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PRIMARY RESEARCH PAPER

Beta diversity patterns of diatom assemblages along the largest north-western river of Cambodia (Sangker River): implication for biomonitoring

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Abstract Benthic diatoms are sensitive indicators of freshwater ecosystem health, yet their spatial diversity patterns in tropical rivers remain poorly understood. This study investigated β-diversity of benthic diatom assemblages along the Sangker River, northwestern Cambodia. β-Diversity was quantified using the Sørensen index and partitioned into turnover (βsim) and nestedness (βsne) components, based on 7 sampling campaigns from 2018 to 2022. Local (LCBD) and taxa (SCBD) contributions identified unique sites and influential taxa (genera). Twelve environmental variables, including nine physical and chemical and three spatial factors, were analyzed along the upstream–downstream gradient. A total of 78 genera were recorded, dominated by *Gomphonema*, *Nitzschia*, *Navicula*, and *Achnanthidium*. Alpha diversity declined downstream, reflecting reduced habitat heterogeneity and increasing nutrient enrichment, while evenness remained stable. Overall β-diversity was high (βsor = 0.748), driven mainly by species turnover (βsim = 0.639), indicating distinct assemblages across river sections. Certain sites located in tributaries exhibited high-LCBD values, whereas total phosphorus and total suspended solids significantly influenced LCBD. These findings highlight the strong roles of environmental filtering and longitudinal (upstream–downstream) gradients in structuring diatom assemblages. Targeting high-LCBD sites and key indicator genera can enhance biomonitoring efficiency and guide freshwater conservation under growing anthropogenic pressures in tropical river systems.

Keywords Benthic diatoms · Beta diversity · River ecosystem health · Biomonitoring · Tonle Sap Basin

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Introduction

Freshwater ecosystems are among the most vital components of the biosphere, providing essential services for human well-being, including clean

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water, food, energy, and transportation (Vörösmarty et al., 2010). These ecosystems support high biodiversity and are crucial for sustaining livelihoods worldwide (Reid et al., 2019). The health of these ecosystems underpins not only biodiversity conservation but also the social and economic stability of the human communities that rely on them (Palmer et al., 2008). Understanding the structure and drivers of biodiversity within freshwater systems is therefore essential for sustainable management and conservation planning (Mooney et al., 2009; Heino et al., 2015). However, anthropogenic activities driven by rapid economic growth over the past few decades have increasingly compromised freshwater ecosystem health globally, resulting in habitat degradation, altered hydrological regimes, and pollution (Dudgeon, 2019; Oberdorff, 2022). Agricultural intensification, urbanization, dam construction, and industrial or sewage discharges all degrade water quality, reduce habitat complexity, and threaten aquatic biodiversity (Keskinen et al., 2015; Winemiller et al., 2016).

Benthic diatoms, microscopic algae that colonize submerged substrates in freshwater environments, are among the most widely used biological indicators of river ecosystem health (Pandey et al., 2017). Their short generation times and strong sensitivity to multiple physical and chemical factors, such as nutrients and sediment loads, light availability, and water ionic composition, make them early responsive to environmental change (Kelly et al., 2008; Rimet & Bouchez, 2012). As primary producers, they form the foundation of aquatic food webs, driving primary productivity and nutrient cycling, while shifts in their assemblages often signal broader ecological changes that affect higher trophic levels (Poulíčková & Manoylov, 2019). Because diatom assemblages respond rapidly and predictably to stressors such as eutrophication, turbidity, and organic pollution, they are considered reliable early warning indicators of ecological degradation (Duong et al., 2006; Solimini et al., 2008; Pham, 2017, 2020; Poulíčková & Manoylov, 2019; Tran et al., 2022; Chrea et al., 2024). In Southeast Asia, the Mekong River Basin and its tributaries, including Cambodia's Tonle Sap Lake system, support agriculture, fisheries, and domestic water use (Kummu et al., 2010). Rapid population growth and economic development have increasingly posed pressures on these ecosystems, causing declines in chemical water quality and altering sediment dynamics (Chea et al., 2020).

Biodiversity in freshwater ecosystems is commonly assessed using multiple complementary metrics. Among these, alpha (α), beta (β), and gamma (γ) diversity indices are widely applied to quantify ecological patterns across flora and fauna (Whittaker, 1972; Magurran, 2021). Alpha (α) diversity describes species richness or diversity within a specific site or community, whereas beta (β) diversity captures the turnover or variation in species composition among sites. Gamma (γ) diversity, in turn, reflects the total diversity at the landscape or regional scale, integrating both local richness and spatial turnover. Of these metrics, β-diversity is particularly valuable for understanding spatial patterns of community structure and the ecological processes that shape them (Anderson et al., 2006; Baselga, 2010). Environmental gradients, habitat heterogeneity, and anthropogenic pressures all strongly influence these diversity components, thereby driving the distribution and composition of aquatic communities along riverine networks (Heino et al., 2015; Soininen et al., 2018). Metrics such as Local Contribution to Beta Diversity (LCBD) and Species Contribution to Beta Diversity (SCBD) provide additional insights by identifying sites and species that substantially influence overall β-diversity (Legendre & De Cáceres, 2013). Sites with high-LCBD values are often ecologically unique and may serve as priority areas for conservation, while species with high SCBD play critical roles in maintaining ecosystem functioning. Despite their utility, the application of LCBD and SCBD metrics remains limited, representing a significant knowledge gap in biodiversity assessment and freshwater biomonitoring. Incorporating β-diversity, LCBD, and SCBD analyses into biomonitoring frameworks offers practical benefits, particularly in countries with limited resources, such as Cambodia (MRC, 2019). Indeed, these approaches may enable the rapid identification of sites with high ecological uniqueness and species that play critical roles in maintaining assemblage structure, thereby enhancing conservation priority-setting in the face of accelerating anthropogenic pressures and climate change (Heino et al., 2015; Jyrkänkallio-Mikkola et al., 2018; Hasan et al., 2023).

This study investigates the patterns of beta diversity, along with LCBD and SCBD metrics, of benthic diatom assemblages along the longitudinal gradient

of Cambodia's largest northwestern river, the Sangker River. Specifically, we aim to characterize the spatial variation of taxonomic diversity (α- and β-diversity) of benthic diatom assemblages along the upstream–downstream river gradient and identify the key physical and chemical drivers influencing beta diversity patterns. We hypothesize that longitudinal environmental gradients significantly structure the α- and β-diversity of benthic diatom assemblages along the Sangker River, with genus turnover contributing more to β-diversity than nestedness. Given the limited taxonomic knowledge of diatom species in the region, genus-level identification was performed; although this may affect some species-specific responses, it still captures the main patterns of diatom diversity and ecological responses relevant for long-term biomonitoring. Ongoing taxonomic work in the Sangker River supports this approach: a new species and a new genus have recently been described (Tudesque et al., 2023), and a preliminary flora of centric, monoraphid, araphid, and brachiraphid diatoms has been published (Chrea, 2024), while studies on biraphid diatoms are still in progress. Based on several sampling campaigns conducted between 2018 and 2022, this study provides novel insights into the spatial distribution of benthic diatom diversity in a tropical river system. Our findings are particularly relevant for biomonitoring in data-scarce regions such as Cambodia and contribute to a broader understanding of the bioecology of benthic diatom flora in tropical rivers.

Materials and methods

Study area

The Sangker River basin covers an area of approximately 6,051 km^2, representing about 10% of the Tonle Sap Lake (TSL) catchment. It is one of the major tributaries feeding into the TSL, flowing west to east across northwestern Cambodia (Fig. 1). Land cover in the basin is dominated by forest (54%) and agricultural land (46%), with only a small proportion classified as urban (0.1%) (Sourn et al., 2022). Agricultural activities prevail in the upstream catchment, while the midstream section around Battambang City is characterized by rapid urban expansion, industrial development, and extensive paddy fields (Fig. 1). After a journey of approximately 200 km, the river discharges into the TSL floodplains. Being part of the Tonle Sap hydrological system, the river is subject to a tropical monsoon climate, experiencing a wet season (May–October) and a dry season (April–November). However, over the past few decades, developments such as the construction of cascade dams (e.g., Sek Sak, Kahot, and Taorn), extensive deforestation, agricultural expansion, and rapid urban growth have significantly impacted both biodiversity and ecological integrity within the river basin (Oeurng et al., 2019).

Nineteen monitoring sites were established to capture the variability of the Sangker River catchment across diverse geographic and environmental settings, including floodplains, uplands, and mountainous zones (Fig. 1). Accordingly, six locations were identified in the headwaters, five in the middle course, and eight downstream, comprising five sites within the TLS floodplains. Five sites were located on tributaries (ORAING, KHUOT, SOPHON, PREKHEV, and PREKPEAM) to improve spatial coverage and provide a more comprehensive understanding of catchment-scale dynamics, thereby supporting more effective river monitoring and management. Detailed environmental characteristics of the monitoring sites are provided in Table S1.

Benthic diatom and environmental data collection

Benthic diatom data were collected twice annually, in the early wet (June) and dry (November) seasons from 2018 to 2022, to capture the spatiotemporal variation of the diatom community along the Sangker River. The first sampling campaign took place in November 2018 and covered only sixteen monitoring sites across the river catchment, aiming to provide an initial assessment of ecosystem health and to identify priority locations for long-term biomonitoring (Fig. 1). In 2019, the monitoring sites were expanded to nineteen sites with the addition of three sites in the Tonle Sap floodplain (PREKPEAM, PEAMSEMA) and Sek Sak reservoir (SEKSAK). This extension allowed for a broader understanding of benthic diatom communities and water quality processes across different aquatic environments (main channel *vs.* tributaries; lotic *vs.* lentic systems). Although the sampling campaign was paused in 2020 due to the COVID-19 pandemic, the dataset successfully captures insights from seven comprehensive campaigns

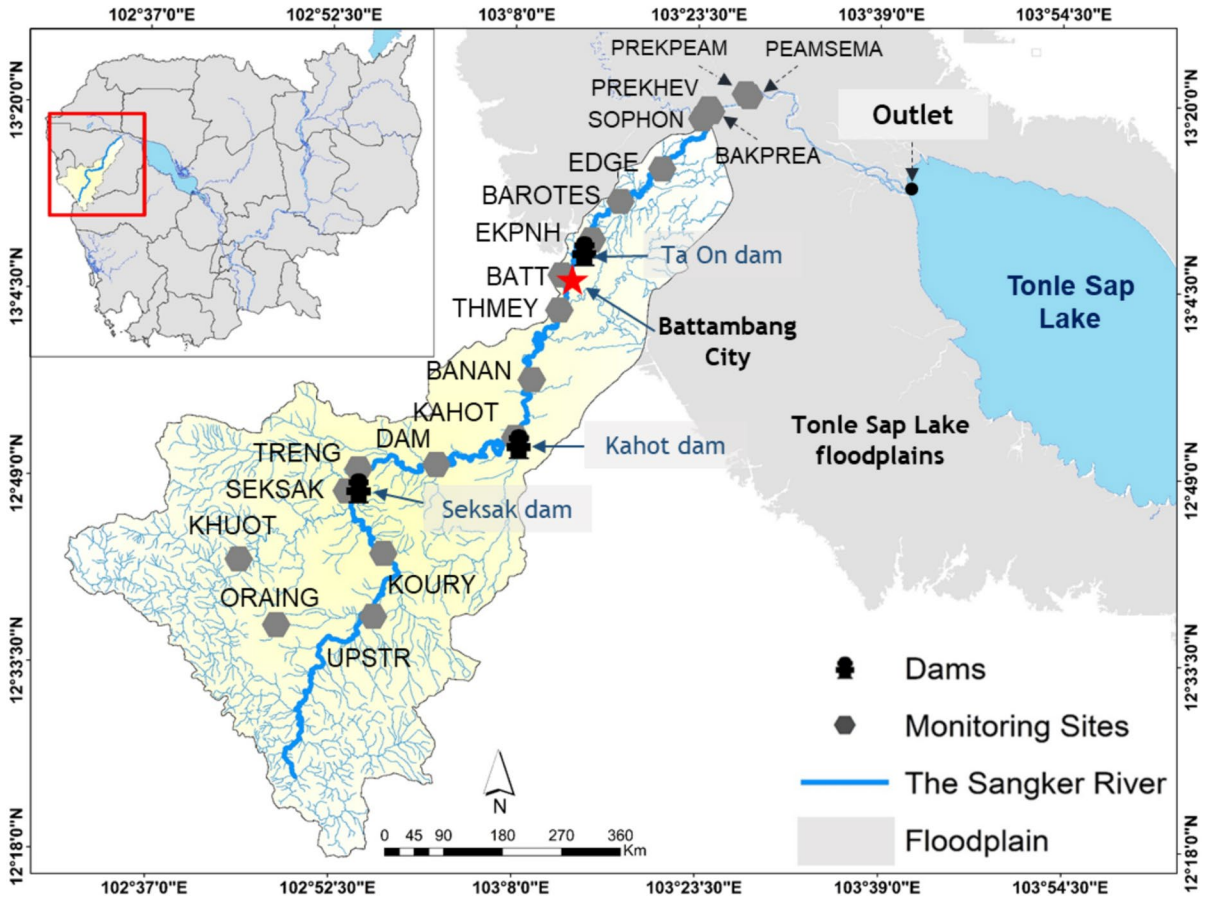


Fig. 1 The map of the Sangker River catchment (Tonle Sap Basin, Cambodia) shows the geographical position of the nineteen monitoring sites (grey polygons) and the outlet of the river in dry season indicated by the black dot. In the wet season, its location varies within the boundaries of the floodplain

in total. Benthic diatoms were collected from available natural substrates in the following order of preference: stones (S), macrophyte stems (Sm), macrophyte roots (R), and wood. Stones and wood were brushed with a toothbrush, while stems and roots were cut and squeezed to extract diatom material. Samples were processed and identified in the laboratory according to standard procedures described in Chrea et al., (2024). Identification was conducted at the genus level using reference materials, primarily diatom floras and taxonomic handbooks from Europe and Asia (Krammer, 2002, 2003; Tanaka, 2007, 2014; Lange-Bertalot et al., 2017). So far, genus-level identification has been performed because species-level determination remains challenging in the Sangker River catchment due to incomplete reference libraries and limited taxonomic and ecological knowledge for many diatom species. Nevertheless, genus-level data capture ecological patterns and environmental responses, providing a holistic insight into diatom diversity and community structure.

A total of twelve environmental variables, nine physical and chemical parameters, and three spatial factors were analyzed to characterize environmental and anthropogenic drivers of benthic diatom diversity along the Sangker River. The physical and chemical parameters included dissolved oxygen (DO), oxygen saturation (OS), electrical conductivity (EC), total nitrogen (TN), total phosphorus (TP), total suspended solids (TSS), chemical oxygen demand (COD), pH, and chloride (Cl). The spatial factors were distance from the lake (DFL), longitude (Lon), and latitude (Lat). Physical and chemical parameters were measured either in situ using a multi-parameter probe

(WTW Multi 3420 Set G) or in the laboratory following ISO standard protocols presented in Table 1 (Chrea et al., 2023), i.e., ISO 10304–1:1995 for Cl^-, ISO 15681–1:2003 for TP, ISO NF EN 12260 for TN, and ISO 15705:2002 for COD. Sampling was conducted twice annually, simultaneous with benthic diatom surveys, at the same monitoring sites. Distance from the lake (DFL) was considered the key spatial factor representing the upstream–downstream gradient. It was calculated in ArcGIS 10.5 (Esri, 2016) from the river outlet (Fig. 1) to each sampling site during the dry season and expressed in kilometers (km).

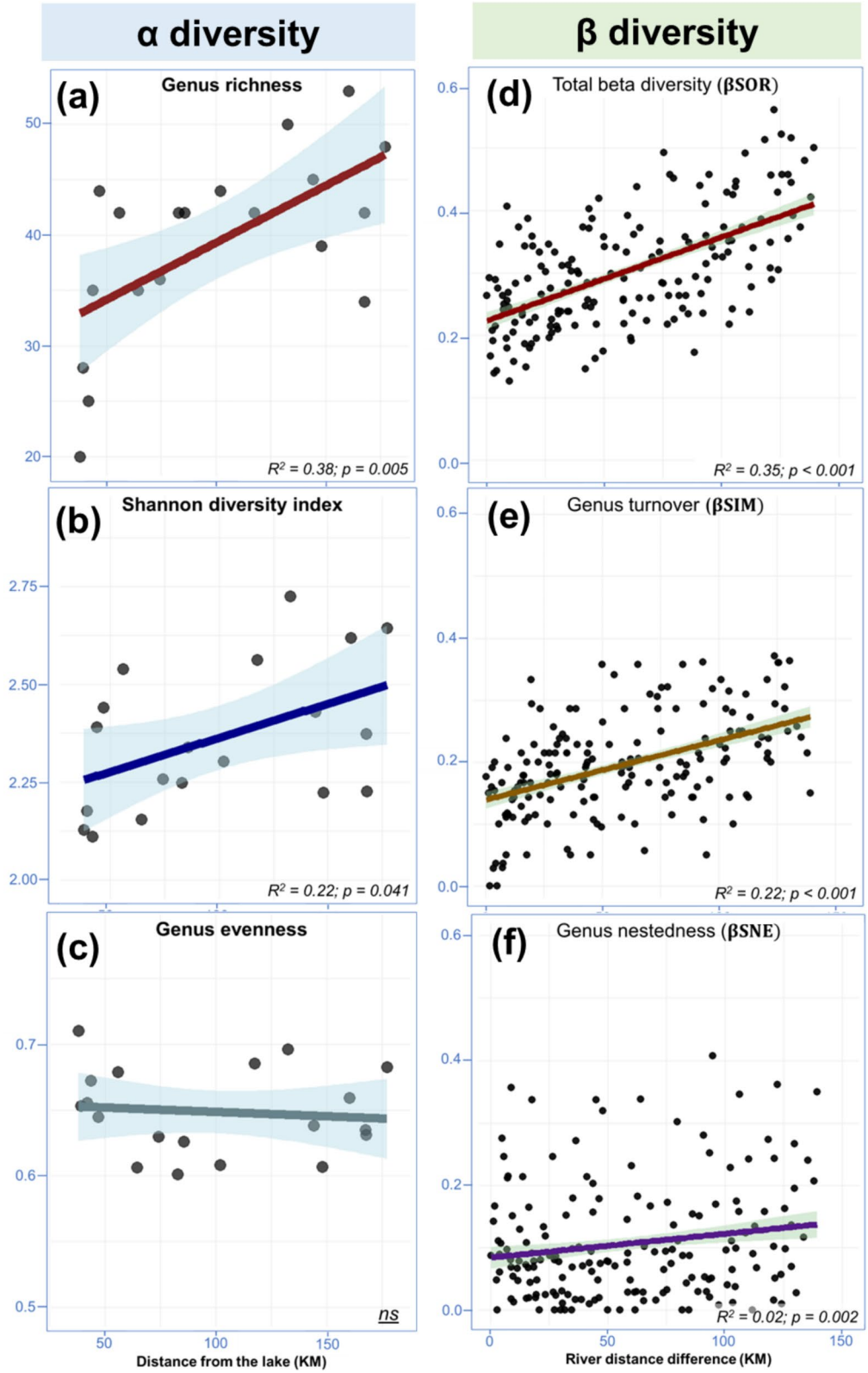
Statistical analyses

First, the benthic diatom table was converted to relative abundances (%) and averaged to standardize assemblage composition across sites. Taxonomic α-diversity metrics, including genus richness, Shannon diversity index (H′), and Pielou's evenness (J), were computed using the "vegan" package in R (Oksanen et al., 2025) to provide a basic snapshot of local diatom assemblage structure in terms of richness, diversity, and evenness. Next, β-diversity, characterizing differences in assemblage composition among sites, was calculated using the Sørensen dissimilarity index with the "betapart" package (Baselga & Orme, 2012). This framework decomposes β-diversity (**βsor**) into two complementary components: turnover (**βsim**), which reflects the replacement of some genera (in our case) by others between sites and indicates genera substitution along environmental/spatial gradients (Baselga, 2010), and nestedness (**βsne**), which captures differences in genus richness among sites resulting from genera loss or gain, without replacement (Baselga, 2010). Indeed, partitioning β-diversity in this framework allows a more detailed understanding of the ecological processes driving benthic diatom assemblage variation, including patterns of genera replacement versus loss along the Sangker environmental gradients. Accordingly, generalized linear models (GLM) were then applied to examine spatial patterns of both α- and β-diversity along the upstream–downstream gradient based on the distance from the lake (DFL), enabling quantification of diversity trends and relationships with river position.

To identify the main contributors to β-diversity across the Sangker River, Local Contribution to Beta Diversity (LCBD) and Species (genera in our case) Contribution to Beta Diversity (SCBD) were calculated following Legendre and De Cáceres, (2013) using Hellinger-transformed assemblage data. LCBD quantifies the degree to which each site's assemblage composition differs from the regional average, thereby highlighting sites with unusual; unique, or distinctive assemblages. SCBD, on the other hand, measures the contribution of each genus to overall β-diversity, identifying taxa that disproportionately drive assemblage differences among sites. Together, these complementary metrics allow a detailed assessment of both spatial patterns and genera-level influences on assemblage variation, providing important insights for biodiversity monitoring, conservation prioritization, and understanding community assembly processes in riverine ecosystems (Anderson et al., 2006; Legendre & De Cáceres, 2013). Both LCBD

Table 1 Effect of physical and chemical variable on local contributions to β-diversity (LCBD) values in the Sangker River catchment

Parameter	Unit	Std. Error	t-value	p-value	Significant levels
Electrical conductivity (EC)	µm/S	0.023	−2.144	0.061	ns
pH	–	9.620	1.527	0.161	ns
Oxygen saturation (Sat)	%	0.231	1.455	0.180	ns
Dissolved oxygen (DO)	mg/L	3.936	−1.967	0.081	ns
Total suspended solid (TSS)	mg/L	0.042	−2.314	0.046	*
Chloride (Cl^-)	mg/L	1.594	1.524	0.311	ns
Chemical oxygen demand (COD)	mg/L	0.307	1.074	0.679	ns
Total nitrogen (TN)	mg/L	0.002	−0.427	0.162	ns
Total phosphorus (TP)	mg/L	10.430	3.542	0.006	**


α diversity
β diversity
(a)
Genus richness
R^2 = 0.38; p = 0.005
(b)
Shannon diversity index
R^2 = 0.22; p = 0.041
(c)
Genus evenness
ns
Distance from the lake (KM)
(d)
Total beta diversity (βSOR)
R^2 = 0.35; p < 0.001
(e)
Genus turnover (βSIM)
R^2 = 0.22; p < 0.001
(f)
Genus nestedness (βSNE)
R^2 = 0.02; p = 0.002
River distance difference (KM)

◂**Fig. 2** Spatial patterns of benthic diatom diversity along the Sangker River. Panels (a-c) show the longitudinal gradient of α-diversity represented by (a) genus richness, (b) Shannon diversity index, and (c) evenness. Panels (d-f) depict β-diversity responses between site pairs, including (d) Sørensen dissimilarity (βsor), (e) species turnover (βsim), and (f) nestedness (βsne) in relation to river distance differences. Solid lines represent trends fitted using generalized linear models (GLMs). *Distance from the lake* (KM) refers to the longitudinal distance of each site from the river mouth, whereas *river distance difference* (KM) denotes the pairwise difference in river distance between monitoring sites

and SCBD were computed using the "beta.div" function from the "vegan" package in R (Oksanen et al., 2025)(Legendre & De Cáceres, 2013). To identify sites with important LCBD values, a Monte Carlo permutation tests with 999 randomizations were performed using the "adespatial" package in R (Legendre & De Cáceres, 2013). Accordingly, sites with $P < 0.05$ were considered to have benthic diatom assemblages significantly different from the regional assemblage. Temporal effects on benthic diatom assemblages in the Sangker River catchment were assessed by examining seasonal variation in α- and β-diversity using Wilcoxon rank-sum tests.

Finally, to examine the effect of physical and chemical variables on site uniqueness along the Sangker River course, a linear model (LM) was used to assess the response of LCBD values to these physical and chemical factors. Variance inflation factors (VIFs) were applied on linear model to assess the multicollinearity among the physical and chemical predictors (O'brien, 2007). Predictors with VIF values greater than 5 were considered highly correlated with other variables, and their effects in the model were interpreted with caution. In other words, their contribution to LCBD variation may be influenced by the presence of other factors. All analyses were carried out using the R program (R Core Team, 2024).

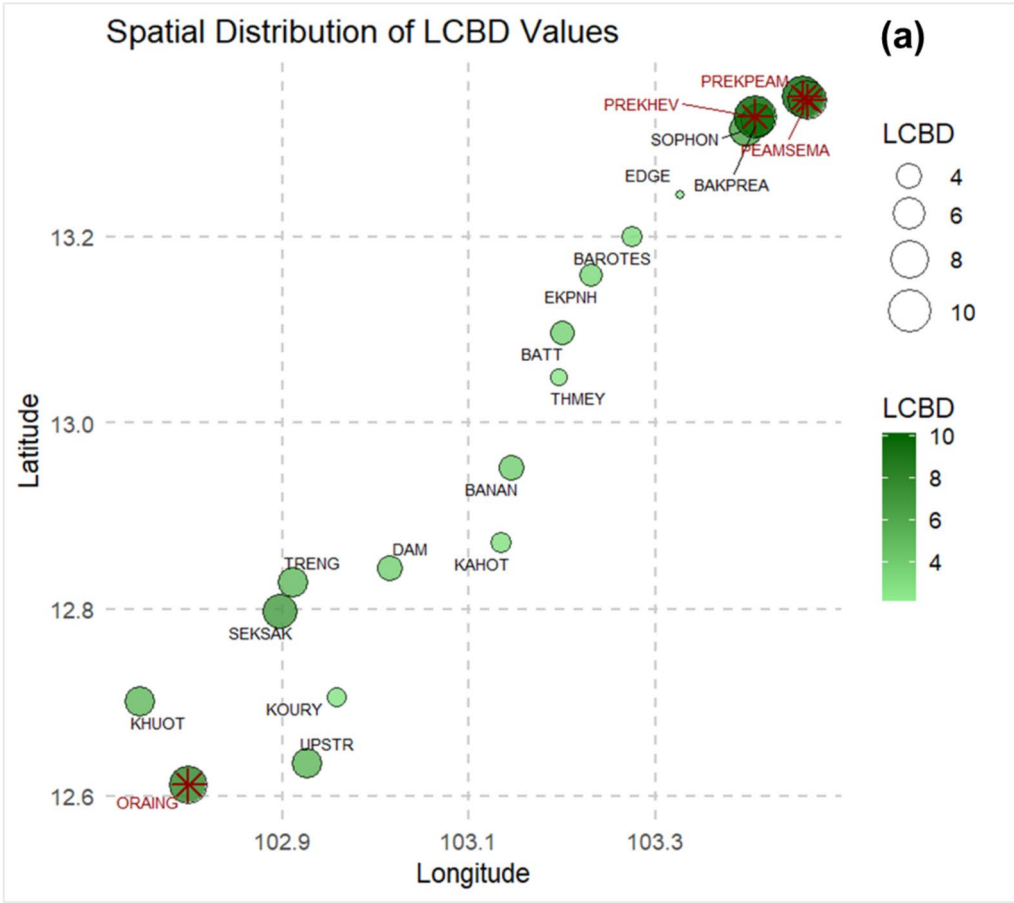
Results

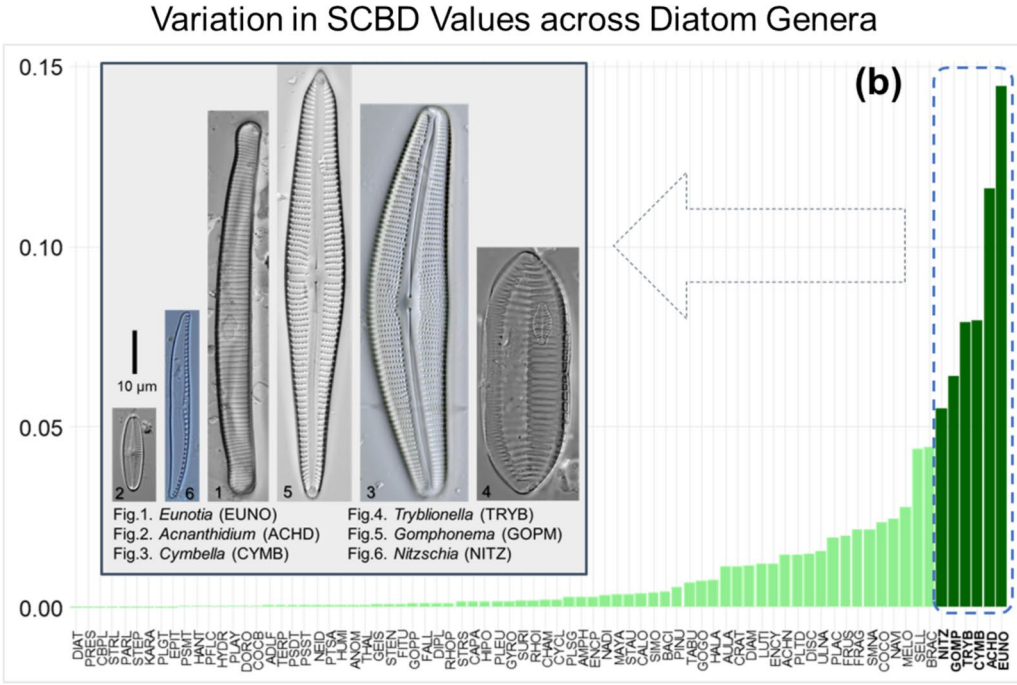
Patterns of α- and β-diversity of benthic diatom community

Across the nineteen monitoring sites of the Sangker River catchment, 78 diatom genera were identified, representing 36 families, 18 orders, and five ecological categories (Fig. S1, Table S1). The community was dominated by biraphid taxa, which comprised two-thirds (67%) of all recorded genera, while centric (13%) and monoraphid forms (10%) were less common (Fig. S1). Naviculales, Cymbellales, and Achnanthales were the most diverse orders, whereas at the family level, Naviculaceae was the most represented (10%), followed by Bacillariaceae and Achnanthidiaceae (8% each), while Cymbellaceae and Stauroneidaceae each contributed 6%. Despite this broad taxonomic diversity, community composition was predominated by a small number of genera, such as *Gomphonema* Ehrenberg (GOMP) (19.44% of total relative abundance), *Nitzschia* Hassal (NITZ) (17.24%), *Navicula* Bory (NAVI) (7.79%), and *Achnanthidium* Kützing (ACHD) (7.19%).

Both α-diversity and β-diversity of the benthic diatom community exhibited important variation along the longitudinal gradient of the Sangker River. A linear model revealed a clear longitudinal gradient of diatom genus richness, showing a significant decline from the upstream sections toward the Tonle Sap floodplains ($R^2 = 0.38$, $P = 0.005$) (Fig. 2a). This suggests that upstream habitats support a higher number of diatom genera compared to the downstream sites as well as within the TSL floodplains. A similar spatial gradient was also observed for the Shannon diversity index; it showed a moderate but significant decline downstream ($R^2 = 0.22$, $P = 0.041$), indicating that the diversity loss was largely attributable to reduced genus richness rather than shifts in community evenness (Fig. 2b). In fact, evenness did not exhibit any systematic longitudinal pattern, suggesting that the relative distribution of individuals among genera remained relatively stable across the river-floodplain gradient (Fig. 2c). More precisely, the number of genera varied widely, from the lowest 20 genera in PEAMSEMA (TLS floodplains) to the highest 53 genera in KOURY (upstream of Sangker). In terms of the Shannon index, diversity values spanned from 2.1 in PREKHEV, indicating comparatively low diversity, to 2.7 in ORAING, KOURY, and DAM, which were defined as the most diverse sites within the catchment. These observations highlight strong spatial heterogeneity in diatom communities, reflecting the combined effects of hydrological connectivity, nutrient gradients, and habitat diversity along the river course.

The average value of the Sørensen beta diversity index (βsor) was calculated as 0.748, indicating


Spatial Distribution of LCBD Values
(a)
PREKPEAM
PREKHEV
SOPHON
PEAMSEMA
EDGE
BAKPREA
BAROTES
EKPNH
BATT
THMEY
BANAN
DAM
KAHOT
TRENG
SEKSAK
KHUOT
KOURY
UPSTR
ORAING
LCBD
4
6
8
10
LCBD
10
8
6
4
Latitude
13.2
13.0
12.8
12.6
102.9
103.1
103.3
Longitude


Variation in SCBD Values across Diatom Genera
(b)
0.15
0.10
0.05
0.00
10 µm
Fig.1. Eunotia (EUNO)
Fig.2. Acnanthidium (ACHD)
Fig.3. Cymbella (CYMB)
Fig.4. Tryblionella (TRYB)
Fig.5. Gomphonema (GOPM)
Fig.6. Nitzschia (NITZ)
DIAT PRES CBRT STRL PARL STEP KARA PLGT PSMT PSMT HANT PFLC HYDR PLAY DORO COCB ADLF TERP PSDT PSST NEID PTSM ANOM THAL GEIS STEN FITU GOPP FRAL RHOP STRS CAPA HIPO PLEU GYRO RHOI CHAM CYCL PLSG AMPH EPIT NADI MAYA STAU CALO SIMO BACI PNAU TABU GOGO HALA ALLA CRAT DIAM LUTI ENCY ACHN PLTD DISC ULNA PLAC FRAS SMNA COCO NAVI MELO SELL BRYO NITZ GOMP TRYB CYMB ACHD EUNO

◂**Fig. 3** Local and species contributions to β-diversity (LCBD and SCBD) along the Sangker River. (a) Spatial distribution of LCBD values across monitoring sites. Circle size and color represent each site's contribution to overall β-diversity, with larger, darker green circles indicating higher LCBD. Sites marked with a red asterisk (*) significantly contribute to β-diversity and contain unique diatom communities ($P < 0.05$, permutation = 999). (b) SCBD values of diatom genera, indicating each genus's contribution to β-diversity. High and dark green bars highlight genera driving site differences, with top contributors: *Eunotia* Ehrenberg (EUNO), *Achnanthidium* Kützing (ACHD), *Cymbella* C.Agardh (CYMB), *Tryblionella* W.Smith (TRYB), *Gomphonema* Lange-Bertalot (GOMP), and *Nitzschia* Hassall (NITZ). Illustrations of these genera are provided at the top left of panel (b) (Fig. 1–6)

significant changes in genera composition between sites along the longitudinal gradient of the Sangker River. To further disentangle the processes underlying this variation, total beta diversity was partitioned into its two components: genus turnover (βsim) and nestedness (βsne) (Fig. 2d–f). The analysis revealed that turnover contributed the most to the observed beta diversity, with βsim = 0.639, whereas the nestedness component was comparatively low for βsne = 0.109. βsor, βsim, and βsne were all positively related to the distance between sites (Fig. 2d, e, f), although the relationship for nestedness (βsne) was much weaker. These results suggest that the spatial variation in diatom communities along the river gradient is primarily driven by species replacement rather than by differences in richness due to genera loss or gain. In other words, communities at different sites are largely composed of distinct genera rather than representing subsets of each other.

Seasonal variation of benthic diatom assemblages in the Sangker River catchment was reflected in α-diversity patterns. Assemblages in the wet season exhibited higher genus richness, Shannon diversity index, and evenness compared to the dry season (Wilcoxon tests, $P < 0.005$; Figure S1). Consequently, seasonal analyses of β-diversity showed similar patterns between interannual and seasonal variation; genus turnover (βsim) largely drove temporal β-diversity in both seasons, whereas nestedness (βnes) contributed only a minor fraction (Table S2).

Local and species contributions to β-diversity (LCBD and SCBD)

The contribution of individual sites and genera to overall β-diversity varied along the Sangker River (Fig. 3a). LCBD analysis revealed that sites such as PEAMSEMA, PREKPEAM, PREKHEV, and ORAING exhibited significantly higher contributions ($P < 0.05$, permutation = 999), indicating unique diatom community composition, whereas sites like EDGE, THMEY, KAHOT, and BAROTES showed lower LCBD values, reflecting more typical communities (Fig. 3a). High-LCBD sites were distributed both upstream and in floodplain sections, suggesting longitudinal and habitat-driven variation. Seasonal changes in LCBD values were not significant, indicating that the uniqueness of benthic diatom assemblages at individual sites remained stable between the dry and wet seasons (Wilcoxon test, $P > 0.05$). This suggests that, despite seasonal fluctuations in α-diversity. SCBD results identified the genera that primarily drive variations in benthic diatom community composition between sites (Fig. 3b). *Eunotia* Ehrenberg (EUNO), *Achnanthidium* (ACHD), *Cymbella* C. Agardh (CYMB), *Tryblionella* W.Smith (TRYB), *Gomphonema* (GOMP), and *Nitzschia* (NITZ) had the greatest SCBD values, indicating their significant contribution to β-diversity in the Sangker River basin. In contrast, the remaining genera made minor contributions to site differentiation (Fig. 3b).

Effect of physical and chemical variables on LCBD values

The multiple linear model showed a significant effect of physical and chemical factors on the local contributions to β-diversity (LCBD) value within the Sangker River catchment ($R^2 = 0.85$, $P = 0.007$) (Table 1). Among the assessed physical and chemical variables, total phosphorus (TP) and total suspended solids (TSS) exhibited significant effects on LCBD values, indicating that sites with higher TP and TSS concentrations contributed more strongly to β-diversity patterns. Dissolved oxygen (DO) seems to have potential influence on LCBD values; however, the relationship was not significant ($P = 0.08$). Other parameters such as electrical conductivity (EC), pH, oxygen saturation (Sat), chloride (Cl^-), chemical oxygen demand (COD), and total nitrogen (TN) did not show any effects on the variation of LCBD within the Sangker River catchment (Table 1).Variance inflation factor (VIF) analysis revealed that several physical and chemical predictors, including EC, pH, Sat, DO, TSS, and Cl^-, were highly correlated (VIF > 5), reflecting

their strong interrelationships along the longitudinal river gradient. In contrast, TP, TN, and COD exhibited low VIF values (< 5), suggesting that their contributions to LCBD variation along the river course are more robust. Overall, the linear model remains reliable, although the influence of highly correlated variables should be interpreted with caution, as it reflects the underlying river gradient.

Discussion

Patterns of α- and β-diversity of benthic diatom communities along the Sangker River.

The current study revealed pronounced spatial patterns in both α- and β-diversity of benthic diatom communities along the Sangker River, emphasizing the role of environmental filtering in structuring diversity and community composition along the river gradient. Taxonomically, the diatom community was highly diverse; however, despite this richness, it was dominated by a few genera, particularly *Gomphonema* (GOMP), *Nitzschia* (NITZ), *Navicula* (NAVI), and *Achnanthidium* (ACHD), which together accounted for more than half of the total relative abundance. Such dominance of specific genera is consistent with previous observations in other tropical rivers, where a small subset of diatom taxa with broad ecological plasticity (e.g., NITZ, GOMP) often drives community structure (Leelahakriengkrai & Peerapornpisal, 2011; Shibabaw et al., 2021; Chrea et al., 2024). Clear patterns of α-diversity (genus richness and Shannon diversity index) were observed along the longitudinal gradient of the Sangker River. Upstream sites exhibited high α-diversity, while downstream floodplain sites showed lower diversity. Similar patterns have been documented in other large tropical rivers, including the Mekong mainstream and its tributaries, where upstream reaches with higher flow variability, substrate heterogeneity, and lower nutrient concentrations tend to support more diverse benthic communities (Dudgeon, 2000; Shibabaw et al., 2021; Chrea et al., 2024; Nunes et al., 2025). Interestingly, community evenness did not exhibit a systematic longitudinal trend, suggesting that the observed decline in diatom diversity downstream of the Sangker River was primarily driven by reductions in genus richness rather than changes in relative abundance among taxa (Liu et al., 2023; Nunes et al., 2025). This finding implies that, although the number of diatom taxa decreases, the relative distribution of individuals among the remaining genera remains stable, reflecting the potential resilience of dominant taxa to environmental pressures. Although the patterns were based on genus-level identification, this approach can still effectively reflect diatom assemblage structure and ecological gradients along the Sangker River. Species-level identification could reveal finer-scale responses to environmental factors, particularly for dominant genera such as *Navicula, Nitzschia,* and *Gomphonema*, which may comprise multiple species with differing ecological preferences. Nevertheless, previous studies in tropical rivers have shown that genus- and species-level data generally produce similar diversity and community patterns, capturing the main spatial turnover and nestedness patterns of taxonomic diversity (Chen et al., 2016; Riato et al., 2022). Therefore, genus-level identification provides reliable insights into α- and β-diversity in response to environmental gradients, forming an essential foundation for long-term biomonitoring and conservation planning in data-scarce regions such as Cambodia.

Patterns of β-diversity revealed strong spatial heterogeneity across the Sangker River catchment. Partitioning total β-diversity into its turnover (βsim) and nestedness (βsne) components further indicated that species replacement accounted for most of the observed variation. The predominance of turnover over nestedness indicates that sites along the Sangker River host distinct diatom assemblages rather than nested subsets of upstream communities. This pattern is consistent with previous studies in tropical, neotropical, and Afrotropical rivers, where turnover-driven β-diversity has been associated with environmental gradients such as flow regime, substrate type, and nutrient availability (Wu et al., 2024; Caballero et al., 2025). This dominance pattern of turnover was observed for other biological communities such as fish (Schmidt et al., 2022), invertebrates (Keke et al., 2022), and phytoplankton (Wojciechowski et al., 2017). Additionally, the positive correlation between β-diversity and geographic distance suggests that both dispersal limitation and habitat heterogeneity jointly shape diatom community assemblages along the Sangker River. The weak nestedness component further implies that downstream assemblages are not simply a reduced subset of upstream communities;

rather, they are structured by local habitat conditions and selective environmental filters, such as substrate type, flow regime, and nutrient availability (Heino et al., 2015). For instance, studies in the Sungai Pahang River in Malaysia have demonstrated that species turnover is influenced by factors such as water chemistry, hydrology, and habitat complexity, leading to distinct diatom assemblages along environmental gradients (yang Terganggu et al., 2010). Similarly, research in the Rio Guainía in Colombia has highlighted the role of environmental filters in shaping diatom communities, with turnover being a dominant component of β-diversity (Tan et al., 2013). Therefore, our current study highlights the critical role of physical and chemical conditions in structuring diatom communities and suggests that the observed genus turnover in the Sangker River likely reflects responses to similar environmental gradients, such as flow regime, substrate type, and nutrient availability (Heino et al., 2015; Shibabaw et al., 2021; Duan et al., 2025). In addition, dispersal limitation may also influence these patterns by restricting the movement of certain genera among sites within the river. Although dispersal limitation is typically stronger between river systems, limited downstream or upstream dispersal can still occur within a single river, influenced by factors such as water flow, substrate characteristics, and habitat connectivity, resulting in distinct assemblages and contributing to the observed β-diversity along the river gradient (Heino et al., 2015; Hu et al., 2024). Overall, the spatial patterns of α- and β-diversity observed in the Sangker River underline the importance of longitudinal gradients, habitat heterogeneity, and environmental filtering in structuring benthic diatom communities. Upstream reaches, with higher genus richness, likely reflect more diverse microhabitats and stable environmental conditions, whereas downstream floodplain sites are characterized by lower richness and higher uniqueness due to sedimentation, nutrient enrichment, and seasonal flood dynamics. These patterns are consistent with global observations in large river systems, emphasizing that tropical rivers exhibit high turnover-driven β-diversity due to pronounced environmental gradients (Keck & Kahlert, 2019; Hu et al., 2024; Duan et al., 2025; Taurozzi et al., 2025).

Moreover, our findings revealed a clear seasonal effect on α-diversity, while β-diversity was less influenced. In particular, diatom assemblages were more diverse during the dry season compared to the wet season. Higher α-diversity in the dry season likely results from a combination of key environmental factors, including stable hydrology, increased habitat heterogeneity, elevated nutrient concentrations, and reduced physical disturbance, which together promote genus turnover and coexistence. In contrast, high flows during the wet season often increase turbidity and substrate disturbance, reducing diatom richness, a pattern also reported in studies where benthic diatom diversity declined during high-flow or wet conditions due to habitat instability and lower light availability (Snell et al., 2019; Ma et al., 2023). The dominance of genus turnover over nestedness in β-diversity in both seasons indicates that seasonal changes are driven primarily by the replacement of genera rather than by the simple loss or gain of taxa. This pattern is consistent with findings from other aquatic ecosystems, where turnover has been shown to dominate community dynamics across contrasting hydrological periods (Ma et al., 2023). Overall, seasonal hydrological and habitat dynamics play a primary role in structuring benthic diatom diversity and compositional turnover in the Sangker River. Given that taxonomic diversity is higher and genus turnover is more pronounced during the dry season, concentrating sampling efforts in this period may be an effective strategy to capture most of the benthic diatom assemblage diversity at the river basin scale. Such an approach could improve the efficiency of biomonitoring programs in data-limited tropical river systems while potentially reducing the need for multiple surveys within a single year.

Drivers of LCBD and SCBD along the Sangker River

LCBD analysis revealed that certain sites in the tributaries, e.g., PEAMSEMA, PREKPEAM, PREKHEV, and ORAING, contributed significantly to overall β-diversity, reflecting their unique community compositions. These high-LCBD sites were found in both upstream and TLS floodplains, indicating that spatial uniqueness is influenced not only by river position but also by local environmental conditions within the Sangker River catchment (Vilmi et al., 2017; Jyrkänkallio-Mikkola et al., 2018). For instance, the floodplain sites PEAMSEMA and PREKHEV may experience periodic inundation and sediment deposition, creating specialized habitats that support unique diatom assemblages. Similarly, upstream

sites like ORAING may provide a diversity of substrates, microhabitats, and lower nutrient concentrations, fostering distinct community structures (Benito et al., 2020; Rodríguez-Lozano et al., 2023). These tributary sites contribute locally to genus replacement and increased community uniqueness; however, β-diversity along the river was consistently dominated by genus turnover, suggesting that the longitudinal gradient along the main channel is the primary driver of assemblage differences. Tributary sites nevertheless play an important role in shaping local turnover patterns, particularly where flow regime, habitat characteristics, or nutrient dynamics differ from the main channel. In contrast, low-LCBD sites reflected more common communities adapted to eurytopic environmental conditions along the river course. In other words, some sections of the river exhibit homogenized diatom assemblages (Schneck et al., 2022). Moreover, species contributions to β-diversity (SCBD) further highlighted the ecological importance of a subset of dominant genera, including EUNO, ACHD, CYMB, TRYB, GOMP, and NITZ. For example, *Eunotia* (EUNO) species are typically stenotopic, thriving in oligotrophic, well-oxygenated upstream habitats, whereas *Nitzschia* (NITZ) and *Gomphonema* (GOMP) are more eurytopic, tolerating a wide range of nutrient and sediment conditions and thus able to colonize diverse environments (Vilmi et al., 2017; Xia et al., 2022). These patterns indicate that both environmental filtering and ecological plasticity jointly determine the influence of particular genera on β-diversity in the Sangker River catchment (Hasan et al., 2023).

Physical and chemical drivers further explained the variation in LCBD across the Sangker River. Our analysis highlighted the significant influence of total phosphorus (TP) and total suspended solids (TSS) on local contributions to β-diversity, indicating that nutrient enrichment and turbidity are central factors shaping unique diatom assemblages in this system. Similar relationships have been reported in tropical and subtropical rivers (Shibabaw et al., 2021; Hasan et al., 2023; Chrea et al., 2024; Wang et al., 2024). High phosphorus concentrations typically promote fast-growing, eutrophic adapted taxa such as NITZ, NAVI, and GOMP, while high suspended solids favor taxa such as TRYB and EUNO, adapted to turbid, low-light, and unstable habitats. Similar findings have been illustrated from the Tonle Sap floodplain and Mekong basin, where seasonal nutrient and sediment suspension shape diatom turnover, favoring tolerant taxa during high-flow periods (Soum et al., 2021). Along the mainstream Mekong, phosphorus inputs from agriculture and sediment dynamics associated with land-use change and hydropower development similarly influence diatom assemblages (Tran et al., 2022). Previous studies from Amazonian rivers (Aprile et al., 2023) and the subtropical Ganges–Brahmaputra rivers (Roshith et al., 2018) reported nutrient enrichment and turbidity were the key determinants of diatom community differentiation, with only tolerant genera dominating the eutrophic and light-limited river conditions. Therefore, TP and TSS could be fundamental drivers of both local uniqueness (LCBD) and species-level contributions (SCBD), as they regulate which taxa can persist under variable nutrient and sediment regimes, thereby structuring site- and species-based β-diversity patterns in the Sangker River catchment.

Ecological implications for biomonitoring and conservation

The observed patterns of α- and β-diversity of benthic diatom community, along with LCBD and SCBD analyses, carry important implications for long-term biomonitoring of the Sangker River. Indeed, high β-diversity driven by genus turnover indicates that sampling multiple sites along the river is essential to capture the full range of diatom diversity. Focusing only on upstream or low-disturbance sites would underestimate regional diversity and overlook the uniqueness of diatom communities, particularly in the nutrient rich environment within the TLS floodplains. More importantly, LCBD result contributed to define the "hotspot" sites with unique community composition, which may serve as indicators of environmental change. For instance, PEAMSEMA and ORAING, exhibiting the highest LCBD values, could be prioritized for monitoring or conservation due to their unique diatom assemblage structure. Besides, based on the SCBD results, dominant genera such as EUNO, ACHD, CYMB, GOMP, and NITZ should be considered key taxa in biomonitoring, as changes in their abundance or distribution are likely to reflect shifts in water quality, nutrient status, or habitat quality. Targeting these indicator genera can enhance the quality and relevance of biomonitoring programs,

particularly in large, spatially heterogeneous river systems where exhaustive taxonomic surveys are logistically challenging.

The significant influence of physical and chemical variables on LCBD highlights the need to manage nutrient inputs and sediment loads to maintain ecosystem health. In tropical river basins, pressures from agriculture, urbanization, and hydropower development commonly drive nutrient enrichment and sedimentation (Dudgeon, 2000; Shibabaw et al., 2021). Monitoring sites with high-LCBD values can serve as early warning indicators of eutrophication or habitat degradation, supporting proactive and targeted river management. Finally, these findings advance our understanding of diatom flora by showing how environmental gradient and local habitat conditions jointly shape community composition. Moreover, this study provides a practical framework for establishing biomonitoring programs in data-scarce regions like Cambodia, offering guidance for conservation and management under increasing anthropogenic pressures and global environmental change.

Conclusion

This study provides the first comprehensive assessment of β-diversity patterns in benthic diatom assemblages along the longitudinal gradient of the Sangker River, the largest northwestern tributary of the Tonle Sap Lake. Results showed that β-diversity was high and predominantly driven by species turnover rather than nestedness, indicating pronounced spatial differentiation of diatom communities along the river continuum. A downstream decline in α-diversity was also detected, likely reflecting increasing anthropogenic influence and related environmental degradation. Local Contributions to Beta Diversity (LCBD) identified ecologically distinctive sites at both upstream and downstream reaches, while Taxa Contributions to Beta Diversity (SCBD) highlighted key genera, *Eunotia*, *Achnanthidium*, *Cymbella*, *Tryblionella*, *Gomphonema*, and *Nitzschia*, as major contributors to assemblage differentiation. Among the environmental variables examined, total phosphorus and total suspended solids were significant predictors of site uniqueness, underscoring the influence of nutrient enrichment and turbidity on diatom community composition. Overall, diatom diversity in the Sangker River is shaped by both longitudinal gradients and environmental filtering. Integrating LCBD and SCBD metrics into biomonitoring frameworks can improve the detection of ecological changes and provide a cost-effective approach for identifying priority sites for conservation and management under increasing anthropogenic pressures within the Tonle Sap catchment.

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Declarations

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