Introduction

Mangroves, a vital component of tropical and subtropical coastal ecosystems, provide invaluable ecological, economic, and cultural services, including shoreline stabilization, carbon sequestration, and habitat for diverse marine and terrestrial species (Tomlinson 1986; Spalding et al. 2010; Polidoro et al. 2010). These unique ecosystems are characterized by woody vegetation featuring viviparous propagules, aerial roots, and remarkable salinity tolerance, exhibiting adaptations to their intertidal habitat. Classified as 'true mangroves', these ecosystems encompass 73 species and hybrids from 20 families, forming extensive mangrove forests in coastal regions across 124 countries and territories globally (Spalding et al. 2010; Bunting et al. 2018).

Despite the vital ecological functions they serve, as highlighted by Barbier et al. (2011), mangroves face threats from both land use changes and the impacts of climate change, as noted by Duke et al. (2022); Abhik et al. (2021); and Sippo et al. (2020). Over the past two decades, a declining trend in global mangrove coverage (accounting for up to 20 to 35%) was witnessed (Valiela et al. 2001; FAO 2007; Polidoro et al. 2010), posing a heightened risk of extinction for mangrove species. Mangrove ecosystems, despite extensive historical losses, are regarded as disturbance-adapted communities (Lugo et al. 1981), exhibiting remarkable resilience and adaptability. They can swiftly respond to sporadic extreme environmental events, including cyclones, flooding, and storm surges (Asbridge et al. 2018; Krauss and Osland 2020). Although these ecosystems may not always regain their original structural attributes, such as tree height and species composition, resilient mangrove forests often recover and establish a new stable ecological state. Over time, mangroves have shown exceptional adaptability, enduring substantial sea level variations throughout the Quaternary period, highlighting their resilience and ecological persistence (Woodroffe 1992). However, when environmental changes become exceptionally severe, rapid, widespread, or prolonged, mangroves may undergo significant structural and functional shifts (Blasco et al. 1996; Sakho et al. 2011).

The Maldives, a tropical archipelago in the Indian Ocean, hosts distinctive mangrove ecosystems that are both ecologically rich and highly vulnerable. Despite their ecological significance, these mangroves remain inadequately studied, particularly regarding species distribution, structural diversity, and responses to environmental stressors. Recent mangrove dieback events (large-scale decline or mortality of mangrove trees), particularly during the 2020-21 period, have significantly affected *Bruguiera cylindrica* in the region. This dieback has been linked to enhanced salinity levels exceeding 35 psu, driven by sea level rise and climate-related factors such as prolonged drought, a positive Indian Ocean Dipole, and the Triple La Niña phenomenon (Sreelekshmi et al. 2025). In contrast, species like *Lumnitzera racemosa*, *Avicennia marina*, *Rhizophora mucronata*, and *Pemphis acidula*, which share the dieback zones with *Bruguiera cylindrica*, demonstrate a greater tolerance to salinity levels around 35 psu (Su et al. 2011). These unusual dieback events raise concerns about the resilience of these ecosystems and the key factors influencing their recovery. Understanding the structural characteristics of these mangroves is crucial for assessing their productivity and carbon sequestration potential. Before initiating conservation and restoration efforts in dieback-affected islands, comprehensive floristic and biodiversity surveys are essential to evaluate species status, distribution, and zonation patterns (Sagar et al. 2003).

Bruguiera hainesii, a critically endangered hybrid mangrove species, adds another layer of complexity to the structural dynamics of Maldivian mangroves (Cerri et al. 2024; Dryden et al. 2020). This species is reported to possess a broad geographic range spanning Myanmar to Thailand across the Malay Archipelago to Papua New Guinea (Tomlinson 1986; Sheue et al. 2005). According to recent accounts, fewer than 300 mature individuals exist, rendering it one of the rarest mangrove species (Kochummen 1989; Sheue et al. 2005; Polidoro et al. 2010). According to genetic evidence presented by Ono et al. (2016), *Bruguiera hainesii* populations in Malaysia and Singapore are naturally occurring hybrids between *B. gymnorhiza* and *B. cylindrica*. This rare species, characterized by intermediate morphological traits and a limited distribution, serves as a vital indicator of mangrove health and genetic diversity (Pham et al. 2025). Therefore, understanding its ecological role, distribution, and structural attributes is crucial for conservation planning. To confirm the hybrid status of Maldivian populations of *B. hainesii* and ascertain whether the same parental species are involved, genetic analysis is necessary.

With this background, the objectives of the present study are (a) examine the structural composition and zonation patterns of mangroves in both dieback and non-dieback islands, (b) evaluate the current status of *Bruguiera hainesii* in the region,*(c)* sequence and assemble nuclear (CesA, UNK) and chloroplast (matK, rbcL, trnS-trnG) genes for *B. hainesii*, *B. cylindrica*, and *B. gymnorhiza* to clarify their species relationships in the Maldives, and (d) propose conservation strategies to protect this valuable ecosystem amidst widespread dieback of *Bruguiera cylindrica* on the islands.

Materials and Methods

Study Area

The Maldivian archipelago, located in the Indian Ocean approximately 650 km southwest of Sri Lanka and 480 km southwest of Cape Comorin, India, is renowned for its unique geographic characteristics (Fig. 1). Comprising 1,190 islands, the Maldives stands as a nation of low-lying landforms, with 80% of its territory situated below one

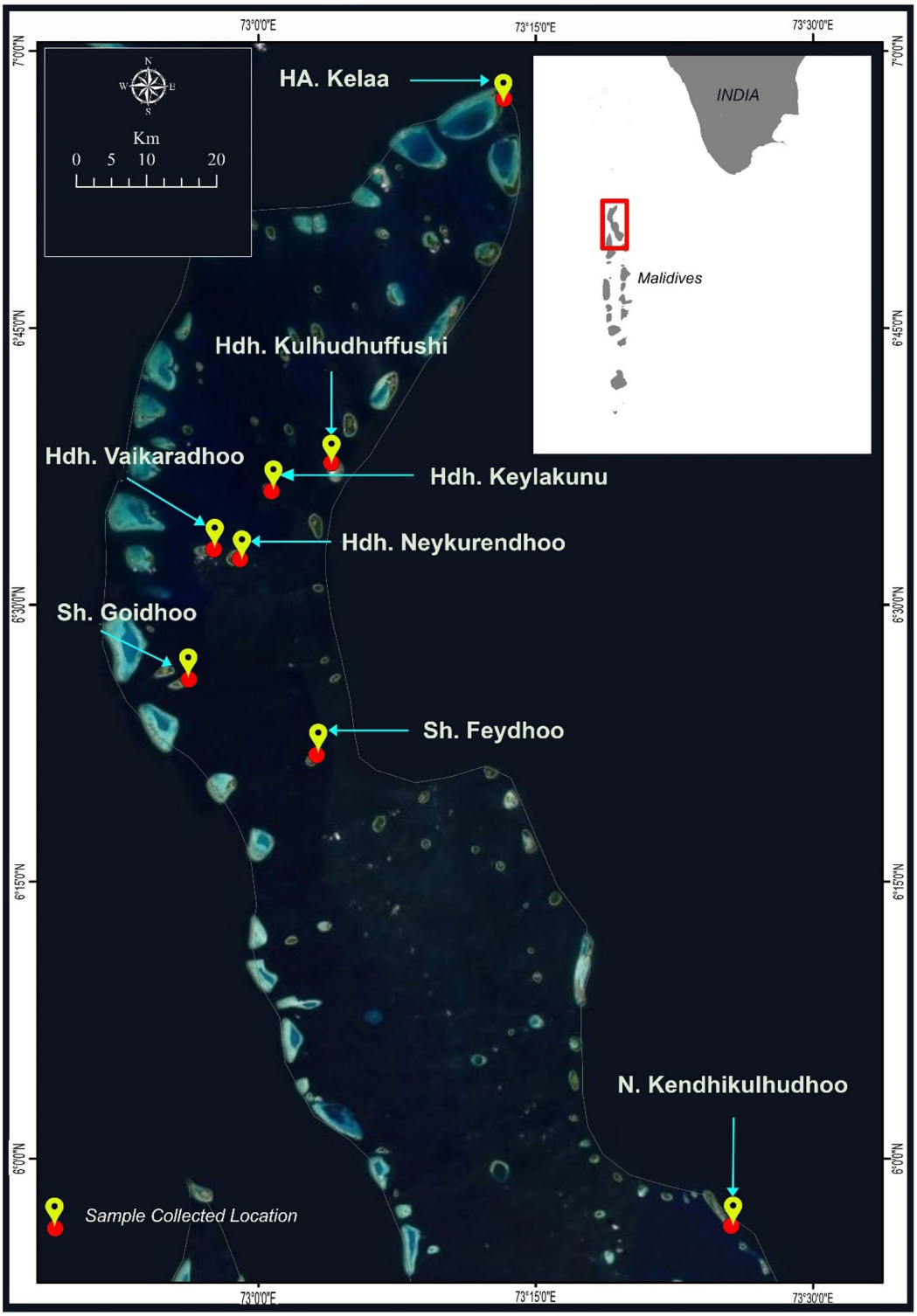

Fig. 1 Map of the Maldives showing the study islands

meter above sea level. Moreover, the majority of the islands cover an area smaller than five square kilometers (Wadey et al. 2017). This topographical layout exposes the nation to the risks of rising sea levels and heightened vulnerability to natural disasters and climate change impacts. The formation of the island reefs of the Maldives can be traced back at least 4,000 years through studies focused on atoll and island development (Perry et al. 2018).

The climate of the Maldives is categorized as a tropical monsoon climate. The southwest monsoon prevails from May to November, while the northeast monsoon occurs from January to March. The daily temperature fluctuates between 23 °C and 31 °C, and the humidity level ranges from 73 to 85% (MEEW 2007). Despite the relatively low population density in the Maldives, there exists ongoing environmental pressure on coastal ecosystems due to the combined effects of climate change and the improper disposal of waste in the ocean and along coastlines. The pressure from aquaculture, tourism, timber harvesting, and land reclamation also contributes to the decline in coastal biodiversity (Roy et al. 2017). Seven islands experiencing mangrove dieback and one control island (no mangrove dieback was observed) from the upper north province and Noonu atoll in the north province of the Maldives were selected for the present study. All these islands stand less than 1 m above sea level. The selection of study islands was facilitated by the Environmental Protection Agency of the Maldives, which gathered information from the local community regarding dieback occurrences. All islands reported to have experienced dieback were incorporated into this study.

Kelaa Island, in the northern Haa Alif Atoll, spans 202.5 ha with agricultural land to the south and east. **Neykurendhoo**, a large inhabited island in central Haa Dhaalu Atoll, covers 169.3 ha and has an inaccessible

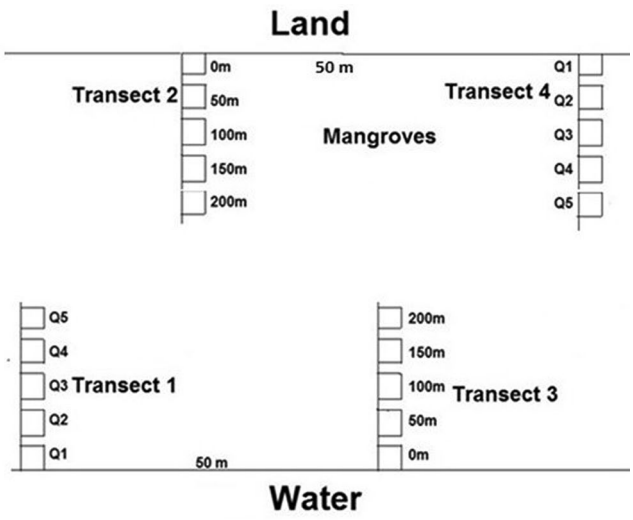

Fig. 2 Schematic diagram showing transect location and quadrats in the study sites

wetland area on its eastern side due to dense vegetation. **Keylakunu** is an uninhabited island (110 ha) in Haa Dhaalu Atoll, with a mangrove swamp formed by seawater seepage through coral rock and surrounded by dense forest. **Vaikaradhoo** is an inhabited island in Haa Dhaalu Atoll. **Feydhoo** (91.2 ha) and **Goidhoo** (99.5 ha) are inhabited islands in Shaviyani Atoll. **Kendhikulhudhoo**, a long, narrow island in Noonu Atoll, has a network of mangroves along its eastern side and is among the 10 largest islands in the Maldives. **Kulhudhuffushi**, (control island) the "Heart of the North" in Thiladhunmathi Atoll, is the Haa Dhaalu administrative center and features renowned mangroves that attract migratory birds, making it a biologically diverse ecosystem.

Field Sampling

Extensive floristic surveys were conducted on seven affected islands and one control island during wet and dry periods of 2020 and 2021 (March 2020, Dec 2020, March 2021, Dec 2021).

Mangrove Identification and Structural Analysis

Fixed-area plot measurement was employed to assess the structural characteristics of the mangrove vegetation on the islands, as proposed by Cintrón & Schaffer-Novelli (1984). Four transects perpendicular to the waterline were placed at 50 m intervals in each site, and five quadrats (10 × 10 m) were laid at 50 m intervals in each transect (Fig. 2). The criteria for choosing sites were extent of mangrove die-back, species diversity, and accessibility. Using standard keys, all mangrove species in the quadrat with a diameter larger than 10 cm were enumerated and identified (Tomlinson 1986). Each species' dbh (diameter at breast height) in the quadrats was measured using a measuring tape. Tree density, basal area, and species dominance (% basal area) were all calculated, as proposed by Cintrón and Schaffer-Novelli (1984).

Zonation Pattern

The zonation pattern of each mangrove species on each island was examined by plotting transects (5 m width) perpendicular to the waterline (from the waterline to the landward zone) to get clarity on the mangrove die-back (Lugo and Snedakar 1974).

Environmental Parameters

In situ measurements of sediment pH, redox potential (Eh), and temperature were carried out using a portable pH meter (Systronics), a redox meter (Systronics), and a thermometer,

respectively (AOAC, 2000). Porewater salinity was assessed on-site with a handheld refractometer (Atago S/Mill-E). Soil texture analysis followed the standard methodology described by Folk (1980). The Total Organic Carbon (TOC) content of sediment samples was quantified using an HT 1300 solid module TOC analyzer (Analytik Jena). For each parameter, triplicate samples were collected from every quadrat to ensure accuracy and consistency.

Morphological Investigations

Morphological details of the leaf, flower, and propagule of *Bruguiera* species were photographed in situ (Cooper et al. 2016).

Sample Collection

Samples of *B. gymnorhiza*, *B. cylindrica*, and *B. hainesii* were collected from Kelaa and Kulhudhufushi islands in the Maldives (Fig. 1). Young leaves were collected from single individual plants representing each species, promptly frozen with liquid nitrogen, and used for DNA extraction (Ono et al. 2016).

Genotyping

Total genomic DNA was isolated from dried leaves (homogenized and powdered using liquid nitrogen) of collected specimens using the NucleoSpin® Plant II Kit (Macherey-Nagel) protocol. Quantification of DNA extracts was performed using a UV spectrophotometer (NanoDrop 2000), and optical density (ratio of absorbance between 260 and 280 nm) was measured to screen good quality DNA extracts (with values between 1.7 and 2.0: data not provided). Targeted gene sequences were amplified from total genomic DNA using a Sigma-Aldrich ReadyMix™ Taq PCR Reaction Mix with $MgCl_2$ using GeneAmp PCR System 9700, Applied Biosystems. Primer pairs and thermal profiles were adopted according to Ono et al. (2024) for amplifying the abovementioned genes (as given in Table S1). Amplicons showing intense bands on a 1.2% agarose gel after electrophoresis were purified using ExoSAP-IT (GE Healthcare). For conducting Sanger sequencing reactions, GeneAmp PCR System 9700, Applied Biosystems, and BigDye Terminator v3.1 Cycle sequencing Kit (Applied Biosystems, USA) were utilized. After post-sequencing PCR clean up, products were sequenced in an ABI 3500 DNA Analyzer (Applied Biosystems).

Nucleotide Sequence Analyses

Quality of nucleotide sequences was checked using Sequence Scanner Software v1 (Applied Biosystems). BioEdit 7.0.9 (Hall 1999) software was used for editing and compilation of gene sequences. Alignment of these sequences was performed with Clustal X (Thompson et al. 1997) followed by their primary screening and comparison with the National Center for Biotechnology Information (NCBI) database based on Basic Local Alignment Search Tool (BLASTn) annotations. The same was also used for ensuring sequence homology (Deepak and Harikrishnan 2016). In Table S2, details regarding the nucleotide sequences submitted to NCBI are provided. Haplotype diversity pertaining to the species employed for this study, based on the sequenced genes, was generated using PopART (Population Analysis with Reticulate Trees) through the TCS network (Clement et al. 2002). Phylogenetic tree (Neighbour joining) and pairwise sequence distance data (Kimura 2-parameter model) were generated based on 1000 bootstraps using MEGA 5 (Tamura et al. 2011).

Statistical Analysis

Multiple regression analysis was performed using SPSS v16 to identify which environmental parameters (independent variables) significantly influenced mangrove structural attributes (dependent variables) across the study islands.

Results and Discussions

Mangrove Species Distribution and Structure

The study identified a total of nine true mangrove species, including *Bruguiera hainesii*, which is classified as "critically endangered" according to the IUCN Red List (Table 1), emphasizing the importance of conserving and protecting these unique ecosystems in the region. The species distribution across eight selected islands revealed that Neykurendhoo and Kulhudhuffushi (control island) had the highest number of species (6), while Keylakunu had the least number of species (3). The differences in species distribution among the islands indicate that various factors may be shaping mangrove communities in different locations (Van Nguyen et al. 2013; Whitmore 1990). Previous studies examining 19 islands across four atolls identified 12 mangrove species from seven genera (Jagtap and Untawala 1999; Saleem and Nileysha 2003). More recent assessments by Sivakumar et al. (2018) documented 15 mangrove species, while Cerri et al. (2024) reported 14 species in the Maldives.

Table 1 Species composition and structural attributes of true mangroves from selected Islands of Maldives

Island	Species	Mean Density (no. ha^{-1})	Mean Basal area (m^2ha^{-1})
Kelaa	*Bruguiera cylindrica* live	5440 ± 2540	2323.9 ± 1025.06
	Bruguiera gymnorhiza live	3760 ± 3015	3626.6 ± 2737.9
	Sonneratia caseolaris	933 ± 1007	2976 ± 2763.15
	Lumnitzera racemosa	6267 ± 3258	122.4 ± 400.44
	Bruguiera hainesii	400 ± 693	93.5 ± 161.99
	Bruguiera cylindrica dead	11,200 ± 7430	3145.7 ± 537.39
Neykurendhoo	*Bruguiera hainesii*	1333 ± 2309	553.4 ± 21.37
	Excoecaria agallocha	4667 ± 1058	2645.6 ± 610.28
	Bruguiera gymnorhiza	3333 ± 611	5193.5 ± 8995.41
	Pemphis acidula	2000 ± 3464	164.7 ± 285.27
	Lumnitzera racemosa	7333 ± 8083	167.2 ± 189.35
	Bruguiera cylindrica live	4533 ± 3107	6412.5 ± 4527.02
	Bruguiera cylindrica dead	10,267 ± 5774	6383.9 ± 5657.71
Kulhudhuffushi (Control)	*Lumnitzera racemosa*	28,000 ± 2000	3772.2 ± 1123.48
	Bruguiera gymnorhiza	1166 ± 833	552.8 ± 226.13
	Bruguiera hainesii	400 ± 231	435.8 ± 272.54
	Bruguiera cylindrica	667 ± 611	165.3 ± 195.40
	Rhizophora mucronata	244 ± 462	108.3 ± 187.64
	Sonneratia caseolaris	400 ± 320	747.6 ± 736.56
Keylakunu	*Avicennia marina*	800 ± 1386	1385.7 ± 2400.19
	Excoecaria agallocha	4400 ± 611	2568 ± 303.37
	Bruguiera cylindrica live	5866 ± 2838	6017.2 ± 2272.52
	Bruguiera cylindrica dead	5067 ± 2663	4933.3 ± 2854.15
Vaikaradhoo	*Lumnitzera racemosa*	2667 ± 4619	284.0 ± 491.9
	Bruguiera cylindrica live	2933 ± 3495	13361.4 ± 22440.5
	Pemphis acidula	933 ± 1617	214.5 ± 371.5
	Sonneratia caseolaris	400 ± 693	273.5 ± 473.8
	Bruguiera cylindrica dead	5333 ± 9238	604.9 ± 1047.7
Goidhoo	*Lumnitzera racemosa*	3067 ± 4619	110 ± 181.34
	Bruguiera cylindrica live	9067 ± 3946	4227.6 ± 3146.95
	Pemphis acidula	1200 ± 1848	375.2 ± 643.36
	Excoecaria agallocha	4533 ± 3464	2424.1 ± 1565.60
	Bruguiera cylindrica dead	3733 ± 6466	2018.8 ± 3496.69
Feydhoo	*Pemphis acidula*	267 ± 462	46.5 ± 80.63
	Lumnitzera racemosa	4933 ± 2838	314.1 ± 148.23
	Bruguiera cylindrica live	933 ± 833	351.8 ± 455.28
	Excoecaria agallocha	2000 ± 1744	948.0 ± 965.16
	Bruguiera cylindrica dead	6667 ± 2498	9555.1 ± 4160.41
Kendhikulhudhoo	*Rhizophora mucronata*	12,667 ± 4163	2196.3 ± 709.82
	Excoecaria agallocha	1867 ± 2013	1096.5 ± 1274.14
	Bruguiera cylindrica live	1733 ± 1058	1369.9 ± 1062.96
	Pemphis acidula	5333 ± 9238	386.3 ± 669.15
	Lumnitzera racemosa	400 ± 693	17.8 ± 30.79
	Bruguiera cylindrica dead	2000 ± 1800	1979.8 ± 1872.81

The structural analysis highlighted the dominance of certain species on different islands. *Bruguiera cylindrica* was found to be dominant on Keylakunnu (5866 ± 2838 $no.ha^{-1}$), Vaikaradhoo (2933 ± 3495 $no.ha^{-1}$), and Goidhoo (9067 ± 3946 $no.ha^{-1}$) islands while *Lumnitzera racemosa* dominated on Kulhudhuffushi, the control island (28000 ± 2000 $no.ha^{-1}$), Kelaa (6267 ± 3258 $no.ha^{-1}$), Neykurendhoo (7333 ± 8083 $no.ha^{-1}$), and Feydhoo (4933 ± 2838 $no.ha^{-1}$). The high dominance of *Lumnitzera racemosa* on affected islands like Kelaa, Neykurendhoo, and Feydhoo is attributed to its high regeneration in the die-back zones, evidenced by its high density and low basal area (Sreelekshmi et al. 2025). Further, the study found a total of 44,267 no ha^{-1} *B. cylindrica* trees to be dead on the seven affected islands. The significant number of dead *B. cylindrica* trees on the affected islands highlights the

vulnerability of the mangroves of the islands to some disturbances (Ward et al. 2016).

The mean density of the mangrove species in the study sites ranged from 244 to 28,000 trees ha^{-1} and the mean basal area was 17.8–13361.4 m^2 ha^{-1} (Table 1) which fell within the range reported in the tropics (Trettin et al. 2016; Sreelekshmi et al. 2017, 2020a, b; Satyanarayana et al. 2002; Das et al. 2014; Hinrichs et al. 2009).

Zonation and Succession Pattern

Most of the mangrove ecosystems in the Maldives islands are of fringing type, where mangroves fringe the banks of the lagoons or ponds/kulhi. However, basin mangroves were found in all of the islands chosen for the present study except for Kulhudhuffushi (control), where pond-based mangroves were observed and the zonation pattern of plants showed significant variation among these two mangrove systems. In basin mangroves, species like *Bruguiera cylindrica*, *B. gymnorhiza*, and *B. hainesii* were found to be restricted to the mid-intertidal region (100–200 m from the waterline), where die-back occurred. In this zone, it was also noticed that *Lumnitzera racemosa* was regenerating rapidly between the dead trees of *Bruguiera cylindrica* (mid intertidal zone). The high intertidal zone (beyond 150 m from the waterline), however, is where *Sonneratia caseolaris* and *Excoecaria agallocha* were found. While *Pemphis acidula* and *Rhizophora mucronata* were found in the low intertidal zone (up to 50 m from the waterline) as shown in Fig. 3a. While, the control island, Kulhudhuffushi, exhibited a different zonation pattern, like, *Rhizophora mucronata*, *Lumnitzera racemosa*, *Bruguiera hainesii* in the low intertidal zone, *B. cylindrica*, *Bruguiera gymnorhiza* in the mid intertidal zone and *Sonneratia caseolaris* in the high intertidal zone (Fig. 3b). Mangrove species respond differently to different tidal regimes (Saenger 2002). Further, the zonation pattern observed in the basin mangroves of the study islands also corroborates the classification suggested by Duke (1992), who described 4 categories of mangroves based on their habitat selection, i.e., intertidal position. These included mangroves preferring low-tide levels (*S. caseolaris* and *(A) officinalis*); low to mid-tide levels (*R. mucronata*); mid-tide levels (*B. cylindrica* and *R. apiculata*), and mid to high tide levels (*L. racemosa*, *(B) gymnorhiza*, *E. agallocha*).

Environmental Parameters

Sediment temperatures remained relatively high across all sites. The highest soil temperature (32 ± 0.49 °C) was recorded in Kelaa, while the lowest (28 ± 0.25 °C) was observed at Vaykaradhoo (Table 2). Soil pH levels varied among the islands, ranging from a maximum of 7.2 ± 0.21 in Feydhoo to a minimum of 6.1 ± 0.15 in Vaykaradhoo. Redox potential (Eh) measurements indicated more strongly reducing conditions across most islands, except Goidhoo, where higher Eh values were recorded—possibly due to lower organic matter content or higher sand composition. Porewater salinity levels in the dieback zones of all study islands, excluding the control site at Kulhudhuffushi, were comparable to seawater salinity. The highest salinity, 34.63 ± 0.38 psu, was observed in Kelaa, while Kulhudhuffushi, with its pond-type mangroves, showed significantly lower salinity levels, likely due to frequent tidal flushing and increased freshwater input (Prihantono et al. 2022). Organic carbon content varied among islands; the highest TOC was recorded at Kelaa (22.76 ± 1.63 g/kg), while the lowest was at Kulhudhufushi (12.14 ± 1.30/kg). All sampled soils exhibited a silty sand texture (Table 2), typical of tropical mangrove sediments (Sreelekshmi et al. 2020b).

Multiple regression analysis of the environmental parameters (independent variables) and structural variables (fixed factors) revealed that factors like sediment temperature, sand%, and salinity had a significant influence on the density (Table 3), whereas sediment pH, sand%, organic carbon, and salinity affect the basal area of mangroves ($p < 0.05$).

Current Status of *Bruguiera hainessii* in the Islands

Bruguiera hainesii C. G. Rogers (Fig. 4) was found in Kelaa (6.95671 N 73.22138 E) and Kulhudufushi (6.62739 N 73.066655 E) islands. On the eastern edge of the pond, located in the northern section of the wetland area on Kelaa Island, at least two individual trees were identified, while three trees were spotted on the western edge of the pond on Kulhudhufushi Island. Despite the presence of dead *Bruguiera cylindrica* and *B. gymnorhiza* species on Kelaa island, the trees of *Bruguiera hainesii* were found to be in good health. However, dying *B. hainesii* specimens were observed on the Kulhudhufushi islands.

Bruguiera, a genus of true mangroves within the Rhizophoraceae family, comprises five species and three natural hybrids (Shearman et al. 2022). These species have adapted to estuarine and sheltered coastal environments by developing roots capable of absorbing water and filtering out salt, a process known as ultrafiltration (Tomlinson 2016). Morphologically, *Bruguiera* species can be divided into two groups. The first group, including *Bruguiera exaristata*, *Bruguiera gymnorhiza*, *and Bruguiera sexangula*, features large leaves and large, solitary-flowered inflorescences. The second group, which includes *B. cylindrica and B. parviflora*, has smaller leaves and inflorescences with multiple flowers (Tomlinson 2016; Sheue et al. 2005). *Bruguiera hainesii* exhibits intermediate morphological traits, leading some to suggest it may be a hybrid species (Ono et al. 2016).

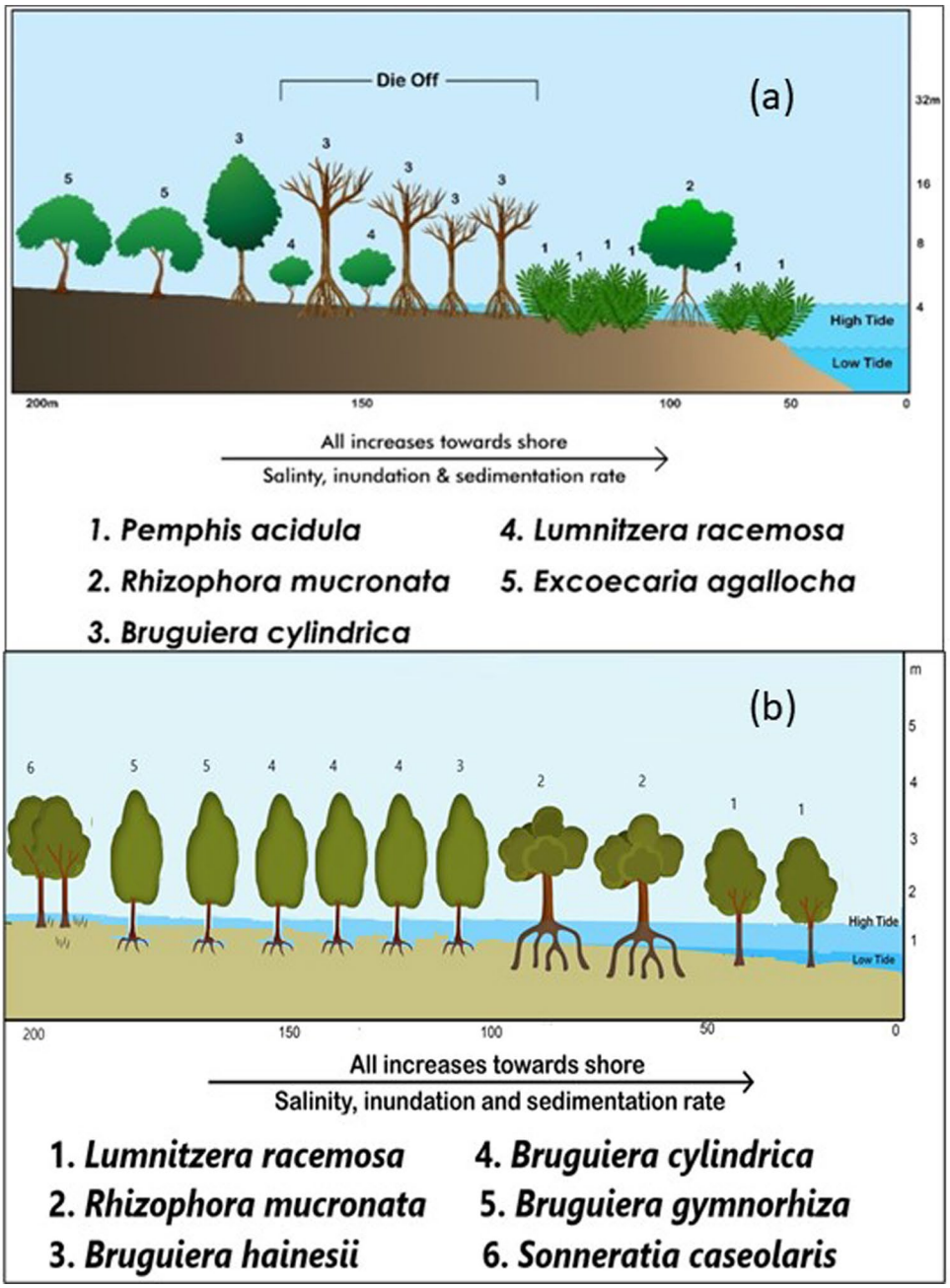

Fig. 3 (**a**) Zonation pattern of true mangrove species observed in the dieback islands (**b**) Zonation pattern of true mangrove species observed in the control islands

Table 2 Environmental parameters prevailed in the study Islands during the study period

Island	Sed Temperature (°C)	Sed pH	Sed Redox potential (mV)	Salinity (psu)	Sand%	Silt%	Clay%	OC(g/kg)
Kelaa	32±0.49	6.2±0.1	-3.49±1.63	34.63±0.38	89.43±2.25	5.55±0.70	5.02±1.73	22.76±1.63
Neykurendhoo	29±0.10	6.8±0.21	-6.6±1.35	34.2±0.25	93.39±2.07	4.65±0.58	1.96±1.56	14.93±1.35
Kelakunnu	31.2±0.15	6.5±0.35	-12.34±7.69	34.6±0.55	91.25±2.05	6.11±1.10	2.64±0.99	14.95±0.69
Vaykaradhoo	28±0.25	6.1±0.15	-20.7±8.52	34.15±0.35	90.53±1.12	4.69±0.34	4.78±0.83	20.57±1.52
Goidhoo	31.64±0.21	6.6±0.23	76±3.96	34.08±0.28	85.22±1.97	8.94±0.73	5.84±2.03	13.67±0.96
Feydhoo	28.07±0.42	7.2±0.21	-15.76±5.99	34.22±0.27	89.37±1.32	8.61±0.23	2.02±1.14	15.39±1.99
Kendhikulhudhoo	29.87±0.46	6.3±0.10	-2.13±5.02	34.13±0.23	85.11±4.36	8.12±1.08	6.77±3.28	15.43±1.02
Kulhudhufushi	31±0.50	6.2±0.15	-156.34±12.02	13.65±0.79	77.98±1.68	17.99±0.85	4.03±1.43	12.14±1.30

Table 3 Multiple regression analysis of environmental parameters influencing Mangrove structure in the study areas. (Density, $R^2 = 0.728$, basal area $R^2 = 0.702$, ∗=statistically significant at 0.05 level of significance)

Density			
Variables	**β**	**t**	***p*** value
Temperature	0.042	0.693	0.000*
pH	0.297	6.233	0.557
Redox potential	-0.032	-0.365	0.682
Sand%	0.121	0.923	0.005*
Silt%	0.204	3.615	0.399
Clay%	-0.060	-2.160	0.323
OC	0.352	2.490	0.121
Salinity	0.462	4.634	0.000*
Basal Area			
Variables	**β**	**t**	**p value**
Temperature	-0.62	-0.842	0.266
pH	0.416	6.709	0.000*
Redox Potential	-0.284	-2.265	0.233
Sand%	0.482	0.389	0.000*
Silt%	-0.529	-6.311	0.644
Clay%	0.011	0.221	0.550
OC	0.298	2.587	0.001*
Salinity	-0.187	-2.368	0.010*

This hybrid origin may partially account for the relatively low number of *B. hainesii* individuals found on Kelaa and Kulhudhufushi islands compared to other coexisting species. However, significant questions remain regarding the determination of hybrid status in *Bruguiera*, particularly since *B. hainesii* in the Maldives shows mature, seemingly viable viviparous propagules.

Haplotype Networks in *Bruguiera* Using Nuclear and Chloroplast Genes

CesA Gene (Cellulose Synthase)

Sequencing of the CesA gene yielded lengths of 594 bp for *Bruguiera hainesii*, 724 bp for *B. gymnorhiza*, and 714 bp for *B. cylindrica*. Combined sequences with other congeners revealed ten haplotypes (Fig. 5a) H1: Two individuals of *B. gymnorhiza* (LC076534-535), H2 & H3: Unique to *B. exaristata* (LC076539-540), H4 & H5: *B. sexangula* (LC076536-538), H6: Shared haplotype (six members) with four *B. hainesii* (LC076503, LC076505, LC076507, LC076511) and two *B. gymnorhiza* (LC076525, LC076527),

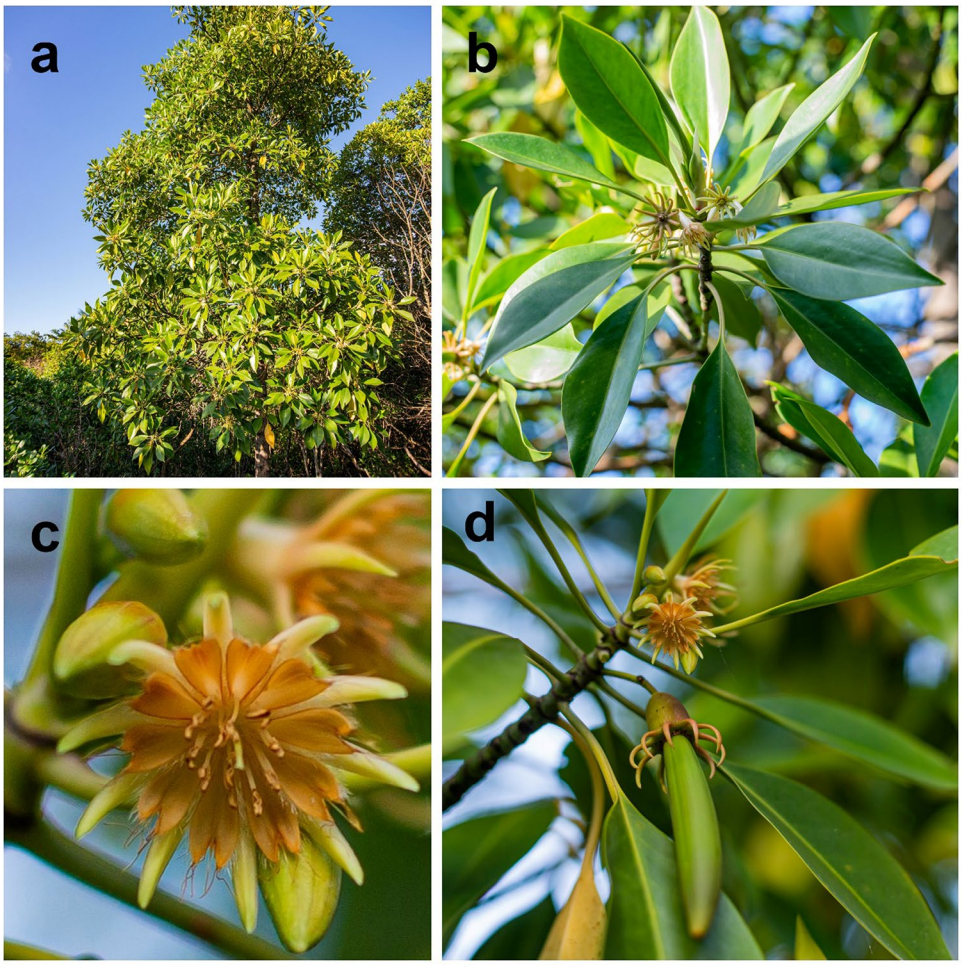

Fig. 4 (**a**) Habitat of *Bruguiera hainesii* in Maldives (**b**) Leaves with flowers (**c**) flower (**d**) propagule

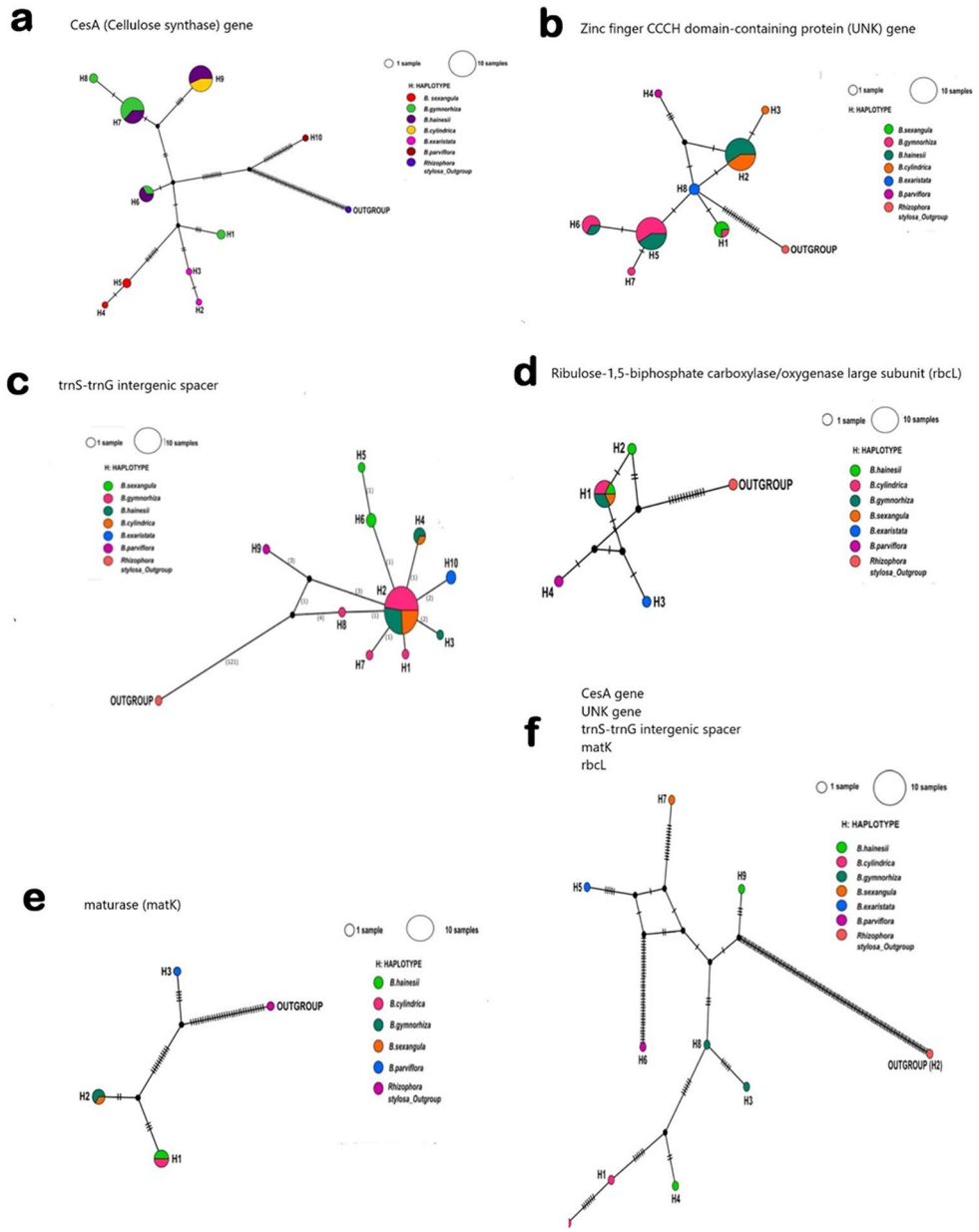

Fig. 5 (**a**) Haplotype networks of genus *Bruguiera* based on CesA (cellulose synthase) gene. Haplotype frequency is represented by the size of circles. Single line is an indication of haplotypes segregated by one mutation apart (No. of mutations) while missing haplotypes (ancestral or unsampled haplotypes) are represented by black dots. (**b**) Haplotype networks of genus *Bruguiera* based on Zinc finger CCCH domain containing protein UNK gene. Haplotype frequency is represented by the size of circles. Single line is an indication of haplotypes segregated by one mutation apart (No. of mutations) while missing haplotypes (ancestral or unsampled haplotypes) are represented by black dots. (**c**) Haplotype networks of genus *Bruguiera* based on trnS-trnG intergenic spacer. Haplotype frequency is represented by the size of circles. Single line is an indication of haplotypes segregated by one mutation apart (No. of mutations) while missing haplotypes (ancestral or unsampled haplotypes) are represented by black dots. (**d**) Haplotype networks of genus *Bruguiera* based on rbcL gene. Haplotype frequency is represented by the size of circles. Single line is an indication of haplotypes segregated by one mutation apart (No. of mutations) while missing haplotypes (ancestral or unsampled haplotypes) are represented by black dots. (**e**) Haplotype networks of genus *Bruguiera* based on matK gene. Haplotype frequency is represented by the size of circles. Single line is an indication of haplotypes segregated by one mutation apart (No. of mutations) while missing haplotypes (ancestral or unsampled haplotypes) are represented by black dots. (**f**) Haplotype networks of genus *Bruguiera* based on concatenated sequences of CesA, UNK and trnS-trnG intergenic spacer, matK and rbcL. Haplotype frequency is represented by the size of circles. Single line is an indication of haplotypes segregated by one mutation apart (No. of mutations) while missing haplotypes (ancestral or unsampled haplotypes) are represented by black dots

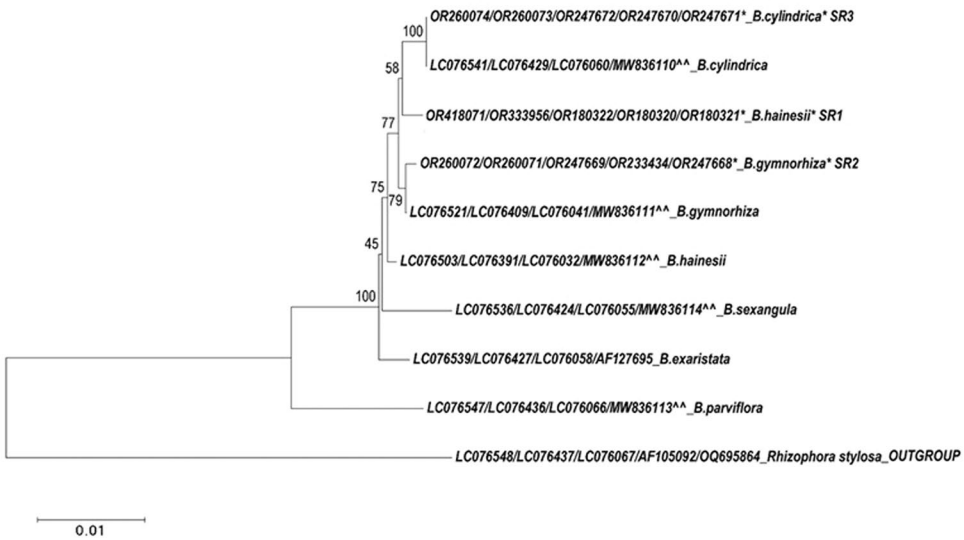

Fig. 6 Phylogenetic tree using concatenated gene sequences based on neighbour joining analysis (1000 bootstraps and Kimura 2 parameter model). '*' indicates gene sequences generated for this study '^^' indicates gene sequences mined from chloroplast genome that are combined with acquired sequences from NCBI

H7: Included six *B. hainesii* and ten *B. gymnorhiza*, H9: Comprised nine *B. hainesii* and seven *B. cylindrica*, H10 & H11: Represented by *B. parviflora* (LC076547) and *Rhizophora stylosa* (LC076548), respectively.

UNK Gene (Zinc Finger CCCH Domain)

The UNK gene sequence was 369 bp across species. Nine haplotypes (Fig. 5b) were identified: H1: Shared by *B. gymnorhiza* (LC076416) and *B. sexangula* (LC076424-426), H2: The largest group with 17 members, including ten *B. hainesii* and seven *B. cylindrica*, H5: Included seven *B. hainesii* and ten *B. gymnorhiza*, H6: Shared by two *B. hainesii* and four *B. gymnorhiza*, Other haplotypes (H3, H4, H7–H9) were unique to specific species, with *Rhizophora stylosa* forming H9.

trnS-trnG Intergenic Spacer

Gene lengths for *B. hainesii*, *B. gymnorhiza*, and *B. cylindrica* were 632 bp, 574 bp, and 606 bp, respectively. Eleven haplotypes (Fig. 5c) were identified: H1: a unique haplotype belonging to *B. gymnorhiza* (OR247669), H2: The largest group with 25 individuals, including seven *B. hainesii*, six *B. cylindrica*, and 12 *B. gymnorhiza*, H3 & H4: Unique haplotypes of *B. hainesii* and shared members of B. cylindrica, H5–H8: Represented by *B. sexangula* and *B. gymnorhiza*, H9 & H10: Unique to *B. parviflora* and *B. exaristata*, H11: Formed by *Rhizophora stylosa*.

RbcL Gene

Gene sequences were 690 bp for *B. hainesii*, 675 bp for *B. gymnorhiza*, and 642 bp for *B. cylindrica*. Five haplotypes (Fig. 5d) were identified: H1: Shared haplotype for six individuals across four species (*B. cylindrica*, *B. hainesii*, *B. gymnorhiza*, and *B. sexangula*), H2–H5: Unique to specific species, including *B. exaristata*, *B. parviflora*, and *Rhizophora stylosa*.

MatK Gene (Maturase)

Gene lengths were 828 bp for *B. hainesii* and 840 bp for both *B. gymnorhiza* and *B. cylindrica*. Four haplotypes (Fig. 5e) were generated: H1: Shared by *B. hainesii* and *B. cylindrica*, H2: Included *B. gymnorhiza* and *B. sexangular*, H3 & H4: Represented by *B. parviflora* and *Rhizophora stylosa*.

Combined Nuclear and Chloroplast Gene Analysis

All chosen genes were amalgamated to create a concatenated file, and molecular analysis was carried out to produce a haplotype network (Fig. 5f). However, contrary to previous findings based on specific genes, each individual formed distinct haplotypes with no shared characters or alleles. This molecular analysis highlights the genetic diversity and evolutionary relationships within the genus *Bruguiera*.

Phylogenetic Tree and Genetic Distance Data

Within the phylogenetic tree (Fig. 6), congeners of the genus *Bruguiera* are arrayed within a major clade with high bootstrap support, demonstrating the high-level genetic congruence among the selected species. However, the precise distinction between selected species at the interspecific level was not clear. To confirm the findings of the phylogenetic tree, genetic distance data (Supplementary file 1) were also generated. The genetic distance data supported the cladistic array of the phylogenetic tree, as the inferred results showed

very low values regarding interspecific delineation, suggesting that it may not be sufficient for species differentiation.

Molecular analysis based on nuclear (CesA, UNK) and chloroplast (matK, rbcL, trnS-trnG) genes revealed considerable sharing of haplotypes between *Bruguiera* species. Nuclear genes revealed the affinity of *B. hainesii* towards *B. cylindrica* and *B. gymnorhiza* as individual haplotypes of *B. hainesii* were shared with these species. However, chloroplast genes (matK, rbcL, trnS-trnG) showed multiple genetic behaviour with respect to employed genes. For the trnS-trnG intergenic spacer, there were two modes of haplotype sharing: (i) haplotype shared between *B. hainesii*, *B. cylindrica*, and *B. gymnorhiza*, (ii) haplotype shared between *B. hainesii* and *B. cylindrica.* For matK, haplotypes were shared between *B. hainesii* and *B. cylindrica* only, and for the rbcL gene, haplotypes were shared between *B. hainesii*, *B. cylindrica*, *B. gymnorhiza*, and *B. sexangula.* However, a combined analysis using nuclear and chloroplast genes revealed no shared haplotypes. Based on these results, it could be inferred that *B. hainesii* might be an F1 hybrid influenced by post-mating isolation, exhibiting very low propagation and germination rates, potentially due to outbreeding depression (Polidoro et al. 2010). These findings have prompted questions about the conservation status of *B. hainesii*, as the International Union for Conservation of Nature (IUCN) focuses on conserving species rather than hybrids. Consequently, deprioritizing *B. hainesii* would redirect attention and resources to other endangered mangrove species.

The wetlands of the Maldives with basin mangroves, one of the rarest mangrove types worldwide, hold significant ecological and social value and require effective protection and management. These areas, home to various species including the critically endangered *B. hainesii*, serve as vital habitats for mangrove-associated species and are of considerable importance to the nation. A mass die-back of *Bruguiera sp.* occurred on the islands in March 2020 (Dryden et al. 2020) due to increased soil salinity resulting from elevated temperatures, prolonged drought caused by the triple La Nina phenomenon, and positive Indian Ocean dipole, as well as localized sea level fluctuations (Bijoy Nandan 2023; Sreelekshmi et al. 2025). Considering the critically endangered status and hybrid characteristics of *Bruguiera hainesii*, along with its low natural regeneration rate, appropriate in-situ and ex-situ conservation strategies should be developed. These strategies might include mass propagation (Tissue culture) and the establishment of marine protected areas or reserves in the mangrove dieback zones. The existing Maldives' principal environmental law, the Environmental Protection and Preservation Act (Law No.4/93), can be strengthened and amended, or even forest conservation laws can be framed and legislated for the conservation of mangroves since the Maldives is not a signatory to the Ramsar Convention. Thus, a concerted nationwide effort is necessary to locate and comprehend these ecosystems, understand their environmental significance, and develop strategies for their sustainable management. Such efforts would contribute significantly to the global understanding of island ecosystems of similar nature.

Conclusion

Based on the findings and field observations, it is strongly advised to establish a real-time monitoring system for the wetland habitats across Maldivian islands to track ecological changes over time. It is imperative to formulate an appropriate management plan, including the designation of additional protected areas, to safeguard these habitats against threats and maintain them at sustainable levels. Given the critical status of *Bruguiera hainesii*, which has been documented on several islands, protecting the habitats where it occurs should be a primary management objective, especially considering the observed decline on Kulhudhufushi island. The significance of mangrove habitats, coupled with their proximity to agricultural lands in the Maldives, underscores the urgent need for the creation of a sustainable management plan.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing Interests The authors declare no competing interests.

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