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Bioclimatic and habitat variability shape the diversity and distribution of aquatic and invasive macrophytes in the floodplains of Indo-Burma biodiversity hotspot

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Abstract

Climate plays a major role in determining plant species richness and distribution patterns at a continental scale. However, a detailed investigation is necessary to understand the effect of climatic variations on species richness and distribution patterns at a regional scale, as other factors such as habitat types and associated environmental conditions exert significant influence at this scale. We conducted a study to test this hypothesis by analyzing species richness data from 1150 aquatic systems categorized into six types i.e., lotic system, marsh, pond, water-logged area, wetland, and wasteland area, located in five bioclimatic zones of Assam (CZ1 to CZ5) in the Indo-Burma biodiversity hotspot. The identification of the bioclimatic zones was based on Iterative Self-Organizing (ISO) clustering of 19 bioclimatic variables, which enabled differentiation of zones based on precipitation and temperature seasonality. The study revealed a total of 90 species of aquatic macrophytes under 67 genera and 34 families. Out of these, 23 species under 20 genera and 18 families were invasive. The richness of aquatic macrophytes including the invasive species increased with extremity of climatic conditions from CZ1 to CZ4. However, the richness decreased substantially in CZ5 that had the highest effect of seasonality of precipitation and temperature. Amongst all the invasive species, species such as *Eichhornia crassipes*, *Ipomoea carnea*, *Cynodon dactylon*, *Pistia stratiotes*, *Mimosa pudica* followed by *Ludwigia adscendens*, *Ipomoea aquatica*, and *Alternanthera philoxeroides* were available in all types of aquatic habitats and across all the bioclimatic zones with greater encountered sites thereby indicating their greater potential for encroachment and landscape spread in the study area.

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Introduction

Climate is a vital factor in determining global plant species richness patterns. However, it is crucial to explore the effects of climatic variations on richness patterns at a regional level, where habitat types and related environmental factors may also play significant roles. Aquatic habitats exhibit a strong mediating effect on species assemblage patterns, often overshadowing the influence of terrestrial factors on terrestrial species assemblages, irrespective of the climate (Kling, 1995; Viana *et al.*, 2014; Manolaki and Papastergiadou, 2016). Unique attributes of aquatic environments, including water chemistry, hydrodynamics, and substrate composition, are crucial in shaping aquatic species assemblages (Elo *et al.*, 2018; Dong *et al.*, 2022).

These factors interact, forming distinct microhabitats that ultimately dictate aquatic species distribution and composition. In contrast, terrestrial species assemblage patterns are more directly influenced by factors such as climate, soil, and vegetation structure.

Although these factors are undeniably important for terrestrial communities, the intricate interaction of environmental conditions in aquatic habitats generally has a more potent effect on species assemblage patterns (John *et al.*, 2007; Teixeira *et al.*, 2008; Heino, 2009; Mikulyuk *et al.*, 2011 and Chaturvedi and Raghubanshi, 2018). This emphasizes the need for a comprehensive understanding on how species assemblages vary in different aquatic habitats under contrasting climatic conditions.

Aquatic macrophytes (AMs) are photosynthetic organisms visible to the naked eye and can grow permanently or temporarily in aquatic systems. They encompass a diverse array of taxonomic groups, including angiosperms, ferns, mosses, liverworts, and some macroalgae (Lacoul and Freedman, 2006). AMs are typically categorized into four groups based on their growth habits: emergent, free-floating, rooted floating, and submerged (Chambers *et al.*, 2007). They serve vital roles in aquatic ecosystems, akin to the functions of terrestrial plants in land-based ecosystems. However, when AMs become invasive, they threaten aquatic ecosystems, human health, and biodiversity by outcompeting native species, disrupting community composition and structure, degrading water quality, impacting fisheries, and creating breeding habitats for disease vectors, ultimately resulting in the loss of ecosystem services in aquatic systems (Brundu, 2015; Wang *et al.*, 2016).

Macrophyte community composition and species richness are influenced by both regional factors, like climate, and local factors, such as habitat quality. Environmental gradients are similarly important in explaining plant community structure and richness (Alahuhta, 2014). Climate change-driven shifts in temperature and precipitation patterns will affect species distribution, abundance, and diversity across various habitats (Osland *et al.*, 2016).

Assam, a northeastern state in India, is part of the Indo-Burma biodiversity hotspot and contains two major river basins: the Brahmaputra and Barak. The region experiences a warm and humid climate influenced by the South-West monsoon, which lasts from April to September (Mahanta and Yamane, 2020). Due to its unique bowl-shaped terrain and distinctive rainfall patterns, Assam boasts an array of water bodies, including ponds, streams, rivers, wetlands, waterlogged areas, and marshes, all of which support diverse aquatic macrophytes (AMs) (Prasad and Das, 2018).

Although the survey and documentation of AMs in Assam began long ago (Hooker, 1872; Kanjilal *et al.*, 1940; Rao and Verma, 1971) and continue to this day (Barooah and Mahanta, 2006; Kalita *et al.*, 2011; Malakar and Boruah, 2017; Prasad and Das, 2018; Sarmah and Das, 2020), efforts to document its diversity have been fragmentary and insufficient for decision-making purposes. Despite the Indo-Burma biodiversity hotspot of Assam being identified as a crucial invasion hotspot area in India (Adhikari *et al.*, 2015), information on the documentation of invasive AMs in the region remains scarce, except for one study by Prasad and Das (2018) in the Barak Valley region.

The hypothesis of this study is that bioclimatic and habitat variability is significant determinants of the diversity and distribution of AMs and their invasive species in Assam, India. Specifically, it is hypothesized that climatic variables and aquatic habitats shape the composition and richness of AMs and their invasive species across different bioclimatic zones and aquatic habitats in Assam.

The primary objective of this study is to explore the influence of bioclimatic zones and aquatic habitats on the diversity and distribution of AMs and their invasive species in Assam, India. The specific objectives are (1) to delineate the study area into different bioclimatic zones based on climatic variables, (2) to assess the diversity and distribution of AMs and their invasive species in different aquatic habitats across the bioclimatic zones, and (3) to examine the relationship between bioclimatic zones, aquatic habitats, and the diversity and distribution of AMs and their invasive species.

Materials and methods:

Study Area

The present study was conducted in Assam (Fig. 2), which has a total area of 78,438 km² out of which 31,500 km² (i.e., 40.2% of the total area) is flood prone (Bhanumurthy *et al.*, 2003; Sharma *et al.*, 2017). Assam is situated between 90° to 96° N latitude, and between 24° to 28° E longitude and is characterized by unique topography comprising hills, riverine systems, extensive floodplain wetlands and lakes, and different seasonal and perennial aquatic bodies. The annual average rainfall in Assam is about 2134.6 mm (Guhathakurta *et al.*, 2020).

Delineating bioclimatic zones

Delineating the study area into different bioclimatic zone is essential as it would be helpful to identify the effect of climatic variables on species distribution (Evans *et al.*, 2005; Yan *et al.*, 2015). We delineated the entire area of Assam into different bioclimatic zones, which are basically the geographical regions characterized by a distinct set of climatic variables like precipitation, moisture availability, and temperature distribution. The bioclimatic zones were differentiated and mapped using 19 bioclimatic variables available at worldclim website (www.worldclim.org) (Table 1).

These variables represent information about annual conditions i.e., annual mean temperature, annual precipitation, annual range in temperature and precipitation, as well as seasonal mean climate conditions and intra-year seasonality i.e., temperature of the coldest and warmest months, precipitation of the wettest and driest quarters. Raster data on global coverage of 19 bioclimatic variables with a spatial resolution of 1km was downloaded from www.worldclim.org.

The bioclimatic data for Assam was extracted in ASCII raster grid format using Q-GIS software. We performed principal component analysis (PCA) with the extracted data using Niche Analyst (NicheA) software (Qiao *et al.*, 2016). This procedure generated 19 principal component images (PCIs) containing the information on the variance in the dataset.

The first three PCIs explained ~99 percent of the variances in the dataset. We then imported the first three principal component images in ArcGIS and made a composite RGB image. Thereafter, we delineated five bioclimatic zones of the study area i.e., Assam using the ISO clustering algorithm in ArcGIS (Fig. 1 and Fig. 2) which were differentiated based on the degree of seasonality of precipitation and temperature. The extremity of the climatic condition (atmospheric temperature and precipitation) increases as we move from bioclimatic zone 1 (CZ1) to bioclimatic zone 5 (CZ5).

The approximate area under each bioclimatic zone varied from each other and it showed the following sequence CZ3 (24,750 km²) > CZ1 (21,600 km²) > CZ4 (18,850 km²) > CZ2 (9000 km²) > CZ5 (4,200 km²).

Table 1. Bioclimatic variables and their ecological interpretations (Source: www.worldclim.org).

Bioclimatic variable name	Ecological interpretation
BIO1 = Annual Mean Temperature	Approximates the total energy inputs for an ecosystem.
BIO2 = Mean Diurnal Range (Mean of monthly (max temp – min temp))	Provide information pertaining to the relevance of temperature fluctuation for different species.
BIO3 = Isothermality (BIO2/BIO7) (* 100)	Provides information on how large the day-to-night temperatures oscillate relative to the summer-to-winter (annual) oscillations. This variable is useful to ascertain how larger or smaller temperature fluctuations within a month relative to the year might affect species distribution.
BIO4 = Temperature Seasonality (standard deviation *100)	It is a measure of temperature change over the course of the year. The larger the value, the greater the temperature variability.
BIO5 = Max Temperature of Warmest Month	This variable is used to determine whether species distributions are affected by warm temperature anomalies throughout the year.
BIO6 = Min Temperature of Coldest Month	This variable is used to determine whether species distributions are affected by cold temperature anomalies throughout the year.
BIO7 = Temperature Annual Range (BIO5-BIO6)	This variable is used to determine whether species distributions are affected by range of extreme temperature conditions.
BIO8 = Mean Temperature of Wettest Quarter	Provides information about mean temperatures during the three wettest months of the year. This is useful to examine how such factors can affect species distributions.
BIO9 = Mean Temperature of Driest Quarter	Provides information about mean temperatures during the three driest months of the year. This is useful to examine how such factors can affect species distributions.
BIO10 = Mean Temperature of Warmest Quarter	Provides information about mean temperatures during the three warmest months of the year. This is useful to examine how such factors can affect species distributions.
BIO11 = Mean Temperature of Coldest Quarter	Provides information about mean temperatures during the three coldest months of the year. This is useful to examine how such factors can affect species distributions.
BIO12 = Annual Precipitation	Provides information on total water inputs and is useful in determining the importance of water availability on species distribution.
BIO13 = Precipitation of Wettest Month	Provides information on the wettest month of the year and is useful if extreme conditions during the year influence species distribution.
BIO14 = Precipitation of Driest Month	Provides information on the driest month of the year and is useful if extreme conditions during the year influence species distribution.
BIO15 = Precipitation Seasonality (Coefficient of Variation)	Provides information on variability of precipitation, and is useful in studying whether species distribution is influenced by variability in precipitation.
BIO16 = Precipitation of Wettest Quarter	Provides information about precipitations during the three wettest months of the year. This is useful to examine how such factors can affect species seasonal distribution.
BIO17 = Precipitation of Driest Quarter	Provides information about precipitations during the three driest months of the year. This is useful to examine how such factors can affect species seasonal distribution.
BIO18 = Precipitation of Warmest Quarter	Provides information about precipitations during the three warmest months of the year. This is useful to examine how such factors can affect species seasonal distribution.
BIO19 = Precipitation of Coldest Quarter	Provides information about precipitations during the three coldest months of the year. This is useful to examine how such factors can affect species seasonal distribution.

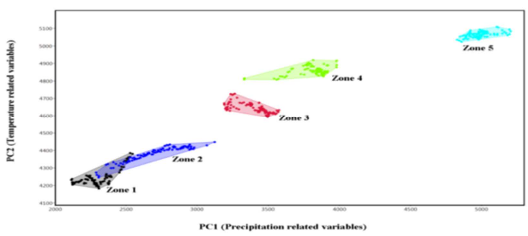

Fig. 1. Differentiation of the five climatic zones of Assam in two-dimensional principal component axis.

The dots inside the convex polygons represent the bioclimatic conditions of 100 random locations in each zone.

PC1 represents linear combination of annual precipitation (Bio12), precipitation of wettest quarter (Bio16), and precipitation of driest quarter (Bio17), and PC2 mainly represent temperature seasonality (Bio4).

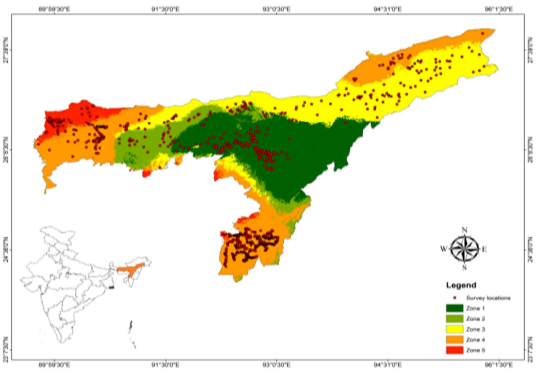

Fig. 2. Map showing the different bioclimatic zones and survey locations in the Brahmaputra and Barak valleys of Assam.

Field survey

Extensive field surveys were conducted to collect and document the AMs including the invasive species occurring in various aquatic systems in the Indo-Burma biodiversity hotspot of Assam comprising ponds, water logged areas, marshy areas, wetlands, streams, canals and rivers for a period of five years from March, 2015 to February, 2020 across the different bio-climatic zones of Assam. The survey was done on a seasonal basis comprising pre-monsoon (March to May), monsoon (June to August) and post-monsoon (September to November). Global Positioning System (GPS) points were recorded for the species encountered in different aquatic systems of the study area. Q-GIS software was used for mapping the surveyed locations and distribution of AMs including the invasive species across the study area (Fig. 2). We have surveyed 30 % of all the bioclimatic zone and selected 30 % water bodies from each bioclimatic zone. Overall, 1150 aquatic systems were surveyed for the present study.

Species composition and richness

Species composition and richness of the AMs were assessed following direct observations in different aquatic systems. Plant samples were collected and identified following standard methods and reference materials (Cook, 1996; Fassett, 2000; www.kew.org, RBG Kew, 2017). For confirmation of the species identity, the herbarium of Botanical Survey of India, Shillong was consulted. The scientific names of all the species were verified using *The World Flora Online* (WFO) (http://www.worldfloraonline.org). The identification of the invasive species was done based on the information from the global database on invasive species (www.issg.org) and the database on invasive species in India (www.bsienvis.nic.in).

Results

Bioclimatic zonation in Assam

In Assam, five distinct bioclimate zones can be identified, labeled as Zone 1 through Zone 5. Bioclimatic Zone 1 (CZ1), encompasses the districts Nagaon, Morigaon, Hojai, Karbi Anglong, and Dima Hasao. Bioclimatic Zone 2 (CZ2), includes the districts Nalbari, Barpeta, and Darang. Bioclimatic Zone 3 (CZ3), comprises the districts Tinsukia, Dibrugarh, Sibsagar, Jorhat, Golaghat, and Sonitpur. Bioclimatic Zone 4 (CZ4), covers the districts Bongaigaon, Dhubri, Goalpara, Barpeta, North-Lakhimpur, Cachar, Karimganj, and Hailakandi. Bioclimatic Zone 5 (CZ5), consists of the districts Kokrajhar, Chirang, Udalguri, Baksa, and Dhubri (Fig. 2).

Habitat diversity in different bioclimatic zones

In CZ1, overall, 152 systems were surveyed, out of them 43 were pond, 10 were water-logged area, 27 were marshy area, 8 were lotic systems and 64 were wetlands. In CZ2, overall, 63 systems were surveyed, out of them 15 were pond, 5 were water-logged area, 6 were marshy area, 5 were lotic systems and 32 were wetlands. In CZ3, overall, 115 systems were surveyed, out of them 18 were pond, 40 were water-logged area, 5 were marshy area, 4 were lotic systems and 48 were wetlands. In CZ4, overall, 757 systems were surveyed, out of them 183 were pond, 261 were water-logged area, 192 were marshy area, 32 were lotic systems and 89 were wetlands. In CZ5, overall, 63 systems were surveyed, out of them 11 were pond, 3 were water-logged area, 16 were marshy area, 12 were lotic systems and 21 were wetlands. The total number of surveyed systems varied in the different climatic zones because of the geographical extent and topography of each of these zones.

Species composition and richness

Overall, a total of 90 aquatic macrophyte (AM) species belonging to 67 genera and 34 families were recorded from the study area. Out of these, 23 species were invasive. Among the invasive species, 19 are listed in the global invasive species database, 8 in the Indian invasive species database, out of which 4 are common to both databases (Table 2). Of the total species, 75 were native to India, while 15 were exotic.

In terms of habit, most species (58) were classified as emergent, followed by rooted floating (12), free-floating (11), and submerged (9). The species were further categorized by their preferred environment: 32 perennial aquatic herbs, 31 perennial herbs (riparian), 18 annual herbs (riparian), 5 aquatic ferns, 3 semi-aquatic herbs, and 1 perennial shrub (riparian) (Table 2). *Eichhornia crassipes* was found in most of the sites (842), followed by *Ipomoea carnea* (680), *Colocasia esculenta* (347), *Cynodon dactylon* (327), *Leucas aspera* (274), *Pistia stratiotes* (231), *Mimosa pudica* (231), and *Ludwigia adscendens* (201). All these species were found across all the bioclimatic zones. All these species, except for *Colocasia esculenta* and *Leucas aspera*, were classified as invasive. Amongst these species the free-floating species like *Eichhornia crassipes* and *Pistia stratiotes* were present in aquatic bodies, while emergent species like *Ipomoea carnea*, *Colocasia esculenta*, *Cynodon dactylon*, *Leucas aspera*, *Mimosa pudica*, and *Ludwigia adscendens* were observed in the riparian regions or partially dried areas of aquatic bodies. Amongst these species, *Eichhornia crassipes*, *Ipomoea carnea*, *Cynodon dactylon*, *Pistia stratiotes*, and *Mimosa pudica* were exotic while, *Colocasia esculenta*, *Leucas aspera* and *Ludwigia adscendens* were native to India (Table 2). Invasive species consisted of 61% from the emergent group, 22% free-floating, and 17% submerged group, with no invasive species in the rooted-floating group (Table 3).

Table 2. List of aquatic macrophytes including the invasive species with their respective habit, growth form, and nativity including the number of sites, type of aquatic habitats, and the bio-climatic zones where each species was encountered.

SL	Species name	Family	Habit	Growth form	Native / Exotic	Number of systems where each species was encounter -ed	Type of aquatic habitats where each species was encounter -ed	Bio-climatic zone under which each species was encountered
1	*Acorus calamus* L.	Acoraceae	Emergent	SAH	Exotic	72	WLA, M, LS, W	1,2,3,4,5
2	*Alocasia cucullata* (Lour.) G.Don	Araceae	Emergent	PH	Native	15	P, LS, W	1,2,3,4,5
3	*Alocasia fornicate* (Roxb.) Schott	Araceae	Emergent	PH	Native	12	P, LS, W	3,4
4	*Alocasia macrorrhizos* (L.) G.Don	Araceae	Emergent	PH	Exotic	37	M, W	1,2,3,4,5
5	***Alternanthera philoxeroides* (Mart.) Griseb. *	Amaranthaceae	Emergent	PH	Exotic	102	P, WLA, M, LS, W	1,2,3,4,5
6	***Alternanthera sessilis* (L.) R. Br. ex DC.	Amaranthaceae	Emergent	PH	Native	23	P, LS, W	3,4,5
7	*Aponogeto natans* (L.) Engl. & K. Krause	Aponogetonaceae	Rooted floating	PAH	Native	13	P, W	3,4
8	*Aponogeton appendiculatus* H.Bruggen	Aponogetonaceae	Submerged	PAH	Native	11	W	1,3,4
9	***Azolla pinnata* R. Br.	Salviniaceae	Free-floating	AF	Native	26	M, LS, W	1,2,3,4,5
10	*Bacopa monnieri* (L.) Wettst.	Plantaginaceae	Emergent	PH	Native	9	M, W	2,3
11	*Bergia capensis* L.	Elatinaceae	Emergent	PH	Native	54	LS, W	2,3,4
12	*Centella asiatica* (L.) Urb.	Apiaceae	Emergent	PH	Native	176	WL A, M, LS, W	1,2,3,4,5
13	***Ceratophyllum demersum* L.	Ceratophyllaceae	Submerg -ed	PAH	Exotic	16	M, W	1,3,4
14	*Colocasia esculenta* (L.) Schott	Araceae	Emergent	PH	Native	347	P, WLA, M, LS, W	1,2,3,4,5
15	***Commelina benghalensis* L.	Commelinaceae	Emergent	PH	Native	23	P, M, W	2,3,4

SL	Species name	Family	Habit	Growth form	Native / Exotic	Number of systems where each species was encounter -ed	Type of aquatic habitats where each species was encounter -ed	Bio-climatic zone under which each species was encountered
16	*Commelina diffusa* Burm.f.	Commelinaceae	Emergent	PH	Native	14	P, M, W	2,3,4,5
17	*Cyanotis axillaries* (L.) D. Don ex Sweet	Commelinaceae	Emergent	AH	Native	17	P, WLA, LS, W	1,3,4,5
18	***Cynodon dactylon* (L.) Pers.	Poaceae	Emergent	PH	Exotic	327	P, WLA, M, LS, W	1,2,3,4,5
19	*Cyperus haspan* L.	Cyperaceae	Emergent	PH	Native	31	WLA, M, W	3,4
20	*Cyperus imbricatus* Retz.	Cyperaceae	Emergent	PH	Native	48	WLA, M, W	2,3,4,5
21	*Cyperus tenuispica* Steud.	Cyperaceae	Emergent	AH	Exotic	29	WLA, M, W	1,2,3,4,5
22	*Cyperus pilosus* Vahl	Cyperaceae	Emergent	PH	Native	22	WLA, M, W	3,4,5
23	***Cyperus rotundus* L.	Cyperaceae	Emergent	PH	Exotic	12	W	1,4
24	*Eclipta prostrata* (L.) L.	Compositae	Emergent	AH	Native	23	P, M, W	4
25	***Eichhornia crassipes* (Mart.) Solms *	Pontederiaceae	Free-floating	PAH	Exotic	842	P, WLA, M, LS, W	1,2,3,4,5
26	*Eleocharis acuta* R.Br.	Cyperaceae	Emergent	PH	Exotic	14	W	4,5
27	*Enydra fluctuans* DC.	Compositae	Emergent	SAH	Native	78	P, WLA, M, LS, W	1,2,3,4,5
28	*Eragrostis unioloides* (Retz.) Nees ex Steud.	Poaceae	Emergent	AH	Native	67	M, WLA, LS, W	2,4,5
29	*Eriocaulon setaceum* L.	Eriocaulaceae	Submerg -ed	PAH	Native	5	W	3,4
30	*Euphorbia hirta* L.	Euphorbiaceae	Emergent	PH	Native	96	P, W	4
31	*Euryale ferox* Salisb.	Nymphaeaceae	Rooted floating	PAH	Native	14	P, WLA, W	1,2,3,4,5
32	*Fimbristylis littoralis* Gaudich.	Cyperaceae	Emergent	AH	Native	39	WLA, W	3,4
33	*Fimbristylis argentea* (Rottb.) Vahl	Cyperaceae	Emergent	AH	Native	12	M	3,4
34	*Floscopa scandens* Lour.	Commelinaceae	Emergent	PH	Native	17	M , WLA	4
35	*Heliotropium indicum* L.	Boraginaceae	Emergent	AH	Native	21	WL, A, M,W	2
36	***Hydrilla verticillata* (L.f.) Royle	Hydrocharitaceae	Emergent	PAH	Native	13	LS, W	1,2,3,4,5
37	***Hygrophila polysperma* (Roxb.) T.Anderson	Acanthaceae	Submerg -ed	PAH	Native	176	M, W	1,2,3,4,5
38	*Hygroryza aristata* (Retz.) Nees ex Wight &Arn.	Poaceae	Rooted floating	PAH	Native	42	W	1,2,3,4,5
39	*Hymenachne amplexicaulis* (Rudge) Nees	Poaceae	Emergent	SAH	Native	93	WLA, M, W	1,2,3,4,5
40	***Ipomoea aquatica* Forssk.	Convolvulaceae	Emergent	PH	Native	137	P, WLA, M, LS, W	1,2,3,4,5
41	*Ipomoea obscura* (L.) Ker Gawl.	Convolvulaceae	Emergent	PH	Native	25	M,W	3,4
42	**Ipomoea carnea* Jacq.	Convolvulaceae	Emergent	PS	Exotic	680	P, WLA, M, LS,W	1,2,3,4,5
43	*Isachne globosa* (Thunb.) Kuntze	Poaceae	Emergent	AH	Native	127	M, WLA	1,2,3,4
44	*Kyllinga brevifolia* Rottb.	Cyperaceae	Emergent	PH	Exotic	23	WLA, M, W	3,4,5
45	*Lasia spinosa* (L.) Thwaites	Araceae	Emergent	PH	Native	2	M, LS	4
46	*Leersia hexandra* Sw.	Poaceae	Emergent	PH	Native	4	W	1
47	*Lemna perpusilla* Torr.	Araceae	Free floating	PAH	Native	11	P,W	2,4
48	*Lemna minor* L.	Araceae	Free-floating	PAH	Native	32	P, M, W	1,2,3,4,5
49	*Leucas aspera* (Willd.) Link	Lamiaceae	Emergent	AH	Native	274	M, WL A, LS, W	1,2,3,4,5
50	***Limnophila sessiliflora* (Vahl) Blume	Plantaginaceae	Submerg -ed	PAH	Native	11	M, LS, W	1,2,3,4,5
51	**Ludwigia adscendens* (L.) H.Hara	Onagraceae	Emergent	PAH	Native	201	P, WLA, M, LS, W	1,2,3,4,5
52	**Ludwigia perennis* L.	Onagraceae	Emergent	AH	Native	41	M, WLA, LS & W	1,2,3,4,5
53	*Marsilea minuta* L.	Marsileaceae	Rooted floating	AF	Native	72	P, WLA, LS, W	1,2,3,4,5
54	*Marsilea quadrifolia* L.	Marsileaceae	Rooted floating	AF	Exotic	93	P, M, W	1,2,3,4,5
55	***Mimosa pudica* L.*	Leguminosae	Emergent	AH	Exotic	231	M, WLA	1,2,3,4,5
56	*Monochoria hastata* (L.) Solms	Pontederiaceae	Emergent	PH	Native	83	M, WLA, W	2,4
57	**Monochoria vaginalis* (Burm.f.) C.Presl	Pontederiaceae	Emergent	AH	Native	43	WLA, W	4
58	***Myriophyllum spicatum* L.	Haloragaceae	Emergent	PAH	Native	15	WLA, W	1,2,3,4,5
59	***Najas minor* All.	Hydrocharitaceae	Free-floating	PAH	Native	11	WLA, LS, W	1,2,3,4,5
60	*Nelumbo nucifera* Gaertn.	Nelumbonaceae	Rooted floating	PAH	Native	8	P, LS, W	1,2,3,4,5
61	*Neptunia oleracea* Lour.	Leguminosae	Rooted floating	PAH	Native	16	M, WLA, W	1,2,3
62	*Nymphaea nouchali* Burm.f.	Nymphaeaceae	Rooted floating	PAH	Native	32	WLA, W	1,2,3,4,5

SL	Species name	Family	Habit	Growth form	Native / Exotic	Number of systems where each species was encounter -ed	Type of aquatic habitats where each species was encounter -ed	Bio-climatic zone under which each species was encountered
63	*Nymphaea pubescens* Willd.	Nymphaeaceae	Rooted floating	PAH	Native	63	LS, W	1,2,3,4,5
64	*Nymphaea lotus* L.	Nymphaeaceae	Rooted floating	PAH	Native	14	LS, W	1,2,3,4,5
65	*Nymphoides indica* (L.) Kuntze	Menyanthaceae	Rooted floating	PAH	Native	135	M, WLA, W	1,2,3,4,5
66	*Nymphoides cristata* (Roxb.) Kuntze	Menyanthaceae	Rooted floating	PAH	Native	87	P, M, W	1,2,3,4,5
67	*Oenanthe javanica* (Blume) DC.	Apiaceae	Emergent	PH	Native	5	W	4
68	*Ottelia alismoides* (L.) Pers.	Hydrocharitaceae	Submerg -ed	PAH	Native	21	P, LS, W	1,3
69	*Paspalum conjugatum* P.J.Bergius	Poaceae	Emergent	PH	Native	4	P, M, W	5
70	*Persicaria barbata* (L.) H.Hara	Polygonaceae	Emergent	PH	Native	136	M, WLA, W	1,2,3,4,5
71	*Persicaria hydropiper* (L.) Delarbre	Polygonaceae	Emergent	AH	Native	29	M. WLA, W	1,2,3,4,5
72	*Persicaria lapathifolia* (L.) Delarbre	Polygonaceae	Emergent	AH	Exotic	31	M, W	1,2,3,4,5
73	***Pistia stratiotes* L. *	Araceae	Free-floating	PAH	Exotic	231	P, WLA, M, LS, W	1,2,3,4,5
74	***Potamogeton crispus* L.	Potamogetona -ceae	Submerg -ed	PAH	Native	8	W	1,2,3,4,5
75	*Pseudoraphis spinescens* (R.Br.) Vickery	Poaceae	Emergent	PH	Native	35	M, LS, W	1,2,3,4,5
76	*Pycreus pumilus* (L.) Nees	Cyperaceae	Emergent	AH	Native	1	M	4
77	*Pycreus stramineus* C.B.Clarke	Cyperaceae	Emergent	PH	Native	80	M, W	2,4,5
78	*Rhynchospora corymbosa* (L.) Britton	Cyperaceae	Emergent	PH	Native	57	M, W	2,3,4,5
79	*Sacciolepis interrupta* (Willd.) Stapf	Poaceae	Emergent	AH	Native	52	W	3,4
80	*Sagittaria guayanensis* Kunth	Alismataceae	Emergent	PAH	Native	11	M, W	2,4
81	***Sagittaria sagittifolia* L.	Alismataceae	Emergent	PAH	Native	78	LS, W	1,2,3,4,5
82	*Salvinia cucullata* Roxb.	Salviniaceae	Free-floating	AF	Native	79	P, M, WLA, W	1,2,3,4,5
83	*Salvinia natans* (L.) All.	Salviniaceae	Free-floating	AF	Native	31	P, M, WLA, LS, W	1,2,3,4,5
84	*Sphaerocaryum malaccense* (Trin.) Pilg.	Poaceae	Emergent	AH	Native	127	WLA & M	1,2,3,4,5
85	*Sphenoclea zeylanica* Gaertn.	Sphenocleaceae	Emergent	AH	Native	5	WLA, W	1,2,3,4,5
86	*Spirodela polyrrhiza* (L.) Schleid.	Araceae	Free-floating	PAH	Native	7	WLA, W	2
87	**Trapa natans* L.	Lythraceae	Free-floating	PAH	Native	143	P, LS, W	1,2,3,4,5
88	*Utricularia aurea* Lour.	Lentibulariaceae	Submerg -ed	PAH	Native	69	P, WLA, W	1,2,3,4,5
89	*Vallisneria spiralis* L.	Hydrocharita -ceae	Submerg -ed	PAH	Native	2	W	1,4
90	*Wolffia globosa* (Roxb.) Hartog &Plas	Araceae	Free floating	PAH	Native	6	W	1,4

Total family=34; Total genus=67; Total species=90; Emergent species=58; Free floating species= 11; Rooted floating species=12; Submerged species=9; Annual herb=18; Perennial herb=31; Perennial aquatic herb=32; Semi aquatic herb=3; Aquatic fern =5; Perennial shrub=1; Native species=75; Exotic species=15; Invasive species as per global invasive species database=19; Species invasive in India as per the database on invasive species in India=8; Invasive species common to both global invasive species database and the database on invasive species in India=4

'**'indicates the species are reported to be invasive as per global invasive species database of Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission (www.issg.org) and '*' indicates the species are reported to be invasive in India as per ENVIS database of Botanical Survey of India (BSI), Kolkata, West Bengal and Ministry of Environment, Forests and Climate Change (MoEF&CC), Government of India (www.bsienvis.nic.in); species with '**' on the left side and '*' on right side indicate that they are reported to be invasive in both the global invasive species database and the invasive species database of India; 'P' indicates pond; 'WLA' indicates water logged area; 'M' indicates marsh; 'LS' indicates lotic system (rivers, streams and channels); 'W' indicates wetland (floodplain wetlands and lakes) 'PAH' indicates Perennial aquatic herb; 'AH' indicates Annual herb; 'SAH' indicates Semi-aquatic herb; 'AF' indicates Aquatic fern; 'PS' indicates Perennial shrub; 'PH' indicates Perennial herb

Table 3. Diversity profile of aquatic macrophytes including the invasive species in different types of aquatic habitats of the study area.

SL	Diversity profile			Pond (270)	Water-logged area (319)	Marsh (246)	Lotic system (61)	Wetland (254)	Total (1150)
1	No. of species			31	43	55	33	83	90
2	No of invasive species			10	12	14	15	22	23
3	No. of families			18	23	23	20	34	34
4	No. of families with invasive species			8	9	12	11	17	18
5	Habit	Submerged	Overall	2	1	3	2	9	9
			Invasive species	0	0	3	1	4	4
		Rooted floating	Overall	6	5	4	4	12	12
			Invasive species	0	0	0	0	0	0
		Free floating	Overall	7	6	7	6	11	11
			Invasive species	3	3	3	5	5	5
		Emergent	Overall	16	31	41	21	51	58
			Invasive species	7	9	8	9	13	14
6	Growth form	Perennial aquatic herb	Overall	12	11	12	12	32	32
			Invasive species	4	5	6	8	12	12
		Annual herb	Overall	2	13	13	4	13	18
			Invasive species	0	3	2	1	2	3
		Semi-aquatic herb	Overall	1	3	3	2	3	3
			Invasive species	0	0	0	0	0	0
		Aquatic fern	Overall	4	3	4	3	5	5
			Invasive species	0	0	1	1	1	1
		Perennial shrub	Overall	1	1	1	1	1	1
			Invasive species	1	1	1	1	1	1
		Perennial herb	Overall	11	12	22	11	29	31
			Invasive species	5	3	4	4	6	6

Number within parenthesis indicates the total number of aquatic systems surveyed; sorting of invasive species is based on information from global invasive species database of Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission (www.issg.org) and ENVIS database of Botanical Survey of India (BSI), Kolkata, West Bengal and Ministry of Environment, Forests and Climate Change (MoEF&CC), Government of India (www.bsienvis.nic.in) based on information presented in Table 1

Species richness patterns

The species richness of aquatic macrophytes (AMs) varied across different bioclimatic zones, following the sequence CZ4 > CZ3 > CZ2 > CZ5 > CZ1. When analyzing the richness of invasive species across these bioclimatic zones, a different pattern emerged: CZ4 > CZ3 > CZ1 > CZ2 = CZ5 (Table 2 and Fig. 3). The richness of AMs also differed among various aquatic habitats, with the sequence being Wetland > Marsh > Waterlogged area > Lotic system > Pond. However, when examining the richness of invasive species across these habitat types, the pattern was as follows: Wetland > Lotic system > Marsh > Waterlogged area > Pond (Table 3).

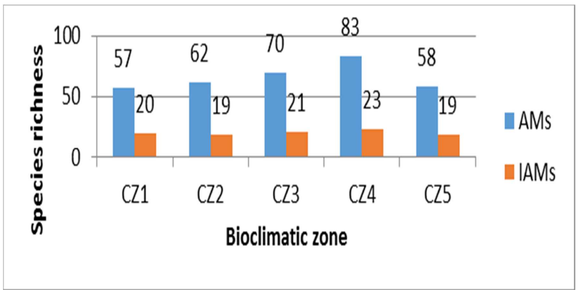

Fig. 3. Species richness of aquatic macrophytes (AMs) including the invasive species (IAMs) found across different bioclimatic zones of Assam.

Discussion

Our study explores the distribution of aquatic macrophytes (AMs), including invasive species, across various bioclimatic zones and habitats within the Indo-Burma biodiversity hotspot in Assam, Northeast India.

The region's diverse habitat conditions and environmental factors, such as temperature and precipitation patterns, influence the AMs found there. Surveys conducted in this area identified 90 species of AMs belonging to 67 genera and 34 families, with 23 species from 20 genera and 18 families considered invasive.

Bioclimatic Zone 1 (CZ1) includes Nagaon, Morigaon, Hojai, Karbi Anglong, and Dima Hasao districts, characterized by a sub-tropical climate due to their hilly terrain. CZ2 comprises Nalbari, Barpeta, and Darang districts, which experience a tropical climate with hot, humid summers and mild winters. CZ3 consists of Tinsukia, Dibrugarh, Sibsagar, Jorhat, Golaghat, and Sonitpur districts, featuring a sub-tropical climate with greater temperature variations and significant rainfall; tea cultivation is a prominent agricultural activity in this area. CZ4 encompasses Bongaigaon, Dhubri, Goalpara, Barpeta, North-Lakhimpur, Cachar, Karimganj, and Hailakandi districts, characterized by a tropical climate with hot, humid summers and heavy monsoon rainfall, leading to frequent flooding in low-lying areas. Finally, CZ5 covers Kokrajhar, Chirang, Udalguri, Baksa, and Dhubri districts, marked by a unique climate with extreme temperature and precipitation variations.

The diversity and distribution of macrophytes across these bioclimatic zones are significantly influenced by distinct environmental factors, including temperature, precipitation, and terrain. Each zone offers unique habitat conditions that support the growth of macrophyte species specially adapted to thrive in those environments. Other factors, such as flooding, agricultural activities, and extreme climate variations, also play a role in shaping macrophyte distribution and diversity. Our study found that species richness of AMs increased with the extremity of precipitation and temperature up to CZ4 (Yan *et al.*, 2015; Velthuis *et al.*, 2017), but declined in CZ5 due to the small size of the study area (Lindgren and Cousins, 2017; Aggemyr *et al.*, 2018). Greater precipitation provides ample water availability (Tabari *et al.*, 2020) and maintains sufficient soil moisture (Rossato *et al.*, 2017), thus promoting the growth of AMs under such conditions. On the other hand, water is often a limiting factor for plant growth in regions with lower rainfall (Schneider *et al.*, 2014; Dodds *et al.*, 2019), which may contribute to the reduced species richness of AMs in CZ1.

Furthermore, we found that 47 AMs, including 18 invasive species, were present in all bioclimatic zones. These species' presence across all bioclimatic zones indicates their greater niche breadth and strong competitive ability, facilitating their spread throughout the entire landscape of Assam. Invasive species such as *Eichhornia crassipes*, *Ipomoea carnea*, *Cynodon dactylon*, *Pistia stratiotes*, *Mimosa pudica*, *Ludwigia adscendens*, *Ipomoea aquatica*, and *Alternanthera philoxeroides* were found in all types of aquatic habitats and across all bioclimatic zones, with greater encountered sites. These species may have reached the final stage of the invasion process-landscape spread. Unless urgent management interventions are implemented for these species, there is a possibility of disruption of the aquatic habitats in the study area, affecting local biodiversity and ecosystem service potential.

While some studies have focused on the management of invasive AMs in India and abroad for species like *Alternanthera philoxeroides*, *Pistia stratiotes*, *Ipomoea aquatica*, *Ipomoea carnea*, *Ludwigia adscendens*, *Cynodon dactylon*, and *Eichhornia crassipes* (Putra *et al.*, 2015; Song *et al.*, 2020; Eid *et al.*, 2020; Shyam *et al.*, 2022), further research is needed on the management of infested aquatic habitats after removing these species. Additionally, it would be beneficial to explore methods for converting these invasive species into useful commodities while protecting the natural environment and human interests.

Our study highlights the importance of understanding the distribution of AMs, including invasive species, across various bioclimatic zones and habitats within the Indo-Burma biodiversity hotspot of Assam. By examining the effects of temperature and precipitation on species richness, we can better predict the potential impacts of invasive species on aquatic habitats and inform management strategies to mitigate their consequences. Continued research in this area will contribute to the preservation of biodiversity and ecosystem services within this vital region.

Conclusion

This study offers important insights on the distribution and richness of aquatic macrophytes, including invasive species, across various bioclimatic zones and different habitats in the Indo-Burma biodiversity hotspot of Assam. This study serves as a comprehensive documentation of aquatic macrophytes, including invasive species of Assam, comprising the Brahmaputra and Barak river basins in North-east India. It demonstrates that diverse habitat types and environmental gradients, along with distinct temperature and rainfall patterns across different bioclimatic zones, create varied aquatic habitat conditions that contribute to the high diversity of aquatic macrophytes, including invasive species, in the region. Additionally, the study identifies several invasive species that are prevalent in all aquatic habitats and bioclimatic zones, indicating their high potential for encroachment and landscape spread in the study area. The study underscores the need for further in-depth ecological investigations and emphasizes the importance of managing these species in a manner that protects both the natural environment and human interests.

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