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Seasonal diversity and community structure of wetland macrophytes in two monsoon-influenced lakes in eastern India

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ABSTRACT

Seasonal diversity and community structure of wetland macrophytes in two monsoon-influenced lakes in eastern India

This study tracked seasonal changes in macrophyte communities in two freshwater lakes in Ranchi, India: Bundu Lake, which shows marked seasonal fluctuation, and Ratu Maharaja Lake, which remains comparatively stable. Field surveys were conducted from October 2023 to April 2025, covering the pre-monsoon, monsoon, and post-monsoon periods. Using 1 m² quadrats, we recorded 87 macrophyte species. Species diversity, including alpha diversity, beta diversity, and its components, importance value index (IVI), relative IVI, evenness, dominance, rank–abundance curves (RACs), and spatial distribution, was analysed using standard ecological indices. All computations were performed in R (v4.4.0). Ratu Maharaja Lake supported more species (50–68) and a balanced mix of emergent, submerged, and rooted floating plants. Bundu Lake had fewer species (36–51) and showed minimal seasonal turnover, with free-floating species dominating. Bundu Lake was dominated by nestedness, reflecting species loss and recolonization, whereas Ratu Maharaja Lake showed higher turnover, indicating active species replacement across seasons. Over 63% of the species changed their ranking between seasons, suggesting that fluctuating water levels strongly influence community stability. The species distribution was relatively stable in Ratu Maharaja Lake but clumped and variable in Bundu Lake. These findings provide a baseline for biodiversity monitoring and show how hydrological stability supports wetland resilience. They also offer a useful reference for predicting how communities may respond to future climate and human pressures.

KEY WORDS: wetland macrophytes, seasonal species dynamics, alpha and beta diversity, relative IVI, ecological turnover, rank abundance curves, freshwater lakes, Eastern India.

RESUMEN

Diversidad estacional y estructura comunitaria de las macrófitas de humedal en dos lagos influenciados por el monzón en el este de la India.

Este estudio realizó un seguimiento de los cambios estacionales en las comunidades de macrófitos en dos lagos de agua dulce en Ranchi, India: el lago Bundu, que muestra una marcada fluctuación estacional, y el lago Ratu Maharaja, que se mantiene relativamente estable. Se llevaron a cabo estudios de campo entre octubre de 2023 y abril de 2025, que abarcaron los períodos premonzónico, monzónico y posmonzónico. Utilizando cuadrantes de 1 m², se registraron 87 especies de macrófitos. Se analizó la diversidad de especies, incluida la diversidad alfa, la diversidad beta y sus componentes, el índice de valor de importancia (IVI), el IVI relativo, la uniformidad, el dominio, las curvas de rango-abundancia (RAC) y la distribución espacial, utilizando índices ecológicos estándar. Todos los cálculos se realizaron en R (v4.4.0). El lago Ratu Maharaja albergaba más especies (50-68) y una mezcla equilibrada de plantas emergentes, sumergidas y flotantes con raíces. El lago Bundu tenía menos especies (36-51) y mostraba una renovación estacional mínima, con predominio de especies flotantes libres. El lago

Bundu estaba dominado por el anidamiento, lo que reflejaba la pérdida y recolonización de especies, mientras que el lago Ratu Maharaja mostraba una mayor renovación, lo que indicaba una sustitución activa de especies a lo largo de las estaciones. Más del 63 % de las especies cambiaron entre estaciones, lo que sugiere que las fluctuaciones en los niveles de agua influyen considerablemente en la estabilidad de la comunidad. La distribución de las especies era relativamente estable en el lago Ratu Maharaja, pero agrupada y variable en el lago Bundu. Estos hallazgos proporcionan una base de referencia para el seguimiento de la biodiversidad y muestran cómo la estabilidad hidrológica favorece la resiliencia de los humedales. También ofrecen una referencia útil para predecir cómo pueden responder las comunidades a las presiones climáticas y humanas futuras.

PALABRAS CLAVE: *macrófitos de humedales, dinámica estacional de especies, diversidad alfa y beta, IVI relativo, renovación ecológica, curvas de abundancia de rango, lagos de agua dulce, este de la India..*

INTRODUCTION

Wetlands are among the most productive and ecologically significant ecosystems on Earth. They support rich biodiversity, regulate water flow, recycle nutrients, and store carbon (Keddy, 2023). Macrophytes form the structural base of these systems. They increase habitat diversity, improve water clarity, and sustain aquatic food webs (Gopal, 2012, Ramachandra et al., 2024). Their growth and spread depend on the climate, water levels, soil conditions, and human activity (Dar et al., 2014, Xia et al., 2022).

Across India, the monsoon cycle drives great seasonal changes in wetland plants. These changes affect which species dominate and how communities are structured. They result from variations in water depth, sediment buildup, and nutrient supply (Lal & Lal, 2023, Singh et al., 2024). Understanding these shifts is crucial for wetland conservation and restoration, particularly as small freshwater bodies face escalating anthropogenic pressures (Regmi et al., 2021, Peng et al., 2022).

Ecologists rely on several well-known indices to track how plant communities are put together and how they shift across seasons. Measures such as Shannon and Simpson indices capture overall diversity, Margalef index reflects richness, and the Berger-Parker index helps show which species dominate. Beta diversity quantifies the variation in community composition among sites, enabling researchers to distinguish whether observed differences arise primarily from species turnover (replacement) or from nested patterns of species gain or loss. The analysis further incorporated relative IVI to evaluate whether individual species maintained stable positions in community structure throughout seasonal changes. Rank abundance curves, along with alpha and beta diversity, help visualize how evenly species are spread in a community and how much one site differs from another (Magurran, 2004, 2013, Legendre & De Cáceres, 2013).

Although research on Indian wetland macrophytes is growing, detailed seasonal and spatial comparative studies on community structure remain limited. This gap is particularly evident for small waterbodies in eastern India, which differ markedly in hydrological regime, water connectivity, degrees of human disturbance, and habitat characteristics. Ranchi district in Jharkhand supports several culturally and ecologically important lakes, yet their macrophyte dynamics remain poorly documented.

Earlier work from Ranchi notes high macrophyte diversity in many water bodies, but these studies rarely link those patterns to clear seasonal shifts. Recent work also shows that urban growth and land use change are starting to alter which species persist and how they are distributed. (Sharma et al., 2020, Kadave & Kumari, 2025).

Bundu Lake (BL) and Ratu Maharaja Lake (RML) fall within this broader hydro-ecological context but have not been examined individually. The present study focused on these two lakes to provide a detailed analysis of their macrophyte communities and seasonal variation. The RML maintains steadier water levels, connects more effectively with surrounding drains, and features gently sloping shores that support a diverse range of vegetation. These contrasts are supported by data from the Jharkhand Water Resources Department (https://wrd.jharkhand.gov.in › node) and field notes.

This study examined how seasonal changes influence macrophyte diversity and community structure in two freshwater lakes located in the Ranchi district. The work follows shifts in species richness, community composition, growth forms, dominance, and stability. Diversity and evenness indices help capture how the communities are organized and how resilient they are across seasons. RML, with its relatively steady water levels, was expected to support higher and more even diversity. BL, with greater fluctuation in water level, was anticipated to show stronger seasonal swings. Together, these expectations frame the study's broader goal of understanding macrophyte dynamics in small tropical lakes, an issue increasingly important for wetland monitoring and management.

MATERIALS AND METHODS

Study areas

This study was conducted in two freshwater lakes, Bundu Lake (BL) and Ratu Maharaja Lake (RML), which are located in the Ranchi district of Jharkhand, eastern India (Fig. 1). These two lakes differ sharply in water behaviour and basin shape, which makes them useful for comparing how macrophyte communities shift with the season.

Bundu Lake (BL)

Located at 23.1621° N, 85.5837° E at an elevation

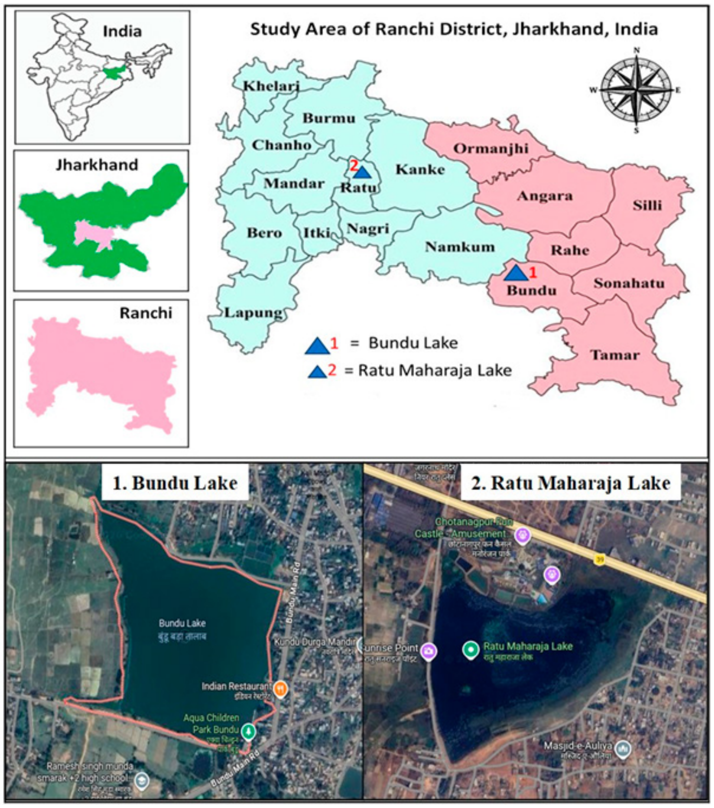

Figure 1. Locations and satellite imagery of the study sites in Ranchi District, Jharkhand, Eastern India. The map includes the positions of Bundu Lake (1) and Ratu Maharaja Lake (2) within the administrative boundaries of India (top left), Jharkhand state (middle left, pink indicating Ranchi District), and Ranchi District (main map). The study sites are marked by blue triangles with red numbers. *Ubicaciones e imágenes satelitales de los sitios de estudio en el distrito de Ranchi, Jharkhand, al este de la India. El mapa incluye las posiciones del lago Bundu (1) y el lago Ratu Maharaja (2) dentro de los límites administrativos de la India (arriba a la izquierda), el estado de Jharkhand (en el centro a la izquierda, en rosa, indicando el distrito de Ranchi) y el distrito de Ranchi (mapa principal). Los sitios de estudio están marcados con triángulos azules con números rojos.*

of approximately 259 m, the BL is a perennial, seminatural, human-modified, urban freshwater wetland spanning approximately 40.5 hectares in the Bundu subdivision of Ranchi. Owing primarily to monsoon rainfall and upland runoff, the lake has limited inlet and outlet connectivity through a broad irrigation canal. Its depth ranges from 2 m near the margins to 7.5 m at the center. The surrounding catchment includes grasslands and agricultural fields, particularly to the south and west. The urban settlements are in the east and north. The lake is used for fishing, irrigation, domestic activities, and recreation, and it also supports local biodiversity and water storage.

Ratu Maharaja Lake (RML)

Also known as Ratu Talab, this man-made, perennial, semiurban lake (23.4132° N, 85.2166° E; elevation ~661 m) lies in the Ratu Block, approximately 18 km northwest of Ranchi city. It was constructed in 1901 by King Udai Pratap Nath Shah Deo for rainwater harvesting and covers approximately 6.9 hectares, with depths ranging from 1.5 m at the edges to 7.5 m in the central basin. The catchment includes agricultural fields, small settlements, and patches of seminatural vegetation. The lake supports livelihoods through fisheries, irrigation, bathing, and recreation. RML connects more freely with nearby drains and low-lying areas, unlike BL, which is more closed off.

Sampling methodology

Extensive field surveys were conducted from October 2023 - April 2025, covering pre-monsoon, monsoon, and post-monsoon seasons. A quadrat-based sampling approach was used to document macrophyte composition through both qualitative (presence-absence) and quantitative (abundance and frequency) measures. In each lake, fourteen 1 m × 1 m quadrats were randomly placed along the littoral zone, with three replicates at each sampling site. The samples were collected from the shoreline to 3 m into the water column. The lakes varied in size, but we used the same number of quadrats in each one to keep the data comparable. This approach follows standard protocols for macrophyte studies in small to medium-sized tropical wetlands (Chambers et al., 2008, Bornette & Puijalon, 2011, Orfanidis et al., 2008, Mormul et al., 2013, Amorim et al., 2015). All macrophyte species occurring within the quadrats were recorded and counted manually (Mahato & Ghosh, 2025).

Identification and nomenclature

Plant species were identified using standard taxonomic keys and diagnostic features from 'Botany of Bihar and Orissa' (Haines, 1978), 'Aquatic and Wetland Plants of India' (Cook, 1996), 'Flora of Bihar: Analysis' (Singh,2001), and 'Wetland Flora of West Bengal' (Chowdhury & Chowdhury, 2022). The scientific names were verified and updated using the Plants of the World Online (POWO, 2025) and the World Flora Online (WFO, 2025).

Voucher specimens were prepared following the methods described in Jain and Rao (1977). They were then deposited in the SKBU Herbarium in the Botany Department so that plant identifications can be verified later if needed. Accession numbers range from SKBU/BOT/RCH/MG-S-001 to SKBU/BOT/RCH/MG-S-320 for the seasonal quadrat collections made between 2023 and 2025. Each sample received a sequential number from 01 to 320, and these numbers appear both in the field notes and on the corresponding herbarium sheets to ensure everything remains traceable for future reference or validation.

Data analysis

Analysis of community composition (taxonomic, growth form, and life cycle composition)

Seasonal macrophyte richness was quantified using quadrat-based species counts. Macrophyte composition was organized into hierarchical categories that encompassed angiosperms (divided into dicots and monocots) with further subdivision into families, genera, and species. Ferns and macroalgae were treated as separate groups. Growth forms were classified as emergent, submerged, free-floating, or rooted with floating leaves, while life cycle patterns distinguished annuals from perennials.

Species dominance and rarity patterns through IVI

For each recorded species, the importance value index (IVI) was calculated using the formula IVI = RD + RF + RA, where RD denotes relative density, RF represents relative frequency, and RA indicates relative abundance. The relative IVI (R-IVI), expressed as a percentage of the total IVI (R-IVI = [IVI/Total IVI] × 100), facilitates interseasonal comparisons and the assessment of community structure (Magurran, 2004; Mahato & Ghosh, 2025). Phytosociological parameters such as percent frequency, relative frequency, abundance, density, and relative density were computed as per Margalef (1969).

Species exhibiting higher IVI values were classified as dominant macrophytes, reflecting their greater contribution to community structure, resilience, and ecological influence within each lake. Conversely, species with lower IVI values (IVI < 5) were considered rare, indicating low abundance or limited spatial distribution. Changes in IVI across seasons made it possible to see which species stayed dominant and which ones were rare. R-IVI was used to compare the stability of different macrophyte growth forms, where higher values reflected stronger ecological stability within the community.

Assessment of alpha diversity

Within-community diversity was evaluated using alpha (α) diversity indices, including the Shannon–Wiener index, Simpson's index, species richness, and evenness, following Magurran (2004).

- **Shannon–Wiener index (H′)**: This index was developed by Claude E. Shannon and Norbert Wiener (Shannon & Wiener, 1963) and is used in ecology to measure species diversity by combining species richness with relative abundance and evenness.

$$H' = -\sum_{i=1}^{S} (p_i) \times \ln(p_i)$$

Where pi = the proportion of individuals belonging to the i^{th} species, S = the total number of species, Pi =n/N (n = the number of individuals of each species; N = the total number of individuals; N = n1+n2+n3+n4+n5………, ln = the natural logarithm. High H′ scores show a more even and diverse community, while low values point to one or a few species dominating.

- **Simpson's diversity index (1 – D)**: This dominance index was developed by Edward H. Simpson (1949). It is used to measure both species richness and evenness. Simpson's index (D) defines the probability that two individuals randomly selected from a sample belong to the same species. Simpson's diversity index (1–D) represents the probability that two randomly selected individuals from a community belong to different species.

$$D = \sum_{i=1}^{S} (p_i)^2$$

(1 − D) represents the diversity status. The index ranges between 0 and 1; values closer to 1 indicate greater diversity, whereas values near 0 reflect low diversity.

- Margalef's species richness index (d): This index was developed by the ecologist Ramon Margalef (1969). This index is used to compare the species richness of different ecosystems, even if the sample sizes are different. This index focuses solely on species richness and does not account for species evenness (relative abundance). It is also used to assess ecosystem health, human influence, and environmental stability.

$$d = \frac{S-1}{\ln N}$$

Where S = the number of species and N = the total number of individuals. Higher d values indicate greater richness. Interpretations include the following: <2.0: low richness; 2.0–3.0: moderate richness; >3.0: high richness; and >5.0: very high richness.

- **Pielou's evenness index (J′):** This index was developed by Evelyn Pielou (1966) and is used to measure the evenness of a community.

$$J' = \frac{H'}{\ln S}$$

Where H' = the observed value of the Shannon index, ln S = the natural logarithm of S, and S = the total number of species. The value of J′ ranges from 0 - 1. '1' indicates perfect evenness, and '0' indicates no evenness (dominance of one or a few species).

Ordination and β-diversity patterns of macrophyte assemblages in BL and RML

Non-metric multidimensional scaling (NMDS) was used to visualize seasonal and inter-lake differences in macrophyte community composition between BL and RML. The ordination was based on Bray–Curtis dissimilarity calculated from summed abundances per species and season (absent species = 0), with no transformation applied. NMDS was performed in three dimensions (k = 3) with a maximum of 500 random starting configurations (trymax = 500) using the metaMDS function from the *vegan* package (v2.7-1; Oksanen, 2015) in R version 4.4.0. The solution with the lowest stress value was retained. Stress values were interpreted following Clarke (1993): <0.05 = excellent, <0.10 = good, <0.20 = fair/useful, and >0.20 = poor.

To assess between-community variation, β-diversity was calculated using presence–absence data and the Sørensen dissimilarity index (β_{sor}), which quantifies overall compositional differences among macrophyte assemblages across seasons and lakes. The Sørensen similarity index was calculated as $S = 2a / (2a + b + c)$ (Magurran, 2013), and its dissimilarity form $(1 - S)$ was used to estimate variation in species composition (Baselga, 2010, Podani & Schmera, 2011, Carvalho et al., 2012).

Pairwise β diversity comparisons were conducted only between consecutive seasonal transitions (pre-monsoon → monsoon, monsoon → post-monsoon, and post-monsoon → pre-monsoon) within each lake. This ensured that each β-diversity value corresponded to a clearly defined temporal or spatial comparison.

Total Sørensen β diversity (β_{sor}) was partitioned into species replacement (β_{sim}) and nestedness-resultant dissimilarity (β_{sne}) using the *betapart* package (v1.6.1) in R (v4.4.0), following Baselga (2010). Species replacement represents compositional change due to species substitution, whereas nestedness reflects differences driven by species loss or gain without replacement.

The partitioned components were visualized to explicitly track seasonal transitions within each lake, with one value per lake per transition, thereby ensuring unambiguous temporal interpretation.

Dominance dynamics and rank-abundance patterns

To assess species dominance and communities across seasons, the Berger-Parker dominance index (BPI) and rank-abundance curves (RACs) were generated following Magurran (2013). The Berger-Parker index (BPI) was calculated as the ratio of the abundance of the most dominant species (Nm) to the total abundance of all species (n) within a lake and season (BPI = Nm/n). When BPI is high and the RAC slope is steep, a few species dominate. Flatter curves suggest a more even community. Rank Abundance Curves (RAC), the Berger-Parker Index (BPI), rank reversal, and rank consistency were analysed in R (v4.4.0) using the packages *vegan* (v2.6-10) for diversity and dominance computations, *ggplot2* (v3.5.2) for graphical representation, and *dplyr* (v1.1.4) and *tidyr* (v1.3.1) for data handling and ranking analyses. These indices were computed using species abundance data derived from quadrat sampling, and the results were interpreted seasonally and between lakes to evaluate community structural stability. The RAC slope was obtained by plotting the $\log_{10}$-transformed abundance of each species against its rank order, where steeper negative slopes indicate greater dominance and lower evenness.

Temporal changes in macrophyte dominance were analysed using rank-based approaches to assess the stability and variability of community composition across seasons, following the framework of Capers et al. (2010). Two complementary indices, Rank Reversal and Rank Consistency, were employed for this purpose. Species were first ranked according to their abundance within each season for each lake. Rank reversal was defined as a shift in a species' position within the dominance hierarchy between seasons (e.g., from rank 1 to rank 5), with a change of two or more positions ($\Delta rank \geq 2$) considered an ecologically significant reversal, indicating shifts in the position of the species.

To evaluate the temporal stability of dominance, the rank consistency index (RCI) was calculated as the ratio of the standard deviation of species ranks across seasons (rank-SD) to the number of seasons in which the species occurred:

$$\mathrm{RCI} = \frac{\text{Standard deviation of species ranks (Rank} - \text{SD)}}{\text{Number of Seasons Present}}$$

Species were classified as having high rank consistency ($\mathrm{RCI} \geq 0.25$) or low rank consistency ($\mathrm{RCI} < 0.25$). Lower RCI values indicate greater temporal stability in species dominance, whereas higher values reflect greater variability across seasons. This made it easier to see which species stayed dominant and which ones changed their position through the seasons.

RESULTS

1. Seasonal variation in taxonomic composition

1.1 Seasonal patterns of species richness

A total of 87 wetland macrophyte species were recorded across BL and RML during the study period. Of these, 35 species were common to both lakes, 17 species were exclusive to BL, and 35 species occurred only in RML, indicating clear differences in community composition between the two systems (Fig. 2).

The macrophyte community of BL represents a moderately diverse assemblage of wetland plants, comprising up to 22 families, 37 genera, and 51 species (Table 1). The community was dominated by angiosperms, with monocotyledonous and dicotyledonous taxa both well represented, although monocots contributed slightly more species. Ferns were consistently present but limited to two species, and macroalgae were absent from the assemblage. Across seasons, the community structure of BL was consistently characterized by the dominance of a small number of widespread taxa, notably *Alternanthera philoxeroides* (Mart.) Griseb., *Pontederia crassipes* Mart., *Hydrilla verticillata* (L.f.) Royle, *Azolla pinnata* R.Br.,

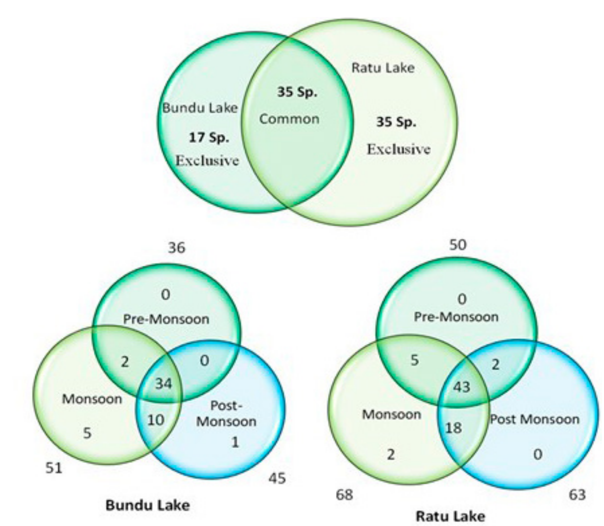

Figure 2. *Venn diagrams illustrating the seasonal abundance of macrophyte species in Bundu Lake and Ratu Maharaja Lake during the pre-monsoon, monsoon, and post-monsoon seasons. Diagramas de Venn que ilustran la abundancia estacional de especies de macrófitos en el lago Bundu y el lago Ratu Maharaja durante las estaciones premonzónica, monzónica y posmonzónica.*

and *Lemna perpusilla* Torr., which together defined the core macrophyte assemblage of the lake.

In contrast, RML supported a richer and more taxonomically extensive macrophyte community, comprising up to 31 families, 49 genera, and 68 species (Table 1). Dicots and monocots contributed almost equally to overall species richness, indicating a more balanced phylogenetic structure. Ferns were regularly represented by two to three species, and macroalgae formed a persistent component of the community, represented by three to four species, including charophytes. Community structure in RML was defined by a broader set of dominant species, with *Alternanthera philoxeroides*, *Eleocharis acutangula* (Roxb.) Schult., and *Hydrilla verticillata* consistently contribute high importance values across seasons.

Seasonal variation in species richness was evident in both lakes, although the magnitude of change differed. In BL, species richness increased from 36 species in the pre-monsoon to 51 species during the monsoon, followed by a decline to 45 species in the post-monsoon. In RML, species richness remained consistently higher across seasons, with 50, 68, and 63 species recorded in the pre-monsoon, monsoon, and post-monsoon periods, respectively (Fig. 2, Tables S1–S3 (supplementary information, available at https://www.limnetica.com/en/limnetica)).

Patterns of seasonal persistence and exclusivity further distinguished the two lakes. In BL, 34 species persisted across all seasons, whereas several taxa were restricted to specific periods. *Lobelia alsinoides* was recorded exclusively during the post-monsoon season, while five species, *Dentella repens* (L.) J.R.Forst. & G.Forst., *Lindernia parviflora* (Roxb.) Haines, *Ludwigia perennis* L., *Murdannia nudiflora* (L.) Brenan, and *Murdannia vaginata* (L.) G.Brückn., occurred only during the monsoon period. No species were shared exclusively between the pre- and post-monsoon seasons.

In RML, seasonal persistence was higher, with 43 species present year-round. Only two species (*Dentella repens* and *Ludwigia perennis*) were restricted to the monsoon season, and no species were exclusive to the pre-monsoon period. Seasonal overlap among assemblages was broader than in BL, indicating greater temporal continuity in species presence.

1.2 Life cycle composition and dominant macrophyte families

Both lakes contained annuals and perennials, yet perennials made up a larger and steadier fraction in RML (59–70 %) than in BL (55–75 %) (Table 2). Annuals increased sharply during the monsoon in both lakes from 25 % to 47 % of the community in BL and from 30 % to 41 % in RML, and then declined again.

Cyperaceae and Poaceae were the leading families in both lakes. Still, their dominance shifted with the seasons (Fig. 3). In BL, Cyperaceae stayed on top throughout the year, while Araceae, Asteraceae, Linderniaceae, and Hydrocharitaceae gained ground in wetter months. RML showed

Table 1. Seasonal variation in macrophyte richness across phylogenetic categories (Families, Genera, Species, Dicots, Monocots, Ferns, and Macroalgae) in Bundu Lake and Ratu Maharaja Lake. *Variación estacional en la riqueza de macrófitos en las diferentes categorías filogenéticas (familias, géneros, especies, dicotiledóneas, monocotiledóneas, helechos y macroalgas) en los lagos Bundu y Ratu Maharaja.*

Parameter	BL			RML		
	Pre-Monsoon	Monsoon	Post-Monsoon	Pre-Monsoon	Monsoon	Post-Monsoon
Families	**18**	**21**	**22**	**24**	**31**	**30**
Genera	**26**	**37**	**35**	**36**	**49**	**46**
Species	**36**	**51**	**45**	**50**	**68**	**63**
Dicots	**15**	**25**	**22**	**21**	**32**	**28**
Monocots	**19**	**24**	**21**	**24**	**30**	**28**
Ferns	**02**	**02**	**02**	**02**	**03**	**03**
Macro Algae	**00**	**00**	**00**	**03**	**03**	**04**

Table 2. Seasonal abundance of annual and perennial macrophytes in Bundu Lake and Ratu Maharaja Lake. *Abundancia estacional de macrófitos, anuales y perennes, en el lago Bundu y el lago Ratu Maharaja.*

Season	Lake	Annuals	Perennials	Total	% Annuals	% Perennials
Pre-Monsoon	Bundu Lake	9	27	36	25.0%	75.0%
Pre-Monsoon	Ratu Lake	15	35	50	30.0%	70.0%
Monsoon	Bundu Lake	24	27	51	47.1%	52.9%
Monsoon	Ratu Lake	28	40	68	41.2%	58.8%
Post-Monsoon	Bundu Lake	20	25	45	44.4%	55.6%
Post-Monsoon	Ratu Lake	22	41	63	34.9%	65.1%

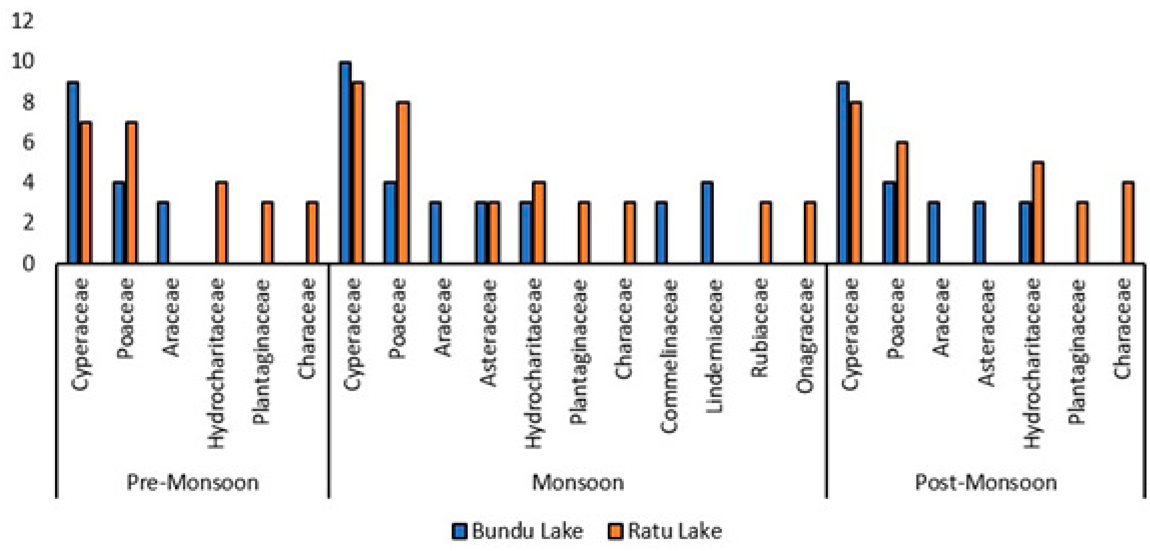

Figure 3. Seasonal abundance of dominant macrophyte families in Bundu Lake and Ratu Maharaja Lake across the pre-monsoon, monsoon, and post-monsoon seasons. *Abundancia estacional de las familias de macrófitos dominantes en los lagos Bundu y Ratu Maharaja durante las estaciones premonzónica, monzónica y posmonzónica*.

more balanced representation among the top families, with Hydrocharitaceae, Characeae, and Plantaginaceae becoming prominent after the monsoon.

1.3 Seasonal patterns of species dominance and rarity

Seasonal IVI analyses revealed distinct patterns of dominance and rarity (Tables S4, supplementary information, available at https://www.limnetica.com/en/limnetica). In the BL, *Alternanthera philoxeroides*, *Pontederia crassipes*, *Hydrilla verticillata*, *Azolla pinnata*, and *Lemna perpusilla* were dominant across all the seasons, although their IVI values fluctuated. Several taxa, including *Ceratophyllum demersum* L., *Nymphaea pubescens* Willd., *N. nouchali* Burm.f., *Nelumbo nucifera* Gaertn., and *Ludwigia* spp., presented low IVI values (<5), indicating their rarity within the community.

In RML, *Alternanthera philoxeroides*, *Eleocharis acutangula*, and *Hydrilla verticillata* remained dominant year-round, with *Alternanthera sessilis* (L.) DC. and *Nymphaea pubescens* Willd. are frequent during the monsoon season and post-monsoon. Rare species, including *Paspalum scrobiculatum* L., *Pontederia vaginalis Burm.f.*, *Grangea maderaspatana* (L.) Desf., *Ceratopteris thalictroides* (L.) Brongn., and *Ipomoea aquatica* Forssk., vary seasonally.

2. Growth form structure and seasonal variability

Across the study period, macrophyte growth-form composition showed a broadly similar pattern in both lakes. Emergent species clearly dominated the vegetation and remained the most prominent growth form in every season (Fig. 4). Their numbers increased during the monsoon, when emergent macrophytes peaked at 33 species in BL and 41 species in RML. By contrast, free-floating and rooted floating-leaved macrophytes changed little through the year and maintained comparable species numbers in both lakes, indicating limited seasonal sensitivity within these groups.

The strongest contrast between the two lakes was evident in the submerged component. In BL, submerged macrophytes were consistently scarce, with only five to six species recorded regardless of season. RML, however, supported a much richer submerged flora. Species numbers increased steadily from the pre-monsoon to the post-monsoon period and reached a maximum of 18 species after the rains, when underwater conditions were most favorable for submerged growth.

The patterns observed in relative importance values closely followed these changes in growth-form composition (Fig. 4). Emergent macrophytes contributed the highest R-IVI% in both lakes throughout the year, although their relative importance fluctuated more strongly in BL than in RML. Submerged macrophytes gained increasing importance across seasons in RML, reflecting their expanding contribution to community structure, while their R-IVI% remained consistently low in BL.

Rooted floating-leaved macrophytes showed little variation in R-IVI% and maintained a relatively stable role in both lakes across seasons. Taken together, emergent and submerged growth forms achieved higher overall importance values in RML, whereas lower values in BL point to clear interlake differences in growth-form dominance and the overall structural organization of macrophyte communities.

3. Seasonal trends in alpha diversity indices

Seasonal trends in alpha-diversity indices closely followed patterns of species richness (Table 3). In BL, nearly all metrics, including Simpson, Shannon, Margalef, and Pielou, peaked during the monsoon season and were lowest before the rains. RML maintained consistently higher values, with Shannon diversity reaching its maximum in the post-monsoon period and evenness showing little seasonal fluctuation. These patterns indicate stronger seasonal sensitivity in BL relative to RML.

4. Ordination and β-diversity patterns of macrophyte assemblages in BL and RML

4.1 Non-metric Multidimensional Scaling (NMDS) ordination

The 3D NMDS ordination based on Bray–Curtis dissimilarity clearly resolved seasonal patterns in macrophyte community structure in both lakes (stress = 0.0475 for BL, 0.0549 for RML; Fig.

Table 3. Seasonal variation in macrophyte alpha diversity indices in Bundu Lake and Ratu Maharaja Lake, showing Simpson's (1–D), Shannon (Hs), Margalef (d), and evenness (J') values. *Variación estacional en los índices de diversidad alfa de macrófitos en el lago Bundu y el lago Ratu Maharaja, mostrando los valores de Simpson (1–D), Shannon (Hs), Margalef (d) y uniformidad (J').*

Lake	Season	Simpson's Index (1-D)	Shannon Index (Hs)	Margalef Index (d)	Evenness (Pielou's J')
Bundu	Pre-monsoon	0.944	3.1826	4.9712	0.8881
	Monsoon	0.9707	3.7339	6.6377	0.9496
	Post-monsoon	0.9623	3.5223	6.0132	0.9253
Ratu	Pre-monsoon	0.9714	3.7321	6.9358	0.9540
	Monsoon	0.9796	3.854783	8.7789	0.9135
	Post-monsoon	0.97663	3.9591	8.2408	0.9555

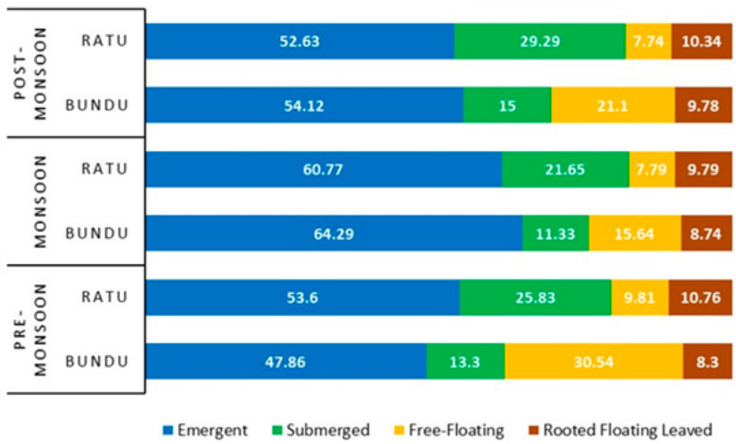

Figure 4. Seasonal distribution of the relative importance value index (R-IVI%) among macrophyte growth forms (emergent, submerged, free-floating, and rooted floating-leaved) in Bundu Lake and Ratu Maharaja Lake. *Distribución estacional del índice de importancia relativa (R-IVI%) entre las formas de crecimiento de los macrófitos (emergentes, sumergidos, flotantes libres y flotantes con raíces) en el lago Bundu y el lago Ratu Maharaja.*

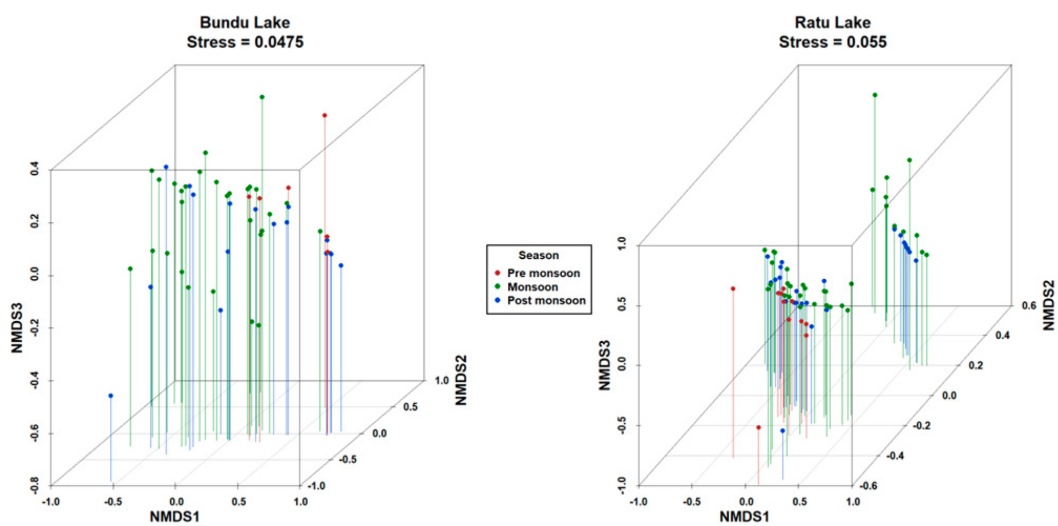

Figure 5. 3D Nonmetric Multidimensional Scaling (NMDS) ordination of macrophyte communities in Bundu Lake (left) and Ratu Maharaja Lake (right) across seasons, pre-monsoon (red), monsoon (green), and post-monsoon (blue), based on Bray–Curtis dissimilarity. *Ordenación mediante escalamiento multidimensional no métrico (NMDS) en 3D de las comunidades de macrófitos en el lago Bundu (izquierda) y el lago Ratu Maharaja (derecha) a lo largo de las estaciones, premonzónica (rojo), monzónica (verde) y posmonzónica (azul), basada en la disimilitud de Bray-Curtis.*

5). In BL, samples formed compact and well-defined seasonal clusters, indicating predictable and stable community reorganization across seasons. Post-monsoon assemblages aligned with emergent and floating-leaved species, including *Alternanthera philoxeroides*, *Azolla pinnata*, and *Panicum repens*, while pre-monsoon samples shifted toward submerged taxa such as *Hydrilla verticillata* and *Ceratophyllum demersum* (Table S5, supplementary information, available at https://www.limnetica.com/en/limnetica). This tight spatial grouping reinforces the nestedness-driven dynamics, where seasonal change is governed mainly by temporary species loss and subsequent recovery.

In RML, NMDS points exhibited broader

dispersion and weaker seasonal segregation, reflecting greater temporal heterogeneity and stronger species turnover (Table S6, supplementary information, available at https://www.limnetica.com/en/limnetica). Monsoon communities were associated with *Alternanthera philoxeroides* and *Eleocharis acutangula*, post-monsoon assemblages with *Hydrilla verticillata* and *Cyperus iria*, and pre-monsoon points with *Vallisneria spiralis*. These ordination trends corroborate the turnover-dominated dynamics identified in beta-diversity partitioning.

4.2 Beta Diversity and Seasonal Compositional Changes

Partitioning of Sørensen β diversity into species turnover (replacement) (β_{sim}) and nestedness (loss or gain) resultant dissimilarity (β_{sne}) revealed clear seasonal variation in macrophyte community composition in both lakes (Fig. 6).

In BL, the pre-monsoon → monsoon transition was entirely driven by nestedness (β_{sne} = 0.172), with no detectable species replacement (β_{sim} = 0.000), indicating that seasonal change was primarily associated with species loss or gain. The monsoon → post-monsoon transition showed relatively low β diversity, reflecting limited compositional change. In contrast, the post-monsoon → pre-monsoon transition exhibited increased species replacement (β_{sim} = 0.056), suggesting partial community restructuring toward the dry season.

In RML, seasonal β diversity was generally higher. The pre-monsoon → monsoon transition showed substantial nestedness (β_{sne} = 0.146) with a modest replacement component. The lowest β diversity occurred during the monsoon → post-monsoon transition, indicating relative seasonal stability. The post-monsoon → pre-monsoon transition exhibited the highest total β diversity (β_{sor} = 0.204), with nearly equal contributions from species replacement (turnover) and nestedness, reflecting pronounced seasonal reorganization.

5. Rank-abundance patterns and dominance dynamics

5.1 Seasonal variation in rank-abundance and community evenness

Rank-abundance curves and the Berger–Parker index revealed how dominance itself shifted (Table 4; Fig. 7). BL curves steepened in pre-monsoon (strongest few-species dominance), flattened dramatically in monsoon, and settled in between post-monsoon. RML curves remained gentler and far more consistent across seasons, which is a hallmark of resilient, equitable assemblages.

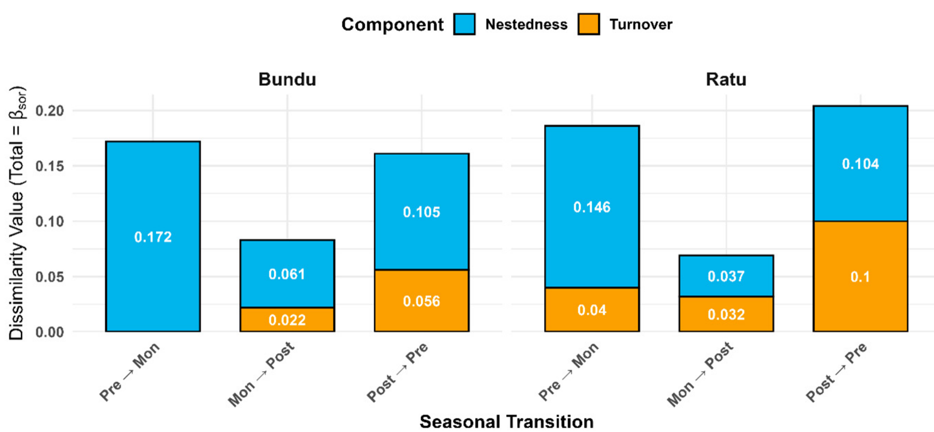

Figure 6. Partitioning of Sørensen-based beta diversity (β_{sor}) into species replacement (β_{sim}) and nestedness-resultant dissimilarity (β_{sne}) across seasonal transitions (Pre-monsoon → Monsoon, Monsoon → Post-monsoon, and Post-monsoon → Pre-monsoon) in Bundu Lake and Ratu Maharaja Lake. Each value represents a single seasonal transition within a lake. *División de la diversidad beta basada en Sørensen (β_{sor}) en sustitución de especies (β_{sim}) y disimilitud resultante del anidamiento (β_{sne}) a lo largo de las transiciones estacionales (pre-monzón → monzón, monzón → posmonzón y posmonzón → premonzón) en el lago Bundu y el lago Ratu Maharaja. Cada valor representa una única transición estacional dentro de un lago.*

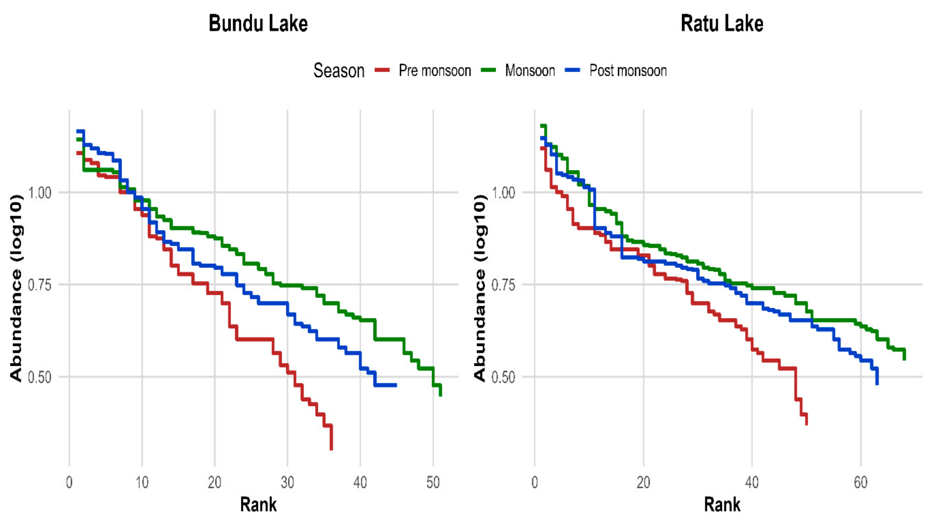

Figure 7. Rank-abundance curves (log_{10} scale) of macrophyte communities in Bundu Lake (left) and Ratu Maharaja Lake (right) across seasons, showing contrasting patterns of dominance and evenness. *Curvas de abundancia por rango (escala log_{10}) de las comunidades de macrófitos en el lago Bundu (izquierda) y el lago Ratu Maharaja (derecha) a lo largo de las estaciones, que muestran patrones contrastados de dominancia y uniformidad.*

Table 4. Seasonal comparison of Berger–Parker index (BPI) and rank–abundance curve (RAC) slopes in Bundu Lake and Ratu Maharaja Lake. *Comparación estacional del índice Berger-Parker (BPI) y las pendientes de la curva de abundancia por rango (RAC) en el lago Bundu y el lago Ratu Maharaja.*

Season	BPI (Bundu)	BPI (RML)	RAC Slope (Bundu)	RAC Slope (RML)
Pre-monsoon	0.0566	0.0439	–0.0218	–0.0118
Monsoon	0.0403	0.0332	–0.0117	–0.0076
Post-monsoon	0.0495	0.0349	–0.0151	–0.0085

Table 5. Seasonal rank consistency index (RCI) summary for macrophytes in Bundu and Ratu Maharaja Lake. *Resumen del índice de consistencia estacional (RCI) para los macrófitos en los lagos Bundu y Ratu Maharaja.*

Lake	Min Consistency	Max Consistency	Mean	SD	Range
Bundu Lake	0.089	0.586	0.2180	0.105	0.089–0.586
Ratu Lake	0.046	1.000	0.1746	0.154	0.046–1.000

5.2 Rank reversal and stability of species dominance

Finally, rank tracking showed that no species kept exactly the same position throughout the year in either lake. Roughly two-thirds (63%-64% in BL and RML, respectively) of the species changed rank from one season to the next. *Alternanthera philoxeroides* was the only one that stayed firmly at or near the top everywhere. The sharp drops included *Marsilea minuta* in the BL and *Limnophila indica* in the RML. Upwards movers in two seasons included in two lakes, are *Ottelia alismoides*, *Cyperus iria* (BL), *Ammannia verticillata*, and *Aponogeton natans* (RML) (Table S7, supplementary information, available at https://www.limnetica.com/en/limnetica).

Rank-consistency indices were low overall (means 0.22 in BL, 0.17 in RML), but RML reached a perfect 1.0 for a few stable perennials (Table 5). The larger hydrological swings in BL simply did not allow most species to hold steady positions from season to season (Table S8, supplementary information, available at https://www.limnetica.com/en/limnetica).

DISCUSSION

The present study compared seasonal macrophyte communities in two monsoon-influenced lakes, RML and BL, using complementary structural, diversity, and ordination-based indices. Alpha diversity metrics consistently indicated higher richness and seasonal stability in RML than in BL, suggesting a more resilient macrophyte assemblage. Although this study did not directly quantify physicochemical or hydrological drivers, the macrophyte assemblage structures observed here closely match community signatures previously reported for disturbed and stable freshwater wetlands, allowing ecological inferences to be drawn from established macrophyte indicator frameworks.

In RML, the persistence of submerged macrophytes and Characeae matches assemblage structures commonly reported from well-illuminated freshwater lakes (Yuan et al., 2022). The occurrence of both short-lived colonizers and long-lived species such as *Hydrilla verticillata* and *Eleocharis acutangula* indicates that RML supports a broader range of life-history strategies, consistent with structurally heterogeneous habitats (Chambers et al., 2008).

Life-form composition analysis showed that the proportion of annual macrophytes increased during the monsoon in both lakes, a pattern widely reported for tropical floodplain wetlands experiencing seasonal inundation (Maltchik et al., 2005). In contrast, perennial macrophytes re-established quickly in RML, while BL continued to be dominated by annual species during the post-monsoon season.

BL's nestedness and high IVI reflect repeated species losses and dominance patterns characteristic of macrophyte assemblages reported from drawdown-prone tropical lakes (Fu et al., 2019). These patterns were reinforced by steep rank-abundance curves before and after the monsoon, high Berger–Parker dominance, and low evenness, together indicating strong competitive exclusion and limited resilience (Michelan et al., 2018). The close clustering of BL samples in NMDS ordination further confirms low compositional variability, consistent with the persistent patterns described by Różańska-Boczula et al. (2025).

In contrast, RML's turnover-dominated beta diversity and even IVI distribution signal dynamic coexistence driven by seasonal reorganization without net species loss (Baselga, 2010). These patterns were supported by gently sloping rank-abundance curves and lower Berger-Parker dominance throughout the year, indicating stable coexistence and weaker competitive exclusion (Barbosa et al., 2024). This pattern was exemplified by the continued presence and seasonal recovery of submerged macrophytes and benthic macroalgae such as *Chara fibrosa*, *Hydrilla verticillata*, and *Ceratophyllum demersum*, taxa widely reported as characteristic of freshwater macrophyte assemblages occurring under stable and well-illuminated lake conditions (Bornette & Puijalon, 2011; Lacoul & Freedman, 2006). Greater dispersion in NMDS reflects habitat heterogeneity and temporal niche differentiation, patterns reported as signatures of structurally stable freshwater lakes (Thomaz et al., 2009).

Converging evidence from alpha diversity, beta diversity partitioning, and ordination analyses highlights macrophyte communities as sensitive and reliable indicators of wetland condition. Integrating community composition, growth form structure, and turnover components into routine monitoring frameworks would allow early detection of ecological degradation and provide a robust ecological basis for wetland conservation and management in freshwater lakes of eastern India.

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CONFLICT OF INTERESTS

The authors affirm that they have no conflicts of interest related to the content of this study.

AUTHOR CONTRIBUTIONS

J.M.[#]: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Taxonomic visualization, Writing-original draft, Writing-review & editing, Correcting original draft, Validation; M.P.[#]: Methodology, Software (R v4.4.0), Data visualization (R), Validation, Writing-review & editing; S.G.: Conceptualization, Methodology, Investigation, Correcting original draft, Writing-review & editing, Supervision, Validation.
[#] J.M. and M.P. contributed equally.

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