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ORIGINAL PAPER

β-diversity of odonate community of the Ganga River: partitioning and insights from local and species contribution

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Abstract The β-diversity studies reveal diversity patterns at a spatial scale and strengthen the process of regional diversity conservation. The aim of the current study was to understand the pattern of local contribution to β-diversity (LCBD) and species contribution to β-diversity (SCBD) of odonates in the Ganga River. We selected 27 sites along the banks of the Ganga River for the study, with an average distance between sites of 75 km, and recorded 30 species of odonate (species richness between 5 and 24) at these sites. Using β-regression analysis, we examined the impact of species richness and habitat variables on the LCBD. The LCBD was found to be negatively correlated with species richness and influenced by creeping macrophytes, water temperature, dissolved oxygen and salinity. We found that species with high SCBD scores (above 0.05) had intermediate occupancy (between 10 and 16 sites), including 5 species of dragonfly and 5 species of dragonfly, and that the second-degree term the relationship between SCBD and the number of declared locations better stocked with species than in the first degree. Since the SCBD is responsible for identifying species that make the greatest contribution to β-diversity and the LCBD is responsible for identifying sites with particular combinations of species, the combined approach using both should be included for ecological assessments, river biodiversity restoration and maintenance plans.

Keywords Dragonflies · Damselflies · LCBD · SCBD · Ganga River

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Introduction

The β-iversity can be defined as spatial differentiation or variation in species composition between sites within a region of interest (Whittaker 1972). As a single value calculated for a specific area, Whittakers β-diversity (Whittaker 1960, 1972) does not allow for statistical comparisons of β-diversity between two or more areas (Anderson et al. 2006). The total β-diversity can be divided into local contribution to β-diversity (LCBD) and species contribution to β-diversity (SCBD) (Legendre and De Cáceres 2013). The LCBD represents the degree of uniqueness of the sample units in terms of community composition and the SCBD represents the degree of variation of individual species in the study area (Legendre and De

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Cáceres 2013). The higher value of the LCBD at a site indicates a more unique species composition, and the higher value of SCBD of a species indicates that it has a greater impact on β-diversity within the region studied (Legendre and De Cáceres 2013; Heino and Grönroos 2016; da Silva et al. 2018; Pozzobom et al. 2020). The LCBD values are the indicator of the uniqueness of the sites; so, large LCBD values therefore indicate sites whose species composition differs from that of other sites (Legendre and De Cáceres 2013).

The insect order Odonata includes both dragonflies (suborder Zygoptera) and dragonflies (suborder Zygoptera), which are amphibious insects as they spend their larval stage in freshwater bodies but the adult stage in terrestrial ecosystems (May 2019). Despite common ecological habits, dragonflies and dragonflies have specific and distinct needs in terms of thermoregulation, oviposition resources, dispersal to new areas, and habitat selection (De Marco Júnior 2015, Suárez-Tovar et al. 2022). For example, while the dragonfly species prefer sunny, open areas, but the dragonflies prefer shady, closed areas of vegetation (Suárez-Tovar et al. 2022). Such differences in ecophysiological requirements along with differential dispersal ability between species are responsible for structuring the Odonata community in a geographic area (Mendes et al. 2015). Most tropical odonates are ectotherms, warming through constant heat exchange with their surroundings, which explains why they are active on bright, sunny days (Batista et al. 2021).

Recently, studies on the spatial distribution pattern of the odonate community have attracted researchers' attention. In the island zoogeographic system, odonate β-diversity distribution is mainly determined by species frequencies at source and by their degree of generalism (Heiser et al. 2013). In the lowland coastal plains, diversity values are low and are related to dissimilarity in scale-specific drivers and geographic distances (Pires et al. 2018). In the river ecosystem, the meta-community pattern of odonates is determined by the environmental and biogeographical predictors as biogeographical region (interfluve), annual mean temperature, habitat integrity, and annual rainfall (Alves-Martins et al. 2019). In the preserved and modified river streams, the variation in the odonate community is determined by environmental factors (Oliveira-Junior and Juen 2019). In rainforest streams, variation in the odonate community depends on local abiotic factors such as canopy cover, and physical and chemical descriptors of the water and regional abiotic factors such as bioclimatic and forest cover variables (Oliveira-Junior 2019).

One of the key issues in conservation ecology is quantifying the distribution pattern of biodiversity in the landscape (ERS 2007) and considering the risk of extinction at regional and local scales to set conservation priorities (Olden et al. 2010). Therefore, understanding β-diversity is essential for protecting regional diversity (Socolar et al. 2016). Although it is extremely important in terms of biodiversity, no studies have been conducted to understand the diversity patterns of odonates and other insects in the riparian areas of the Ganga River. In this work, we aimed to study the pattern of LCBD and SCBD of odonates in the Ganga River. We hypothesized that [1] the LCBD of odonates would have a significant relationship with species richness because ecologically unique sites that are generally poor in species (Brito et al. 2020), [2] the LCBD of odonates had significant relationship with environmental variables because environmental factors influence β-diversity of odonates (Johansson et al. 2019) and [3] the odonate species with intermediate occurrence across the river would have a higher contribution to SCBD values than the species with the high and low occurrence because the intermediate species show most variation in occupancy among sites (Gaston et al. 2006; Heino and Grönroos 2016).

Materials and methods

We conducted the work in the Ganga River which has the largest river basin in India, with a channel length of about 2974 km and a basin area of about 965,936 km^2 (Khan et al. 2018). The hydrology of the Ganga River system is influenced by the complexity of glacier and snow melt, monsoon run-off, groundwater resources, and several dams, barrages, and canals (De at al. 2018b). It is estimated that the discharge size of the Ganga River varies from less than 1000 m^3 s^{-1} in the non-monsoon period to more than 20,000 m^3 s^{-1} in the monsoon period, and it experiences 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 is about 1955 km long and passes through four

Indian states namely Uttar Pradesh, Bihar, Jharkhand and West Bengal. This region fall within the tropical wet dry climate (Aw) and humid subtropical climate (Cwa) zone as per Köppen-Geiger climate classification system (Beck et al. 2018) and two ecoregions namely Lower Gangetic Plains moist deciduous forests and Upper Gangetic Plains moist deciduous forests (Olson et al. 2001). We selected a total of 27 sampling sites with an interval of every – 75 km across the river (Fig. 1). These sites were influenced by several anthropogenic disturbances such as agricultural activities, effluent discharge, garbage dump, grazing, sand mining (De et al. 2021, 2023a, b). For a detail descriptions of each study site refer Ali et al. (2019).

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. We adopted the point count method for odonates proposed by Buchsbaum et al. (2016). In this method, we selected a 5 km long stretch in each site and in each stretch we chose 6 points having a distance of 1 km for point count. We stood at an observation point for 10 min and rerecorded the odoantes that pass within 5 m of the observation point. We surveyed odonates and aquatic macrophytes along the edge of the water body from 10 a.m. to 3 p.m. on a day with bright sunlight and a clear sky, because in such an environment the activity of odonates is highest. We observed the only adult odonates with the aid of binoculars and we noted all species found up to 5 m to the right and left of the edge. We identified most of the odonates without capturing and if necessary we used an insect net of 40 cm diameter and 65 cm depth attached to an aluminium rod to catch odonates for identification. We identified odonates from published field guides (Andrew et al. 2008; Nair 2011) and web resource (https://www.indianodonata.org/). We selected only one bank for study (either left or right, depending on the convenience and accessibility) of the main channel of the river. We focused only on adult odonates because the activity and abundance of adult odonates can be observed in and around the breeding sites (Bried and Ervin 2006; Butler and deMaynadier 2007) which weakens the conventional view that adult odonates cannot indicate the condition of the breeding sites (Raebel et al. 2010). In addition, adult odonates can be seen on the water and in the surrounding region, and are relatively easy to identify at the species level than larvae and exuvia (Raebel et al. 2010; Bried et al. 2011), especially in our study area since there is no reference describing odonate larvae of the Ganga River. Moreover studies found that the odonata larvae and adult follow the same distribution, richness and abundance patterns (Silva et al. 2021).

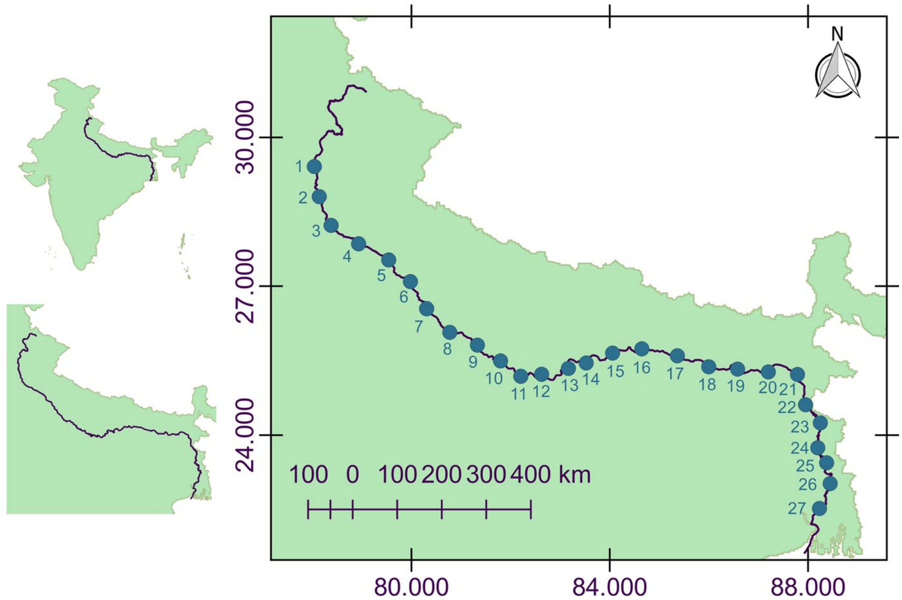

Fig. 1 Location of 27 sampling sites along the Ganga River

We used YSI ProDSS multi-parameter water quality meter for measurement of the physio-chemical parameters of water in situ. We measured eight physio-chemical parameters of water namely ammonium, dissolved oxygen, nitrate, pH, salinity, specific conductivity, total dissolved solids and water temperature.

For plants, we observed the presence of five types of aquatic macrophytes (according to Wetzel and Hutchinson 1976) namely erect emergent macrophytes, creeping emergent macrophytes, floating leaved macrophytes, submersed macrophytes and freely floating macrophytes in each site.

For analyses, we used summed species and habitat variable matrix (i.e. pooled across all months) for each site. Before, analyses we normalized (mean = 0 and SD = 1) the data (Miyazono and Taylor 2013; Datry et al. 2016) for all habitat variables (physio-chemical parameters of water and aquatic macrophyte species richness). To avoid multicollinearity, we performed Pearson correlation and removed strongly correlated ($r > 0.60$) variables for analyses (Pozzobom et al. 2020). We removed three physio-chemical parameters of water namely specific conductivity, ammonium and total dissolved solids (TDS) to avoid multicollinearity. We also did not include floating leaved macrophytes in the analyses as they were found in only two sites.

We applied the Principal Component Analysis (PCA) to understand spatial changes in the habitat parameters which helps to reduce the dataset with minimum loss of original information and to get less numbers of overt factors. Prior to 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 and 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 and Rice 1974). We found that the Bartlett's test of sphericity was significant ($p = 0.02$) and KMO criterion was 0.601 for our data which proof eligibility of the data for PCA. After performing PCA we noticed that the contribution of habitat parameters to the first PCA (PC1) was more that 25%, thus we we kept it for further analysis. As species richness data was positively skewed, we used generalized linear regression model (glm) with a gamma family and log link function to fit a curve to explore relationship between species richness and PC1 (Ng and Cribbie 2016; von Königslöw et al. 2021; Xie et al. 2023; Godó et al. 2023).

We used Hellinger-transformation for presence-absence data, and then calculated the LCBD, and SCBD using the package 'adespatial' (Dray et al. 2019). As the LCBD values are continuous variables restricted to unit interval (0 to 1), we used β-regression using the package 'betareg' (Cribari-Neto and Zeileis 2010) between LCBD and species richness and between LCBD and habitat variables. This method also does not need assumptions for normality, skewness and heteroscedasticity (Zimprich 2010). We analyzed the spatial autocorrelation (Moran´s I) present in LCBD values and the residuals of the β-regression model. To find the relationship between SCBD and the number of sites occupied by species we used first-order and second-order polynomial regression (Pozzobom et al. 2020).

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

Results

We recorded total 30 species of odonates from the study sites (for the list of odonate species refer Fig. 6). The species richness was ranged from 5 to 24 (Fig. 2) (Mean = 10.963, SD = 4.661) across the sites.

In principal component analysis (PCA) (Fig. 3), we found that the first two axes accounted for 48.89% of the total habitat variance, within which the first axis accounted 26.68% (eigenvalue 2.401) and the second accounted for 22.21% (eigenvalue 1.998). The main explanatory parameters for the first PC axis were erect emergent macrophyte which was negatively correlated, followed by salinity and pH, which were positively correlated. The main explanatory parameters for the second PC axis were creeping emergent macrophyte, submersed macrophyte and freely floating macrophyte, all of which were positively correlated. The Table 1 shows the values of the scores obtained for each habitat variables. We found that the species richness was significantly related with first PC axis of habitat variables. (Fig. 4).

The LCBD was significantly and negatively related to species richness (Model pseudo $R^2 = 0.122$,

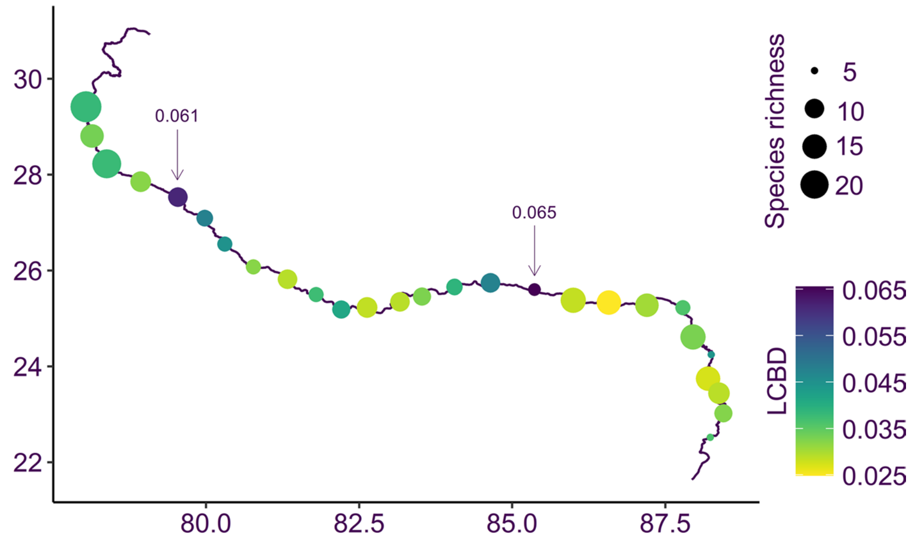

Fig. 2 Geographical position of 27 sampling sites (represented by the circles) in the Ganga river. The sizes of the circles are proportional to the species richness and the shades are proportional to the local contribution to β-diversity (LCBD). The arrows are indicating two sites which have maximum LCBD values

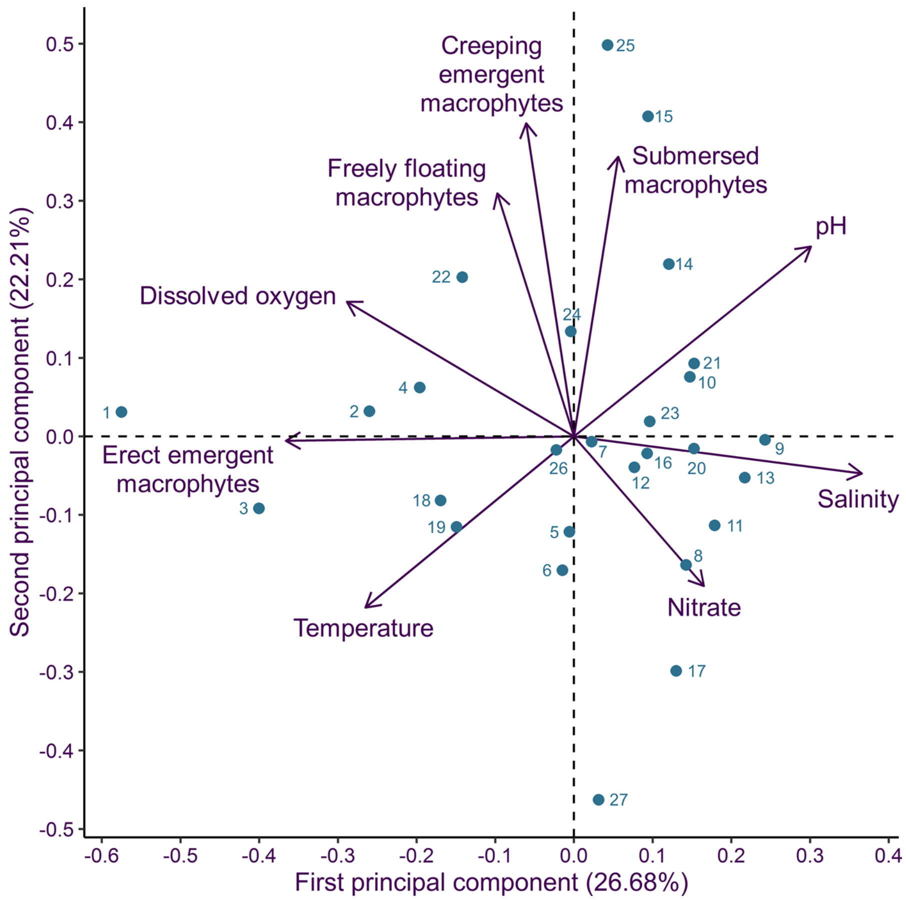

Fig. 3 Comparative account of species contribution to β-diversity of 30 species of odonates found in the study sites. The dark circles represent the ten species with high contributions (more than 0.05) to β-diversity

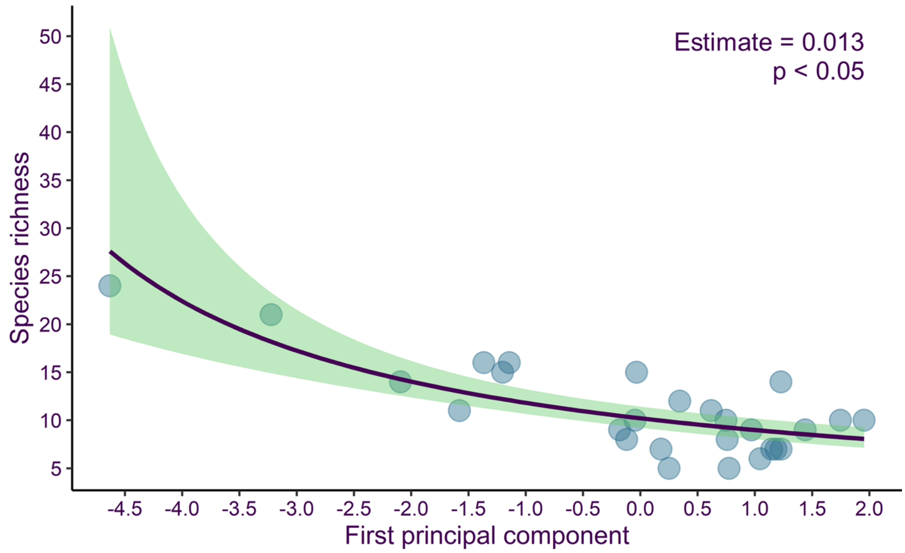

Fig. 4 Principal component analysis (PCA) ordination biplots for nine habitat parameters at the 27 sites sampled in the Ganga River

Table 1 Results of the principal component analysis (PCA). The table shows the values of the scores obtained for each habitat variables

Variables	PC1	PC2	PC3	PC4
Creeping emergent macrophytes	− 0.081	0.535	− 0.268	0.281
Erect emergent macrophytes	− 0.491	− 0.007	0.302	0.057
Freely floating macrophytes	− 0.131	0.415	− 0.221	− 0.604
Submersed macrophytes	0.075	0.478	− 0.346	0.278
Water temperature	− 0.356	− 0.293	− 0.422	− 0.019
Dissolved oxygen	− 0.387	0.230	0.233	− 0.511
Salinity	0.491	− 0.064	0.166	− 0.287
pH	0.404	0.324	0.273	− 0.087
Nitrate	0.221	− 0.256	− 0.577	− 0.352

Table 2 Results of β-regression analyses evaluating the effects of total species richness on the local contribution to β-diversity (LCBD)

	Estimate	SE	z	p	Model pseudo R^2
Intercept	− 3.036	0.117	− 25.977	2×10^{-16}	
Species richness	− 0.021	0.010	− 2.024	0.043	0.123

$p<0.05$; Table 2; Fig. 5). The LCBD was negatively affected by creeping emergent macrophytes, water temperature, dissolved oxygen and salinity (Table 3). We did not found any significant spatial autocorrelation in the LCBD values (Moran's I = − 0.039, $p>0.05$) and in the residuals of the β-regression model (Moran's I = − 0.017, $p>0.05$).

The species with high SCBD values (above 0.05) showed intermediate occupancy (between 10 and 16 sites). Among ten species of odonates with high contributions to β-diversity (above 0.05), five were damselflies (*Ischnura rubilio*, *Pseudagrion rubriceps*, *Agriocnemis lacteola*, *Agriocnemis pygmaea*, *Agriocnemis femina*) and five were dragonflies (*Brachydiplax sobrina*, *Brachydiplax farinose, Acisoma panorpoides*, *Pantala flavescens*, *Diplacodes trivialis*) (Fig. 6). The second degree term ($R^2=0.907$, $p<0.05$, AIC = − 215.776; Table 4; Fig. 7) explained better relationship between SCBD and number of sites occupied by species than the first degree term

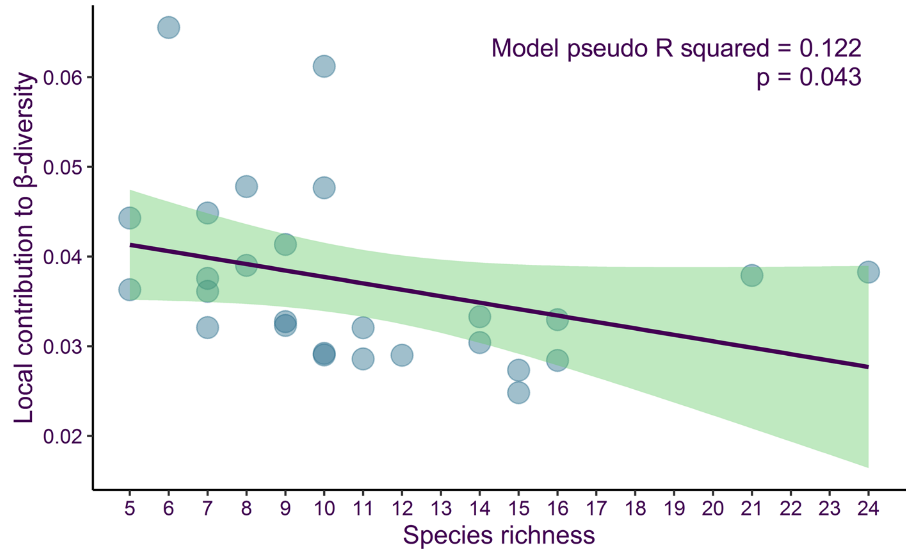

Fig. 5 Relationship between species richness and first principal component

Table 3 Result of β-regression analyses using water quality variables as predictors of variation in the local contribution to β-diversity (LCBD) values

	Estimate	SE	z	p	Model pseudo R^2
Intercept	− 3.276	0.031	− 104.361	2×10^{-16}	
Creeping emergent macrophytes	− 0.104	0.039	− 2.619	0.00882	
Erect emergent macrophytes	0.039	0.044	0.898	0.369	
Freely floating macrophytes	− 0.041	0.039	− 1.044	0.296	
Submersed macrophytes	0.011	0.038	0.276	0.782	
Temperature	− 0.109	0.039	− 2.787	0.005	
Dissolved oxygen	− 0.128	0.042	− 3.053	0.002	
Salinity	− 0.132	0.041	− 3.224	0.001	
pH	− 0.011	0.040	− 0.271	0.786	
Nitrate	0.005	0.039	0.136	0.892	0.587

($R^2=0.148$, $p<0.05$, AIC = − 151.285; Table 4; Fig. 8).

Discussion

Information on species composition and distribution and spatial variation in diversity is required to design the conservation strategies that can reduce the increasing rates of biodiversity loss, especially in aquatic systems (Brooks et al. 2004; ERőS 2007; Rodrigues and Brooks 2007; Lopes et al. 2011). The changes in species composition across the geographical distances between their habitats occur due to the changes in biotic and abiotic factors of those habitats (Axmacher et al. 2009; Tojo et al. 2017; Chesters et al. 2019). Information about these ecological requirements is a useful tool for the evaluation of the overall conservation status and bio-monitoring of aquatic environments (Stewart and Downing 2008; Bouhala et al. 2019). Odonates are semi-aquatic predatory insects as their early stages of life spend in the freshwater, so the physio-chemical properties of the water and habitat variability shape their diversity and distribution in the aquatic ecosystem (Campos et al. 2014; Sakai et al. 2017; Tippler et al. 2018; Sareein et al. 2019).

As ultimate goal of conservation is to protect the greatest number of species and habitats within limited

Fig. 6 Relationship between local contribution to β-diversity (LCBD) and species richness

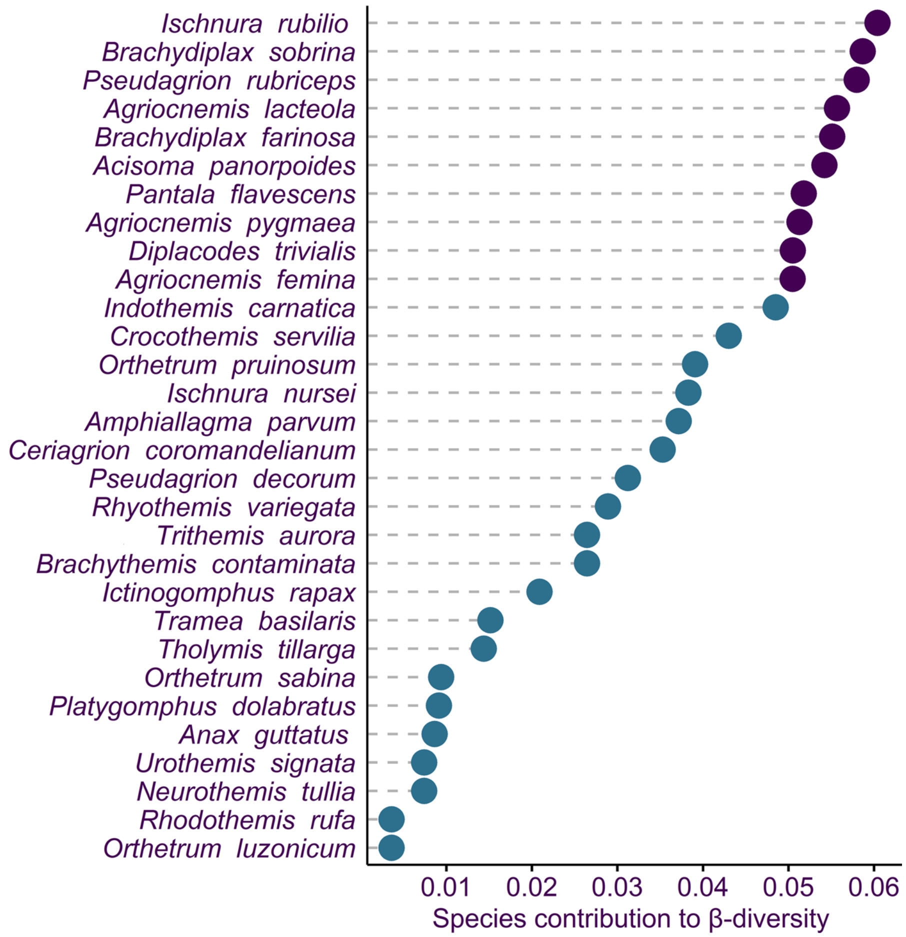

Fig. 7 Relationship between species contribution to β-diversity (SCBD) and number of sites occupied by each species. The curved line depicts the model that contained the second degree term ($R^2 = 0.907$, $p < 0.05$). The species that showed higher SCBD values showed intermediate occupancy (between 10 and 16 sites). The size of the bubbles represents SCBD values

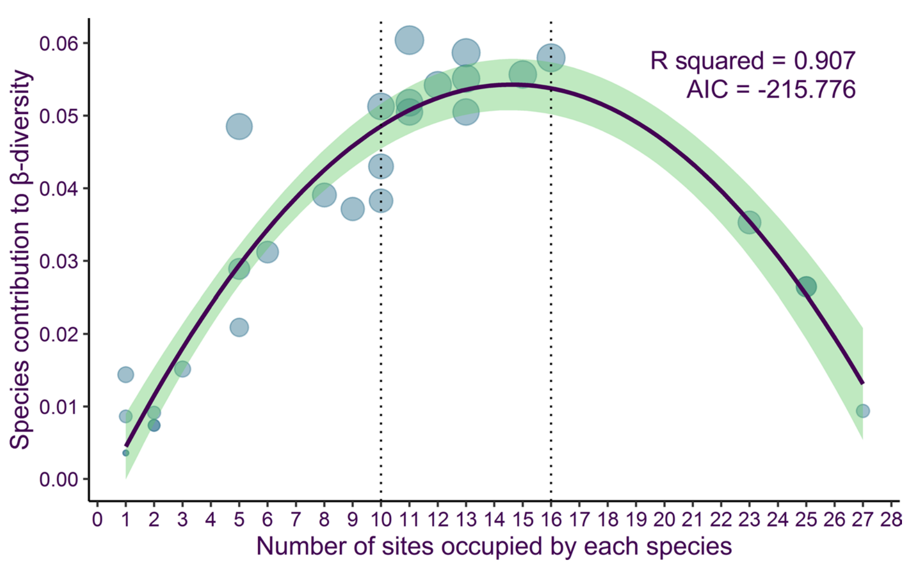

Table 4 Model statistics evaluating the relationships between species contributions to β-diversity (SCBD) and the number of sites occupied by each species

	p	R^2	AIC
Sites occupied by odonate species			
Occupancy[a]	0.036	0.147	− 151.285
Occupancy[b]	< 0.001	0.907	− 215.776

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

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

resources; therefore, β-diversity study is important for optimizing conservation efforts (Wiersma and Urban 2005). For the conservation planning of aquatic environments, the SCBD and the LCBD are useful in two ways i.e. SCBD values indicate which species contribute the most to β-diversity (Pozzobom et al. 2020), and the LCBD values indicate which site has unique assemblage characteristics (Legendre and De Cáceres 2013; Pozzobom et al. 2020). The LCBD values generally indicate the sites which have unusual species combinations and high conservation value or degraded and species-poor sites in need of ecological restoration (Legendre and De Cáceres 2013).

The environmental factors could account for the co-variation in shaping odonate assemblages (Bouhala et al. 2019). The physio-chemical parameters of water such as water temperature, pH, conductivity and dissolved oxygen had significant impacts on the abundance and species richness of adult odonates (Villalobos-Jimenez et al. 2016; Briggs et al. 2019; Jooste et al. 2020). The adult odonates prefer the aquatic vegetation above the water surface such as the emergent and floating vegetation as these provide perching sites, foraging sites, hiding places and breeding sites (Buchwald 1992; Schindler et al. 2003; Corbet 2004; Hofmann and Mason 2005; Thomaz and Cunha 2010). In our study we observed that creeping emergent macrophytes, water temperature, dissolved oxygen and salinity were the main environmental variables related to local contribution to β-diversity (LCBD), indicating that these variables are important factors differentiating the odonate assemblages of the Ganga River.

In aquatic ecosystem, some studies reported negative relationships between species richness and LCBD values such as for zooplankton (Mimouni et al. 2015), aquatic insects (Heino and Grönroos 2016) and diatoms (Vilmi et al. 2017), while some studies reported a positive relationship between them such as for fish (Kong et al. 2017) and riparian spiders (De et al. 2023a) and some studies reported no relationship such as for aquatic macrophytes (Pozzobom et al. 2020), which indicate that the relationship is not obligatory (Legendre and De Cáceres 2013). In the present study, we found a negative relationship between species richness and LCBD values which indicates that less species rich sites has more unique species and vice-versa. Thus our findings suggest that the variation in LCBD of odonates across in the Ganga River is governed by variation in species

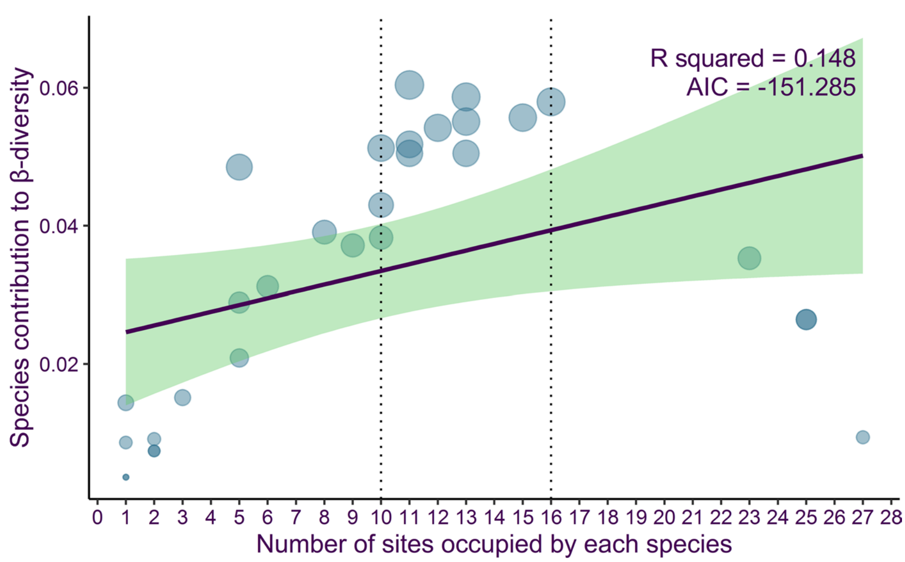

Fig. 8 Relationship between species contribution to β-diversity (SCBD) and number of sites occupied by each species. The straight line depicts the model that contained the first degree term ($R^2 = 0.148$, $p < 0.05$). The species that showed higher SCBD values showed intermediate occupancy (between 10 and 16 sites). The size of the bubbles represents SCBD values

richness which in turn may be reined by different habitat factors as suggested by Heino and Grönroos (2016) for stream insects.

We found that SCBD values increased with the number of sites occupied by species until intermediate occurrences were reached, resulting in a hump-shaped curve indicating that species with intermediate occurrences contribute higher to β-diversity. This result indicates that the intermediate species contribute most to the β-diversity as they show the greatest variation in occupancy among sites as observed for stream insects (Heino and Grönroos 2016), stream and lake diatom communities (Vilmi et al. 2017), benthic diatom communities (Szabó et al. 2018), aquatic macrophytes (Pozzobom et al. 2020) and riparian spiders (De et al. 2023a).

We recorded total of 30 species of odonates from the study sites and this number seems to be low. This is because it seems that we surveyed only along the narrow river bank strips in the sites, most of which are nuisance by several anthropogenic activities (De et al. 2021). Although each of the 30 species of odonates we found is in the Least Concern (LC) category, the current population trend of 26 of these 30 species is currently unknown and the population status of three species (*Diplacodes trivialis*, *Orthetrum sabina* and *Pantala flavescens*) is stable and one species (*Crocothemis servilia*) is increasing (https://www.iucnredlist.org). We need to keep in mind that keeping common species common is important. This is a complex process, especially in the case of insects, because the slightest variation in the environment can greatly damage the population of these species and inadvertently endanger them locally, with detrimental effects on the ecosystem. Similarly, if the biodiversity of a region exists at a high level, there is no guarantee that the biodiversity of that region will remain high forever, particularly on the banks of the Ganga River, where anthropogenic pressure and consequent ecological damage are likely to be high. It is commonly assumed that only species-rich sites should be protected but in practice this is not correct as being species-poor does not necessarily make a site unworthy of conservation (Kareiva and Marvier 2003). And this is where the importance of LCBD is immense as it helps to find sites with unique species combination which are competent for conservation. In our study, we initially identified two sites (Fig. 2) whose LCBD values were higher than those of other regions. It is noteworthy that one of these two sites is located in the rural area and the other in the urban area. That is, it may be assumed that biodiversity and species distribution do not depend on the village or town, but on whether it has a suitable habitat, which in many cases is affected by anthropogenic pressure.

River hydrology and geomorphology change over time as rainfall, vegetation cover, and land-use patterns change, leading to changes in aquatic animal community patterns. Depending on the nature and extent of habitat changes, species that were once rare in a region may become common and vice versa. Thus, LCBD and SCBD could be remodelled in an area over time. However, the species which is best able to adapt to environmental changes may become ubiquitous and contribute little to assemblage patterns. The present study is the first to examine the β-diversity pattern of odonate community and its relationship to the physicochemical properties of water and aquatic macrophytes of an Indian River. We recommend that further studies be conducted on the diversity pattern of odonates and other freshwater organisms to explain the spatial turnover of riverine organisms in the Indian River systems and to understand community composition for effective planning and implementation of habitat conservation and restoration plans. We call on researchers to combine LCBD and SCBD approaches for ecological assessment, restoration and conservation of riverine and aquatic ecosystems where SCBD will be responsible for identifying species, which are major contributors to diversity, and LCBD will be responsible for identifying sites with idiosyncratic assemblages.

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Author contributions KD: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft; DD: Data curation, Investigation, Methodology, Validation; MS: Data curation, Investigation, Methodology, Validation; VPU: Project administration, Resources, Supervision, Validation, Writing – review & editing; BSA: Project administration, Resources, Supervision, Validation, Writing – review & editing; JAJ: Project administration, Resources, Supervision, Validation, Writing – review & editing; SAH: Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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