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# Local and species contribution of beta diversity of macrophytes in perspective of conservation and restoration of Ganga River, India

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**Abstract** The biodiversity of freshwater ecosystems especially macrophytes are threatened by various anthropogenic factors. We performed this study to investigate the beta diversity pattern of macrophyte communities in the Ganga River to find out their relationship with the physio-chemical properties of the habitat and to identify their life forms with conservation priorities and ensuring priority areas for conservation and restoration. We found that the species replacement (Repl) contributes more to beta diversity than similarity (S) and richness difference (RichDiff) component indicating continuous macrophyte turnover along the Ganga river. We found that the local contribution to beta diversity (LCBD) has a significant positive relationship with organic carbon and nitrate. We identified seven sites in the middle and lower reach of the Ganga River whose LCBD values lie within the top 75% indicating that these sites have unique species composition. The species with the highest species contribution to beta diversity (SCBD) values were mostly emergent macrophytes, which have a greater influence on the beta diversity in the studied region. Thus, when developing models and action plans for Ganga River management, which includes both biodiversity conservation and restoration, the middle and lower sections of the river, as well as emergent macrophytes, should be considered.

**Keywords** Aquatic plants · Life forms · LCBD · SCBD · Repl · RichDiff

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## Introduction

To define the rate of change in species composition across various habitats along spatial gradients, Whittaker (1960) used the term beta diversity. With advancements in the mathematical interpretation of beta diversity over past decades, identification of

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the stochastic and deterministic processes that promote variation in biodiversity at the spatial scale became a central and growing issue in ecology and biogeography (Li et al., 2023). As beta diversity represents the connectivity between local communities and regional species pools, it is considered a key asset of ecological denominations that can help us to infer about community assembly processes, especially at a spatial scale (Marathe et al., 2021). Beta diversity is also independent from alpha diversity, thus it offers insights into the factors responsible for relative diversity changes and functional processes across functional groups which is also essential for guiding biodiversity conservation efforts (Garbowski et al., 2023; Serra et al., 2023; Teittinen et al., 2023).

The beta diversity can be partitioned into a LCBD and SCBD in which the uniqueness of the sampling units in terms of community composition is represented by the LCBD and the variation of individual species across the study area is represented by the SCBD (Legendre & De Cáceres, 2013). The values of LCBD range from 0 to 1, and a higher value of the LCBD in a site indicates unique species composition and the higher value of SCBD of a species indicates that it has more influence in the beta diversity within the studied region as it is related to the intrinsic characteristics of each species (Legendre & De Cáceres, 2013; Bomfim et al., 2023; Rodríguez-Lozano et al., 2023). The LCBD and SCBD allows to identify specific sites and species respectively that contribute most to the regional diversity, and can address specific bioassessment, conservation and restoration programs (Bona et al., 2023).

The beta diversity can also be decomposed into two components namely species replacement (Repl) and richness difference (RichDiff) (Podani & Schmera, 2011; Baselga, 2012; Podani et al., 2013). The Repl refers to the fact that species tend to replace each other along ecological gradients that are sufficiently long and the RichDiff refers to the fact that one community may include a larger number of species than another which reflects the diversity of niches available at different locations along the sampling axis or throughout the study area (Legendre, 2014). The sum of Repl and RichDiff is called community dissimilarity (D). Podani & Schmera (2011) and Podani et al. (2013) noted that the sum of similarity (S) and D is 1. To summarize, the relationship between dissimilarity (D), similarity (S), species replacement (Repl) and richness difference (RichDiff) are following—

$$\mathrm{Repl} + \mathrm{RichDiff} = \mathrm{D}$$

$$1 - \mathrm{S} = \mathrm{D}$$

$$\mathrm{S} + \mathrm{Repl} + \mathrm{RichDiff} = 1$$

Aquatic macrophytes are a diverse category of macroscopic plants with a life cycle that takes place wholly or periodically in water bodies (Ogamba et al., 2023). Their different life forms reflect varying responses to the changes in environmental conditions, representing different patterns and occupancy from those observed for other biological groups (Alahuhta et al., 2018). The richness and diversity of macrophytes play a vital role in sustaining the ecology, structure, function and ecosystem services of aquatic systems (O'Hare et al., 2017). The macrophytes supply food to the first consumers such as several herbivore species (Mussy et al., 2022). They provide habitats and refuges for several biotas such as periphytons, zooplanktons, invertebrates and vertebrates such as fish and amphibians (Iquematsu et al., 2022; Alcocer et al., 2023; Bendary et al., 2023; Nemes-Kókai et al., 2023; Stefanidis et al., 2023). The macrophyte-rich water bodies offer a diversity of microhabitats which are less exposed to predation risk (Nessi et al., 2023). They play key functions in biochemical cycles by taking part in the organic carbon production, nutrient mobilization, transfer of trace elements and nitrogen fixation (Polechońska & Klink, 2022; Fastner et al., 2023; Panhota et al., 2023; Pastor et al., 2023). They influence the hydrology of freshwater ecosystems by altering or reducing current velocity (Lind et al., 2022), affecting the sediment dynamics by reinforcing the clogging process as they trap and release fine sediment in the riverbed (Dubuis & De Cesare, 2023) and act as biological filters as they purify the water bodies by accumulating heavy metals their tissue (Serafini et al., 2022; Ge et al., 2023). Macrophytes are considered ecosystem engineers because they play an essential ecological role in aquatic ecosystems by modifying the physical and chemical environment (Pastor et al., 2023).

Globally freshwater ecosystems are at risk from multiple factors which include agricultural, industrial and domestic activity, extraction of water, exotic species, construction of dams and reservoirs, overexploitation, organic and inorganic pollution and climate change (Dudgeon et al., 2005; Strayer & Dudgeon, 2010; Vörösmarty et al., 2010; Collen et al., 2013) and the Ganga River is not an exception as is threatened by alterations of the magnitude of discharge, pollution, sedimentation, and riparian attributes (Paudel & Koprowski, 2020). The alarming decline in biodiversity highlights the need to understand the relationship between ecological factors and biodiversity at different levels to properly protect and manage diverse life forms (De & Dwivedi, 2023b). Understanding the mechanisms underlying species coexistence within plant communities in abiotically constrained habitats, like freshwater ecosystems is crucial to predict their fate given the current context of biodiversity loss (Douce et al. 2023). Considering the present status of rivers in India, including the Ganga River, there is an urgent requirement to know which parts of the river and which biota of the river are to be considered for conservation and restoration management. However, because this approach suggests that conserving a large number of sites may be optimal for protecting regional diversity, limited financial budgets often make it impractical to protect many sites simultaneously (Li et al., 2023). In these situations, when available resources are limited, conservation biologists must strategically prioritize the allocation of conservation efforts to specific sites and species or life forms that cannot be achieved by focusing solely on taxonomic diversity (Fernández-Aláez et al., 2020; Li et al., 2023). In such a scenario, analysing multiple aspects of beta diversity patterns and understanding its components is important for freshwater ecosystem management (Dubois et al., 2020; Li et al., 2023). The spatial variation in species composition or beta diversity provides valuable information about the unique contribution of some hotspots to biodiversity at a regional scale (Wiersma & Urban, 2005; Socolar et al., 2016; Dubois et al., 2020). The freshwater ecosystem hosts clonal macrophyte communities and in this ecosystem, the functional composition and diversity of macrophytes are influenced by strong habitat filtering that determines the local spatial arrangement between species (Douce et al., 2023). In recent years several researchers worked on the process and determinants of beta diversity patterns of macrophytes around the world on both regional scales (Dubois et al., 2020; Fernández-Aláez et al., 2020) and the global scale (Alahuhta et al., 2017; García-Girón et al., 2020). But, so far, no studies have been conducted to understand the beta diversity pattern of plants or animals of the Ganga River, except for works on odonates (De et al., 2023a) and spiders (De et al., 2023b, c).

We conducted this study to identify the life forms of macrophytes with conservation priority and to ascertain areas with conservation and restoration precedence in the Ganga River using LCBD and SCBD approaches of beta diversity. We hypothesized that (1) the LCBD of macrophytes would have a significant relationship with total species richness because ecologically unique sites that are generally poor in species (Brito et al., 2020), (we did not hypothesized 'positive' or 'negative' relationship because according to Legendre & De Cáceres, 2013 this relationship is not always positive or negative), (2) the LCBD of macrophytes had significant relationship with environmental variables because environmental factors influencing macrophytes assemblages (Manolaki & Papastergiadou, 2015), (we did not hypothesized 'positive' or 'negative' relationship between specific environmental factor and specific life forms as Bubíková & Hrivnák (2018)) and Thompson (2021) suggested that the environmental factors affect macrophyte diversity in a complex manner both positive and negative ways) and (3) the macrophytes with intermediate occurrence across the river would have a higher contribution to beta diversity (SCBD values) than the species with high and low occurrence because the species with intermediate occurrence across the river can vary largely across the sites (***Heino & Grönroos, 2016; De et al. 2023b).

## Methods

### Study area

We conducted the work in the Ganga River, which has a channel length of about 2974 km and a basin area of about 965,936 km$^2$, making it the largest river basin in India (Khan et al., 2018). The hydrology of this river system is influenced by the snow melt and glacier dynamics, monsoon precipitation, groundwater resources as well as anthropogenic factors such as the presence of dams, barrages, and canals. The discharge variation of the Ganga River is largely seasonal, as it may be less than 1000 $m^3\ s^{-1}$ in the non-monsoon period or more than 20,000 $m^3\ s^{-1}$ in the monsoon period and it carries a high suspended sediment load of about 356 × 106 t $year^{-1}$ (Khan et al., 2018; Rai et al., 2021).

For the study, we selected the stretch of the Ganga River from Bijnour in Uttar Pradesh to Nischintapur in West Bengal, which passes through four Indian states namely Uttar Pradesh, Bihar, Jharkhand and West Bengal. We selected this stretch of the Ganga because it lies in the Ganga alluvial plain. The area upstream of the study stretch is in the Himalayan region and downstream of the study stretch is highly influenced by salinity due to tidal action, resulting in the assemblage of different plants such as temperate vegetation in the Himalayas and mangroves in the lower stretch. We selected a total of 27 sampling sites with an interval of every ~ 75 km across the river for work (Fig. 1). For a detailed description of each study site refer Ali et al. (2019).

## Data collection

We carried out the fieldwork in the summer of 2018 (May and June) and 2019 (May and June) and the winter of 2018 (November and December) and 2019 (November and December). We visited each site once in each month in each season in each year. At each of these 27 sites, we selected a 5 km stretch along the river on both sides of the river depending on accessibility. For data collection, we selected 6 locations along this 5 km stretch with an interval of 1 km between each consecutive location. Following Szoszkiewicz et al. (2016), in each of these 6 locations, we selected a 100 m long survey reach and identified all macrophytes from there. The plants were identified using published literature (Duthie et al., 1903–1929; Naskar, 1990, 1993a, b; Cook, 1996; Kehimkar, 2000; Naidu, 2012). We classified plants into four life forms namely creeping emergent, erect emergent, floating and submersed. We measured eight physio-chemical parameters of water namely ammonium, dissolved oxygen, nitrate, pH, salinity, specific conductivity, total dissolved solids and water temperature with YSI ProDSS multi-parameter water quality meter. Although Ganga is a freshwater river we considered salinity in the physio-chemical parameters of the water as freshwater rivers all over the world are oppressed by several anthropogenic and other reasons like artificial flow alternation, households and industrial effluents, changes of land-use in the catchment, introduction of exotic species and climate change which alter physiochemical nature of the river water including salinity (Cañedo-Argüelles et al., 2013; Berger et al., 2018). For organic carbon, we collected soil samples in the field and brought them to the laboratory for the estimation of soil organic carbon following Walkely and Black method (1934).

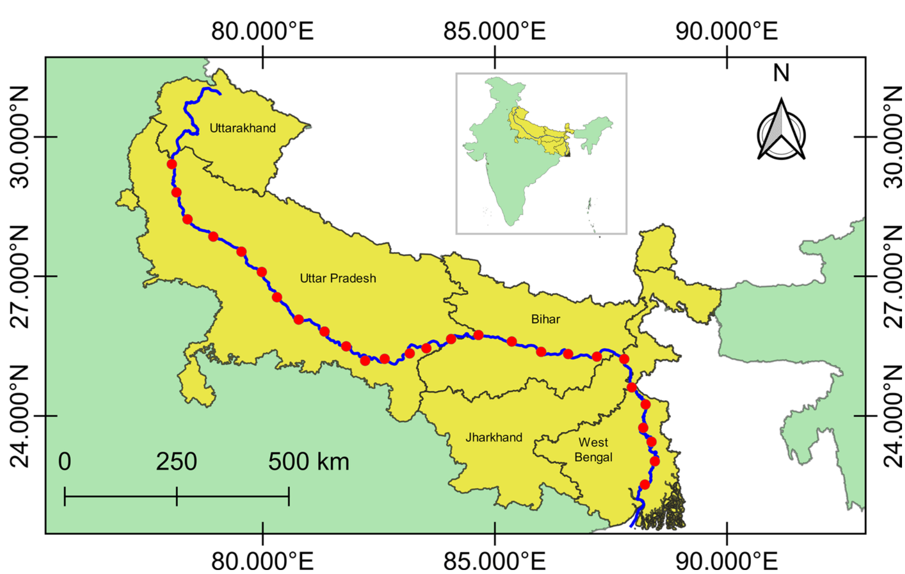


**Fig. 1** Location of 27 sampling sites in the Ganga River

Statistical analysis

We pooled macrophyte presence data and physio-chemical data across all seasons for each study site. We calculate the arithmetic mean of physio-chemical parameters except for pH, for which we calculated the geometric mean as recommended by IUPAC (1997). Then, we normalized (i.e., mean = 0 and variance = 1) the physiochemical parameters to account for differences in measurement scales (Long and Fisher, 2006) and then removed strongly correlated (Pearson's $r > 0.60$) variables for analysis to avoid multicollinearity (Pozzobom et al 2020).

We used Hellinger-transformation for presence-absence data (Legendre et al., 2005; Rey et al., 2023) of macrophyte distribution, and then calculated LCBD and SCBD values by using package 'adespatial' (Dray et al., 2019). We calculated the community dissimilarity (D) (based on Jaccard dissimilarity measurement), species replacement (Repl) and richness difference (RichDiff) between each pair of sites in the R package 'adespatial' (Dray et al., 2019). We prepared SDR-simplex plot (Podani & Schmera, 2011; Podani et al., 2013)—the triangular graph to represent Repl, RichDiff and S graphically.

To understand the relationship between LCBD and species richness, we performed beta-regression between LCBD (as response variable) and species richness (as predictor variable) using the package 'betareg' (Cribari-Neto & Zeileis, 2010). We chose beta-regression because the values of LCBD are continuous variable restricted to unit interval (0–1).

We performed redundancy analysis (RDA) in R package 'vegan' (Oksanen et al., 2019) to investigate the relationship between the macrophyte distribution and environmental variables. To assess the significance of constraints, we performed the permutation test (with 999 permutations) using both the direct model (which permutes community data) and the reduced model (which permutes residuals of the community data). Then we ran the automatic backward step-wise model with 999 iteration steps to know which environmental variable affected macrophyte distribution in RDA ordination space. We used this process because it can assess the joint predictive potential of variables as this process starts with all potential predictors in the model and removes the least important predictors early on, leaving only the most important predictors in the model (Chowdhury & Turin, 2020; Pham et al., 2020; De et al., 2021).

We applied the principal component analysis (PCA) to understand spatial changes in the physio-chemical parameters which helps to reduce the dataset with minimum loss of original information and to get fewer numbers of overt factors. Before PCA, we checked the efficacy of the data to run PCA with both Bartlett's test of sphericity (Bartlett, 1951) and Kaiser–Meyer–Olkin (KMO) criterion (Kaiser, 1970) by using package 'EFAtools' (Steiner & Grieder, 2020). The data is considered to be eligible for PCA analysis if Bartlett's test of sphericity is significant (Bartlett, 1951) and the value of KMO criterion is above 0.5 (Kaiser & Rice, 1974). We found that Bartlett's test of sphericity was significant ($P = 0.019$) and KMO criterion was 0.646 for our data which proved the eligibility of the data for PCA. We used the Kaiser–Guttman criterion (Kaiser, 1958) using the package 'EFAtools' to determine the number of principal components because this criterion consists in selecting only those components associated with eigenvalues larger than 1.0 (Leguendre & Leguendre, 2012) and this procedure tends to be more accurate when applied to the reduced (factor analytic) correlation matrix (McGrath et al., 2021). As this criterion suggested, we shortlisted the first two principal components (PC 1 and PC 2). After shortlisting the first two PCs, we noticed that the contribution of physio-chemical parameters to any one of the two PCs was at least greater than 0.35 (positive or negative) thus we we kept them for further analysis (Tripathi and Singal, 2019).

To understand the relationship between environmental variables and LCBD, we performed beta-regression between LCBD (as response variable) and PC axis (first and second, as predictor variables). Then, we performed multiple beta-regression analysis between LCBD (as response variable) and environmental variables (as predictor variables). We analysed the spatial autocorrelation (Moran´s I) present in the residuals of the multiple beta-regression model and LCBD values for all species.

To find the relationship between SCBD and the number of sites occupied by species we used the first-order term (straight-line response) and the second-order term (curvilinear response) of occupancy. To know if there is any difference in the SCBD values between the macrophyte life forms we performed the analysis of variance (ANOVA) followed by the Tukey post-HOC test.

We performed all the analyses in the R language and environment for statistical computing and graphics (R Core Team, 2020).

## Results

A total number of 37 aquatic hydrophytes belonging to 27 genera under 16 families were listed during the field survey. Among these 37 species, 19 species were creeping emergent, 6 species were erect emergent, 5 species were floating leaved and 7 species were submersed macrophytes. The nativity status of recorded plants showed, that 32 species were native and the 5 species were exotic. Across various sites, the species richness ranged from 1 to 10 (Fig. 2).

We found that the mean S across the study sites for the entire river stretch was 0.147 ± SD 0.162 and mean Repl was 0.486 ± SD 0.258 and mean RichDiff was 0.366 ± SD 0.231. The simplex plot indicated maximum variation in Repl than S and RichDiff across the sites for the entire stretch of the Ganga River (Fig. 3).The relationship between LCBD

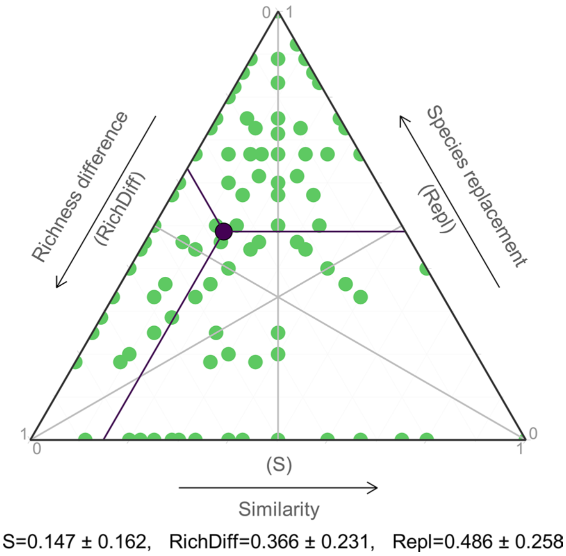


**Fig. 3** SDR simplex plots for beta-diversity of macrophytes of the Ganga River. Dots represent site pairs included in the datasets for entire river stretch. Big dot depicts position of mean values of Similarity (S), Richness difference (RichDiff) and Species replacement(Repl)

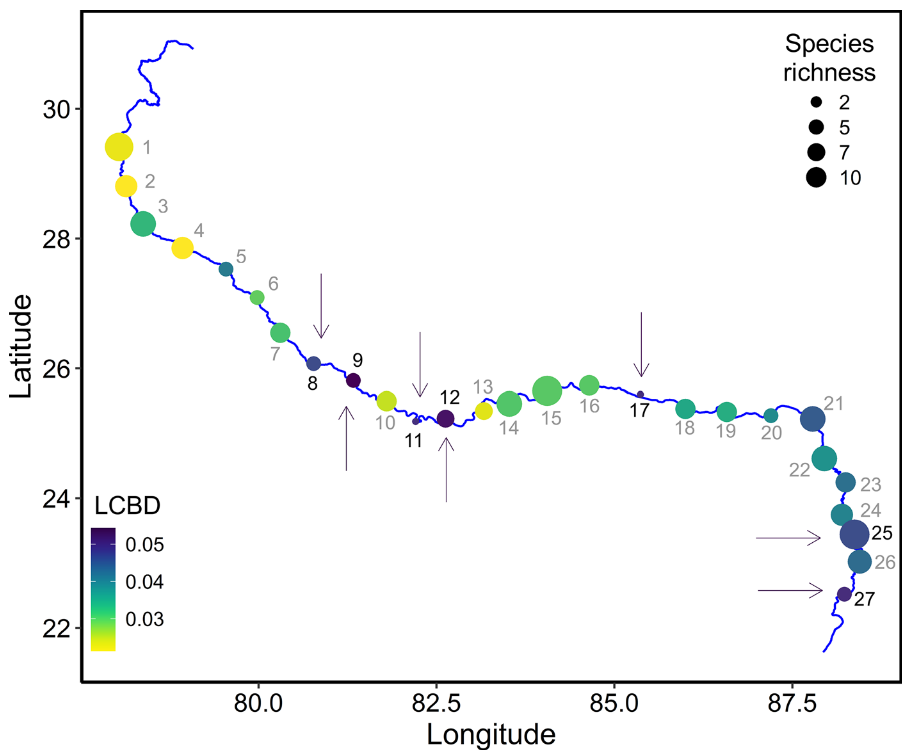


**Fig. 2** Geographical position of 27 sampling sites (represented by the circles) in the Ganga River. The sizes of the circles are proportional to the species richness and the shades are proportional to the LCBD. The arrows represent seven sites with top 75% LCBD scores

and species richness was not significant but marginal (Model Pseudo $R^2=0.102$, $P=0.055$) (Fig. 4, Table 1).

We found that the permutation test for RDA under the direct model ($F=1.346$, $P=0.022$) and reduced model ($F=1.458$, $P=0.019$) were significant. The variance of the RDA biplot (Fig. 5) of macrophyte distribution metrics and environmental variables based on the first two axes explained 65.18% of the variance. Axes 1 and 2 explained 46.01% and 19.17% of the variation in macrophyte assemblages, respectively. This first axis was positively correlated with the entire environmental variables except dissolved oxygen, the second axis was positively correlated with organic carbon, pH and salinity but negatively correlated with dissolved oxygen, nitrate and temperature. The automatic backward step-wise model resulted in six steps and we found that the organic carbon had a significant ($P<0.05$) effect on the macrophyte distribution in RDA ordination space.

The PC axes (Fig. 6) accounted for 60.98% of the observed variance in environmental variables. The first contributed 35.40% of the explained variance and it was positively correlated with nitrate, organic carbon, pH and salinity and negatively correlated with dissolved oxygen and water temperature. The second PC contributed 25.58% of the explained variance and it was positively correlated with nitrate, organic carbon salinity and water temperature but negatively correlated with dissolved oxygen and pH.

We found that the LCBD had significant positive relationship with PC1 (Estimate$=0.103$, $P=0.003$, Model Pseudo $R^2=0.277$; Fig. 7A, Table 2) and with PC2 (Estimate$=0.117$, $P=0.0009$, Model Pseudo $R^2=0.278$; Fig. 7B, Table 3). We found that the LCBD was positively affected by nitrate ($P<0.005$) and soil organic carbon ($P<0.001$) (Fig. 8, Table 4). We did not find any significant spatial autocorrelation in the residuals of the beta regression model (Moran's $I=-0.062$, $P=0.403$).

The species with higher SCBD values ($>0.06$) had occupancy between 6 and 13 sites and mostly belonged to the creeping group (Fig. 9). The first-order term (straight line response) model of occupancy explained 70.0% of the variance (AIC$=-197.119$) (Table 5, Fig. 9A) and the second-order term (curvilinear response) of occupancy explained 78.60% of the variance (AIC$=-207.686$) (Table 5, Fig. 9B).

We found a significant difference in the SCBD values between the life forms (ANOVA $F=5.078$, $P<0.01$), with the Tukey test indicating that erect emergent differed from creeping emergent ($P=0.012$) and submersed ($P=0.004$) macrophytes (Fig. 10).

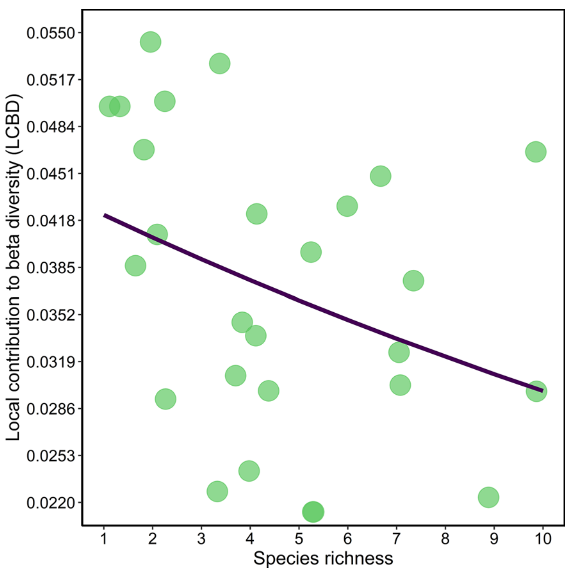


**Fig. 4** Beta regression between LCBD and species richness

## Discussion

As biodiversity is not equally distributed on earth and it is being affected by anthropogenic activities, understanding the distribution of biodiversity has important implications in conservation and management plans, in studying species' niches, and in the assessment of anthropogenic impacts (Gavioli et al., 2022). Considering the degradation of river ecosystems and loss of aquatic biodiversity government agencies and various stakeholders now

**Table 1** Results of beta regression analyses evaluating the effects of species richness on the LCBD

| | Estimate | SE | $z$ | $P$ | Model pseudo $R^2$ |
|---|---|---|---|---|---|
| (Intercept) | − 3.083 | 0.104 | − 29.769 | < 0.001 | 0.102 |
| Species richness | − 0.039 | 0.021 | − 1.914 | 0.055 | |

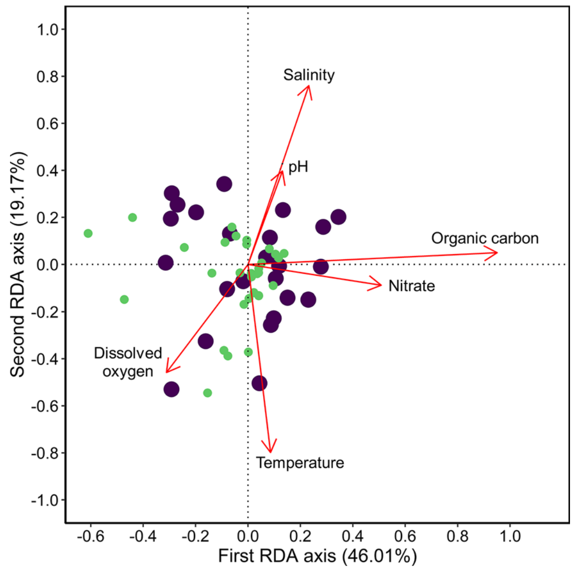


**Fig. 5** Ordination diagram of the RDA of the macrophyte community. Arrows represent the direction of change of the environmental variables. The length of the arrow indicates the variable's importance in explaining the macrophyte community. Sites locations (dark dots) and species locations (light dots) relative to each other indicate their similarity in ordination space

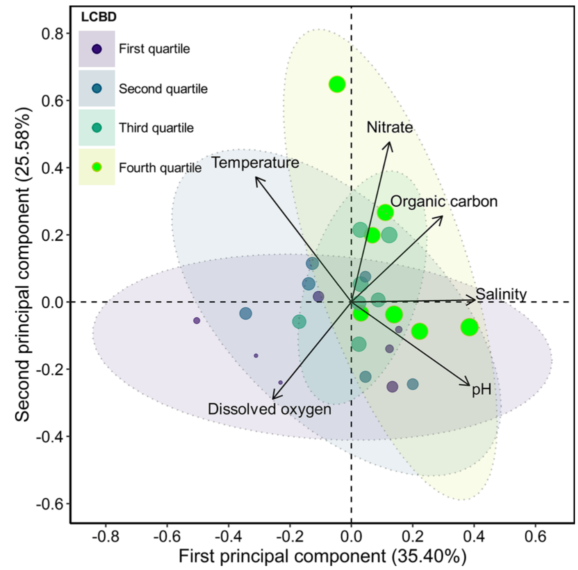


**Fig. 6** Principal component analysis biplot representing factor loadings of first two components and related distribution of sampling locations which are represented by bubbles. Size of the bubbles is proportional to the LCBD scores. The length of the vectors is proportional to its importance. Vectors pointing in similar directions indicate positively correlated variables and vectors pointing in opposite directions indicate negatively correlated variables. Coloured concentration ellipses (size determined by a 0.95 probability level) show the observations groups

support river restoration through hydrologic, geomorphic, and ecological processes as an essential part of conservation and natural resource management (Wohl et al. 2005, 2015). Because ecosystem function, ecosystem service provision, and ecosystem stability are enhanced by macrophyte diversity, it has received much attention in river restoration programs in recent years as an integral part of in-stream habitat enhancement and species management (Wohl et al., 2015; Thomaz, 2021; Haroon, 2022). In the river restoration programmes among all organisms, the macrophytes showed the most pronounced response (Kail et al. 2015). In India, major rivers face serious threats to aquatic biodiversity and hence flagship projects are being conducted to restore freshwater biodiversity using various methods where macrophytes can play an important role. In this work, we investigated the contribution of sites and species to total β-biodiversity of macrophytes in the Ganga River in LCBD and SCBD approaches, respectively. We also investigated which life forms of macrophytes are important in shaping LCBD and which environmental parameters are related to the change in the LCBD across the river length.

At the spatial scale, beta diversity patterns of macrophyte communities showed compositional heterogeneity across the length of the Ganga River. We found that the Repl was the dominating component of community variation and contributed more to beta diversity indicating continuous macrophyte turnover along the Ganga river. Relatively low contribution of S indicated that even sites assigned to the same community type are also different. These findings are similar to the beta diversity pattern of macroinvertebrates in Danube River and rocky grassland communities of the Carpathian basin (Podani and Schmera 2011; Podani et al. 2013).

We found a marginal non-significant relationship between LCBD and species richness and this result is acceptable because according to Legendre & De Cáceres (2013), their relationship is not obligatorily positive or negative. This result is also consistent with the work by Pozzobom et al (2020) and Brito et al.

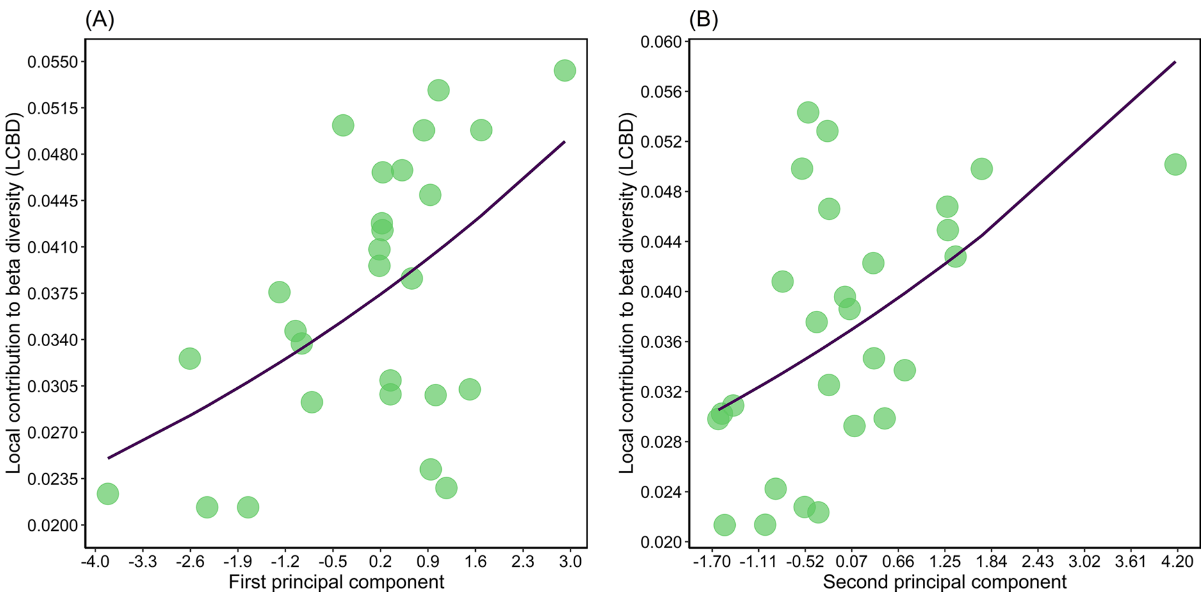


**Fig. 7** **A** Beta regression between LCBD and first principal component axis and **B** beta regression between LCBD and second principal component axis

**Table 2** Results of beta regression analyses evaluating the effects of first principal component axis (PC1) on the LCBD

| | Estimate | SE | *z* | *P* | Model pseudo $R^2$ |
|---|---|---|---|---|---|
| (Intercept) | − 3.268 | 0.048 | − 67.826 | < 0.001 | 0.277 |
| PC1 | 0.103 | 0.035 | 2.991 | 0.003 | |

**Table 3** Results of beta regression analyses evaluating the effects of second principal component axis (PC2) on the LCBD

| | Estimate | SE | *z* | *P* | Model pseudo $R^2$ |
|---|---|---|---|---|---|
| (Intercept) | − 3.268 | 0.048 | − 68.565 | < 0.001 | 0.278 |
| PC2 | 0.117 | 0.035 | 3.332 | 0.0009 | |

(2020) who also did not find any relationship between LCBD and species richness of macrophytes and cladocerans zooplankton, respectively. It means higher species richness does not necessarily mean higher uniqueness of species combination across the study sites and such relationship also varies according to the biological group concern.

Though the macrophytes play an important role as primary producers in the aquatic carbon cycle, but they can be affected by increasing carbon concentrations (Reitsema et al., 2018). The organic carbon can limit macrophyte establishment by changing soil properties (Bociąg, 2003). We found that the LCBD has a significant positive relationship with organic

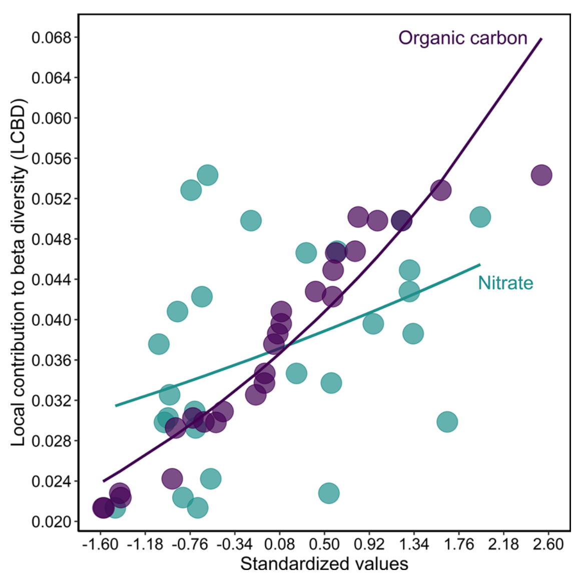


**Fig. 8** The multiple beta regression plot showing significant positive relationship of LCBD with nitrate and organic carbon

**Table 4** Result of beta regression analyses using environmental variables as predictors of variation in LCBD values

| | Estimate | SE | *z* | *P* | Model Pseudo $R^2$ |
|---|---|---|---|---|---|
| (Intercept) | − 3.293 | 0.014 | − 229.122 | < 0.001 | 0.942 |
| Temperature | − 0.019 | 0.019 | − 1.010 | 0.312 | |
| Dissolved oxygen | − 0.015 | 0.015 | − 0.995 | 0.319 | |
| Salinity | − 0.022 | 0.019 | − 1.185 | 0.236 | |
| pH | − 0.031 | 0.019 | − 1.592 | 0.111 | |
| Nitrate | 0.046 | 0.016 | 2.821 | < 0.005 | |
| Soil organic carbon | 0.273 | 0.017 | 16.092 | < 0.001 | |

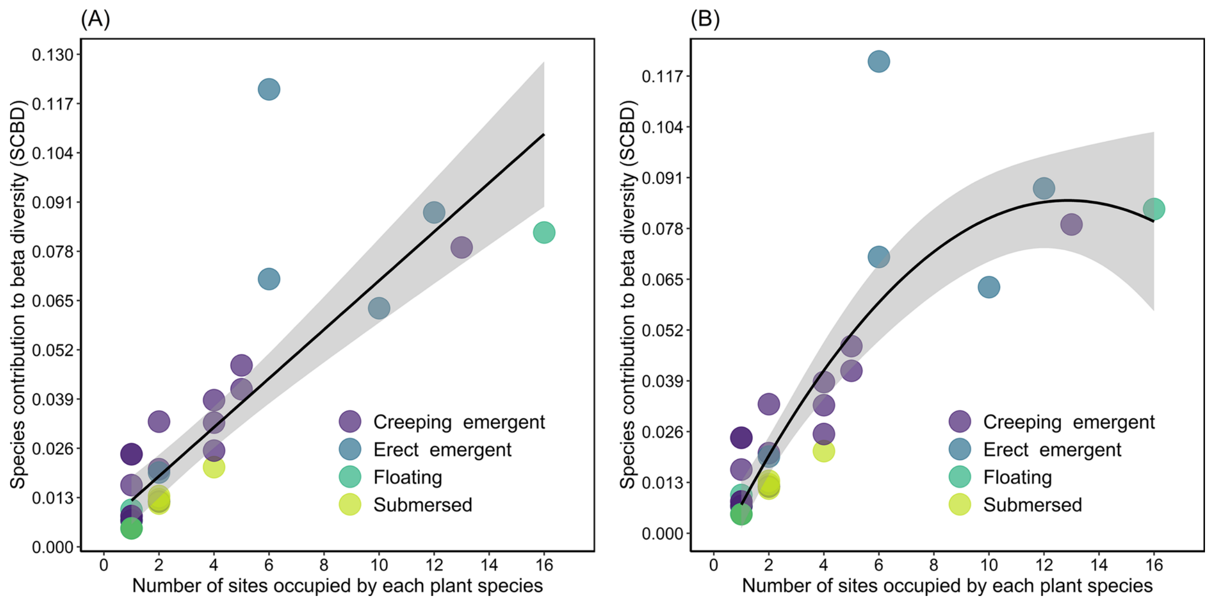


**Fig. 9** **A** Relationship (first-degree term) between SCBD and the number of sites occupied by each species ($R^2 = 0.70$, $P < 0.001$) and **B** relationship (second-degree term) between SCBD and the number of sites occupied by each species ($R^2 = 0.786$, $P < 0.001$)

**Table 5** Model statistics evaluating the relationships between species contributions to beta diversity (SCBD) and the number of sites occupied by macrophytes

| | *P* | $R^2$ | AIC |
|---|---|---|---|
| *Sites occupied by macrophytes* | | | |
| Occupancy[a] | < 0.001 | 0.700 | − 197.119 |
| Occupancy[b] | < 0.001 | 0.786 | − 207.686 |

[a]First-order term (straight-line response) of occupancy

[b]Second-order term (curvilinear response) of occupancy

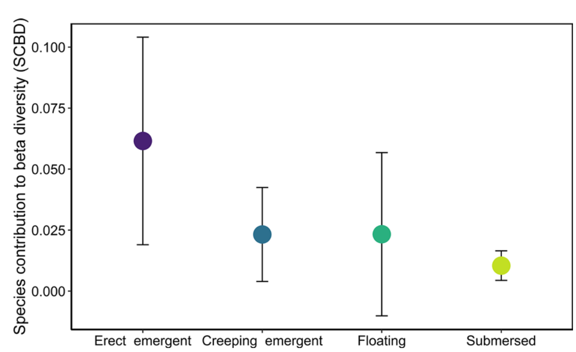


**Fig. 10** Differences in SCBD between the four life forms of macrophytes

carbon. Similarly, we found that the nitrate showed a positive correlation with the LCBD values. The variation in the availability of nutrients such as nitrate in water can affect the biodynamics of trophic levels and the assemblage of macrophytes (Zhang et al., 2021;

Gayol et al., 2022). Thus, the increasing LCBD values (which indicates increasing unique species assemblage) had a significant relationship with nitrate. Moreover, increasing nitrate concentration in aquatic ecosystems may cause decreasing phosphorus uptake by macrophytes and an increase in phytoplankton biomass which eventually leads to declination of macrophyte species richness and biomass (James et al., 2005; Vijayaraj et al. 2022; Polst et al. 2023).

We identified seven sites (Fig. 2) in the middle and lower stretch of the Ganga River whose LCBD values lie within the top 75% (fourth quartile) and these sites have a unique species composition than others. It is noteworthy that these sites include rural areas as well as downstream of large cities, particularly in the middle and lower segments of the Ganga River. Urban-industrial releases, domestic sewage, agricultural runoff and atmospheric deposition add large amounts of N, C and other nutrients in the Ganga River, particularly in the middle and lower stretch (Siddiqui et al. 2018) and such nutrient enhancement may increase primary productivity (Siddiqui et al., 2020). The nutrient enrichment can increase the harshness of environmental conditions for biota, irrespective of changes in productivity which also leads to changes in beta diversity (Donohue et al., 2009). The species with higher SCBD values mostly belonged to the emergent macrophytes that are rooted in water-saturated soil, with foliage extending into the air and having more influence on the beta diversity within the studied region. They grow on the gently sloping shore of the river and provide beneficial ecological services, such as prevention of erosion, nutrient absorption and the provision of shelter, habitat and food for organisms such as fish and water birds (van der Heide et al. 2011; Jia et al., 2016). Moreover, as these plants have better adaptability to even drought conditions (de Morais et al., 2022), they can be used for all-season conservation management.

Pip (1989) and Kaijser et al. (2022) reported that water temperature and pH have negligible direct impact on distribution of macrophytes, though they may have indirect effect. In this sudy we also did not obseve any significant effect of water temperature and pH on LCBD of macrophytes. Since our study sites are located within the freshwater ecosystem of the Ganga River and are away from the estuarine region, we did not observe any significant effect of salinity on the LCBD of macrophytes because these sites do not undergo major changes in salinity. Dissolved oxygen is an important environmental factor in the life cycle and distribution of submerged macrophytes, but in contrast, emergent macrophytes exchange oxygen primarily with the atmosphere, rather than directly with the water column (Bunch et al., 2010; Parveen et al., 2017). Because we got more than 67% emergent macrophytes across the study sites, we probably did not observe any significant relationship between LCBD of total macrophytes and dissolved oxygen. Nitrate and organic carbon concentrations in the Ganga River vary with seasonal changes. It is reported that during the monsoon and post-monsoon season concentration of these nutrients is increased but during winter and pre-monsson concentration of these nutrients is decreased (Singh & Pandey, 2018; Siddiqui & Pandey, 2019; Kumar et al., 2023). A recent study reported that in the Ganga River, the level of carbon is increasing which is accompanied by increasing nitrogen input, especially from anthropogenic activities (Jaiswal et al., 2023). The seasonal variation in the sediment and water nutrients affects the distribution of the macrophytes (Meng et al., 2023). Although in this work, we did not study the seasonal variation of macrophytes our analysis showed that fragmentation and beta-diversity are mainly influenced by organic carbon and nitrate which may result from seasonal changes in sediment and water nutrients. We recommend that further studies should be conducted to investigate the effect of seasonal variation on the assemblage and diversity patterns of riparian vegetation in the Ganga River.

About 13.5% of the macrophytes we observed from the Ganga River were invasive plants. Such plants have a considerable impact on river geomorphology by increasing hydraulic roughness and resistance to bank failure, as well as promoting sediment deposition, bank stabilisation, and channel narrowing (Pollen-Bankhead et al., 2009; Wieting et al., 2022). Invasive vegetation also reduces native species diversity and has an impact on ecosystem functioning by raising primary productivity and accelerating nutrient fluxes (Vilà et al., 2011; Bando et al., 2023; Nguyen et al., 2023). Previous studies showed that the degree of invasion controls the pattern of beta diversity in macrophytes (Lolis et al., 2020; Bando et al., 2023). In this study, we analysed patterns of macrophyte diversity that also included these invasive plants and we did not separately evaluate their effect on the macrophyte distribution. We recommend that further studies should be conducted to investigate the impact of invasive plants on the assemblage and diversity patterns of riparian vegetation in the Ganga River.

The Ganga River ecosystem is under severe anthropogenic stress, especially by flow regulations through structural barriers which alter the geomorphic and hydraulic geometry of riverine habitats (Sonkar et al., 2022). Over the past 32 years, about 40% of the river channel has been altered in the Ganga River and it lost approximately 13.3% of seasonal water flow especially due to anthropogenic changes in the river morphology (Aman & Chu, 2023). Due to these changes in the geological characteristics of the river, the ecosystem of the river changes over time which changes the pattern of river-dependent biota assembly. Thus, depending on the nature and extent of habitat change, previously common species in an area may become rare and vice versa but, most adaptable species become omnipresent in the ecosystem and contribute trivially to the assemblage pattern. As a result, LCBDs and SCBDs could be recast over time in an area.

## Conclusion

India's freshwater biodiversity is in a critical state due to multiple stressors and its conservation faces several challenges (De & Dwivedi, 2023a). Among organisms in aquatic ecosystems, macrophytes are the first to be affected by anthropogenic activities and the survival of animals dependent on those plants is also threatened. For the conservation of biodiversity in the Ganga River, the creation of 'optimal biodiversity sites' and 'strategically prioritised zones' is required (Hussain et al., 2020). Understanding the LCBD and SCBD of macrophytes, as well as their governing factors, can be extremely beneficial for effective conservation, management, and restoration of aquatic ecosystems as they can help in identifying such conservation priority sites as well as species and life forms. Based on our findings, we concluded that during the casting of action plans for Ganga River management in which both conservation and restoration are comprehended, special consideration should be given to emergent macrophytes and agricultural areas along river banks where artificial fertilisers are used, as well as downstream of large cities where domestic and industrial waste is discharged into rivers, particularly in the middle and lower stretches. The present study was the first to explore the beta diversity pattern of the macrophyte community and its relationship with the physio-chemical properties of water in any Indian river. We recommend that further study on the spatial turnover of diversity of macrophytes as well as other freshwater organisms of Indian River systems should be accomplished to understand community assemblage patterns for effective conservation and restoration of riverine ecosystem.

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**Data availability** The datasets used for the current study are available from the corresponding author upon reasonable request.

### Declarations

**Competing interests** The authors declare that they have no competing interests.

**Ethical approval** Not applicable.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

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