

## RESEARCH ARTICLE

# Environment regimes play an important role in structuring trait- and taxonomy-based temporal beta diversity of riverine diatoms

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## Abstract

1. A sound understanding of the community changes over time and its driving forces is at the centre of biodiversity conservation and ecology research. In this study, we examined: (i) the relative roles of turnover and nestedness components to trait- and taxonomy-based temporal beta diversity of riverine diatoms; (ii) whether trait-based temporal beta diversity provides complementary information to taxonomy-based temporal beta diversity; (iii) the relative roles of hydrology (e.g. discharge, antecedent precipitation index), metal ions (e.g.  $Mg^{2+}$ ,  $Si^{2+}$ ) and nutrients (e.g. nitrogen, orthophosphate) to the both facets of temporal beta diversity and their components (i.e. total beta diversity, turnover and nestedness); and (iv) whether inclusion of environment regimes increase their explained variations.
2. A total of 338 daily samples of riverine diatom communities were collected. We employed Mantel tests to evaluate the complementarities between trait- and taxonomy-based temporal beta diversity. Using distance-based redundancy analysis (db-RDA) and variation partitioning, we investigated the relative roles of hydrology, metal ions and nutrients to each facet of temporal beta diversity and its components.
3. Correlations between trait- and taxonomy-based temporal beta diversity and their components were weak, which showed their complementary ecological information. Taxonomy-based total beta diversity had a high contribution by turnover component, whereas trait-based total beta diversity was largely driven by nestedness component. Results of variation partitioning demonstrated that the pure and shared fractions of hydrology, metal ions and nutrient differed among the components of trait- and taxonomy-based temporal beta diversity. Furthermore, addition of environment regimes could dramatically increase the explained variation of temporal beta diversity and its components.

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4. *Synthesis*. Our results highlighted the importance of the two facets of temporal beta diversity as well as their decomposition for exploring diversity patterns of riverine diatoms in relation to abiotic factors, particularly the environment regimes. Although a high temporal taxonomic divergence was detected, the high level of temporal trait convergence indicated that species turnover with similar biological traits occurred during our study period. Our study, for the first time, provides a new perspective into temporal beta diversity of daily riverine diatom communities, which has not yet been documented by previous freshwater studies.

#### KEYWORDS

anthropogenic impacts, beta diversity decomposition, convergence, flow regime, lowland river, nestedness, nutrient regime, turnover

## 1 | INTRODUCTION

Under the Anthropocene (Crutzen, 2002), human disturbances (e.g. urbanization, deforestation, industry) have caused considerable impacts on ecosystems, resulting in a decrease in world-wide biodiversity (Waldron et al., 2017). This is particularly true for freshwater ecosystems, which as a diverse habitat on the Earth, is threatened by multiple concurrent stressors like overexploitation, climate change, flow alteration, habitat fragmentation, pollution and exotic species invasions (Reid et al., 2019). Although freshwater habitats cover only <1% of the planet surface, they support ~10% of all known species and ~1/3 of vertebrate species (Strayer & Dudgeon, 2010), and thus are invaluable for biodiversity (Altermatt et al., 2013). Nevertheless, freshwater biodiversity is declining with an unprecedented speed, faster than in marine and terrestrial ecosystems (Albert et al., 2021), in spite of huge efforts to forestall such loss (Epele et al., 2019; Voulvoulis et al., 2017). Therefore, understanding the interaction among water quality, habitat condition and freshwater biodiversity has become a major challenge of community ecology and conservation biology, as this is crucial for sustainable managing ecological resources and prioritizing conservation efforts (Gaston, 2000; Myers et al., 2000).

Among the three terms of biological diversity (i.e. alpha, beta and gamma), alpha and gamma diversity account for species numbers, whereas beta diversity (i.e. the temporal and spatial differentiation in species composition) links alpha (i.e. local biodiversity) and gamma (i.e. the regional species pool) diversities (Whittaker, 1960; Whittaker, 1972). During the past several decades, researchers have paid considerable attention to beta diversity (Anderson et al., 2011; Lebourcier et al., 2019). However, a common limitation of those investigations is that community information was often collected from a single date (Heino et al., 2015; Sinclair et al., 2021), either because of the complications involved in sampling across seasons or due to the study objective that did not consider temporal variation. This constraint hinders our inference about the major drivers of community structure to one 'snapshot' community, which has missed

the temporal variation with different mechanisms. For instance, the role of environmental variables on species composition relies upon the extent of their gradients that might change over time (Qu et al., 2019; Wu et al., 2018). Similarly, the biotic interactions and dispersal could also temporally vary that affect species composition. Indeed, there is growing evidence of community shifts at catchment and local scales over time (McGill et al., 2015). Particularly, recent studies (e.g. Blowes et al., 2019; Finderup Nielsen et al., 2019; Hendershot et al., 2020; Lindholm et al., 2021) have shown that even though temporal alpha diversity remains stable, species composition may be shifting continuously. In this regard, the identified drivers that shape one time snapshot community composition might not be sufficient when temporal variations were considered (Vagle & McCain, 2020). Therefore, further examination of temporal biodiversity and its relationships with environmental variables is essential for practical management. In fact, the temporal beta diversity, which is defined as the temporal change in community composition at one location (Legendre & Gauthier, 2014; Shimadzu et al., 2015), has become a hotspot in recent freshwater biodiversity studies on distinct organism groups, such as fishes (Kuczynski et al., 2018), zooplankton (Sinclair et al., 2021) and lake plants (Lindholm et al., 2021). Nevertheless, compared with the huge effort to spatial beta diversity, the temporal beta diversity is still less documented to date.

There are several methods to measure temporal beta diversity (Magurran et al., 2019), one among which is the temporal beta diversity index (TBI; Legendre, 2019). Some recent studies have examined the changes in TBI patterns (e.g. Cook et al., 2018; Sinclair et al., 2021), but the TBI can go further and help to identify the mechanisms regulating community assembly (Baselga & Leprieur, 2015; Legendre, 2019). Recent advances in ecology allowed us to decompose TBI into turnover and nestedness components (Baselga, 2010; Legendre, 2019). A high contribution of turnover underlies a large rate of species replacement between sampling dates, whereas a high nestedness rate indicates differences in species richness among sampling dates (i.e. a date with low richness is a subset of date with high richness) (Baselga, 2010).

This decomposition can help identify the dates that have changed in species composition in an exceptional way, thereby leading to a further exploration in more detail. TBI is further useful in guiding management actions by pointing out dates with temporally stable communities, and on the other hand, dates when species loss is causing biodiversity decline. The decomposition of temporal beta diversity has proven its usefulness in detecting temporal beta diversity patterns in different organisms (Soininen et al., 2018), such as trees (Brice et al., 2019), lake plants (Lindholm et al., 2021) and mollusc communities (Legendre & Salvat, 2015), and fish (Kuczynski et al., 2018). However, to our best knowledge, there is no study on riverine diatoms, a key component of riverine algae, that considered the various facets (trait and taxonomy-based) and components (turnover and nestedness) of temporal beta diversity.

As an important primary producer in aquatic ecosystems, diatoms were increasingly involved as environmental indicators in freshwater ecosystems due to their well-known distinct features (Wijewardene et al., 2021; Wu et al., 2017). Consequently, diatom-based biodiversity studies have been widely carried out around the world (Benito et al., 2018; Branco et al., 2020; Lebourcher et al., 2019; Wu et al., 2021). However, most of these studies used only taxonomic composition, which was highly influenced by micro-evolutionary processes and less suitable for large spatial and temporal scale studies of environmental changes (Soininen et al., 2016). Therefore, many ecologists have started to probe functional traits in addition to taxonomic composition because traits reflect a species' functional adaptation to their environment and show a greater stability in their responses to large-scale spatial and temporal environmental changes (McGill et al., 2006).

Trait-based studies have been widely considered in stream macroinvertebrates (Menezes et al., 2010), aquatic plants (Baattrup-Pedersen et al., 2016) and fish communities (López-Delgado et al., 2020), but only recently were implemented for riverine diatoms (Guo et al., 2020; Wu et al., 2017, 2019). Several studies have shown their advantage in freshwater biomonitoring and biodiversity conservation (Perez Rocha et al., 2018; Wang et al., 2022; White et al., 2017; Wijewardene et al., 2021). At the meanwhile, several trait categories have been proposed and implemented recently, such as diatom guilds, biovolumes and life-forms (Lange et al., 2016; Passy, 2007; Rimet & Bouchez, 2012; Witteveen et al., 2020). Nevertheless, most investigations that studied beta diversity of riverine diatoms usually highlighted taxonomic composition, while comparisons among different facets of beta diversity and their relationship to multiple environmental stressors were still scarce (but see Branco et al., 2020; Jamoneau et al., 2018; Perez Rocha et al., 2019; Wu et al., 2021). To our best knowledge, no study has focused on temporal beta diversity patterns of riverine diatoms with consideration of both taxonomy and functional trait yet.

In this study, we explored the relative importance of different factors (i.e. hydrology, metal ions and nutrients) that structure trait and taxonomy-based temporal beta diversity and their components in riverine diatom community from a lowland German river (i.e. the Kielstau Basin; Figure 1). We collected the daily samples of riverine

diatoms over a 1-year period (25 April 2013–30 April 2014) and aimed to answer four research questions: (i) What are the relative roles of turnover and nestedness components to total temporal trait- and taxonomy-based beta diversity of riverine diatom community? (ii) Whether these two facets of temporal beta diversity provide complementary information to each other? (iii) What are the relative roles of hydrology, metal ions and nutrient to both facets of temporal beta diversity and their components? (iv) Can inclusion of environment regimes increase their explained variations? Since taxa with similar niches are grouped into common traits, species replacements (i.e. turnover) do not necessarily lead to trait turnover. Therefore, we expected that taxonomy-based temporal beta diversity should be higher (particularly a higher turnover) than trait-based temporal beta diversity (H1). Furthermore, as species shifts do not always induce trait replacements, we assumed that the correlation between the two facets of temporal beta diversity, particularly turnover, should be low (H2). Given that snapshot diatoms may be affected by both instant and previous environmental situations, we hypothesized that environment regimes (e.g. flow and nutrient regimes) play an important role in explaining the variation of temporal beta diversity and its components (H3).

## 2 | MATERIALS AND METHODS

### 2.1 | Description of the study area

Kielstau catchment is a lowland watershed with a drainage area of 50 km<sup>2</sup> in the northern Germany. Since 2010, it has become an UNESCO Demosite for Ecohydrology. It is an important tributary of the Treene River, which originates in the upper part of Lake Winderatt (Figure 1a). This catchment has two major tributaries—Hennebach and Moorau. The typical soil types are sandy, loamy and peat soils, while agriculture and pasture are dominant land use types, which take ~55% and ~26% respectively (Fohrer et al., 2007). There are six wastewater treatment plants within the catchment (main stream: Ausacker and Freienwill; Moorau: Husby; Hennebach: Hürup Nord, Hürup Weseby and Hürup Süd) (Figure 1b). More details about this catchment have been explicitly introduced by previous studies (Pfanterstill et al., 2014; Sun et al., 2018, 2022; Wu et al., 2011a, 2011b).

This basin is ideal to enhance our understanding of temporal beta diversity patterns and their underlying mechanisms. First, there is still a lack of temporal sampling at a daily or sub-daily interval in previous studies. Thus, researches with daily diatom samples can be particularly important for understanding the responses of temporal beta diversity and its components to environmental change. Second, the long-term monitoring on physicochemical parameters (e.g. nutrients, metal ions) and hydrological variables (e.g. discharge, precipitation) allows calculating both flow and nutrient regimes. Numerous surveys have been conducted in this basin, most of which focused on water balance (Guse et al., 2014; Pfanterstill et al., 2014), community structures and functional groups of riverine phytoplankton

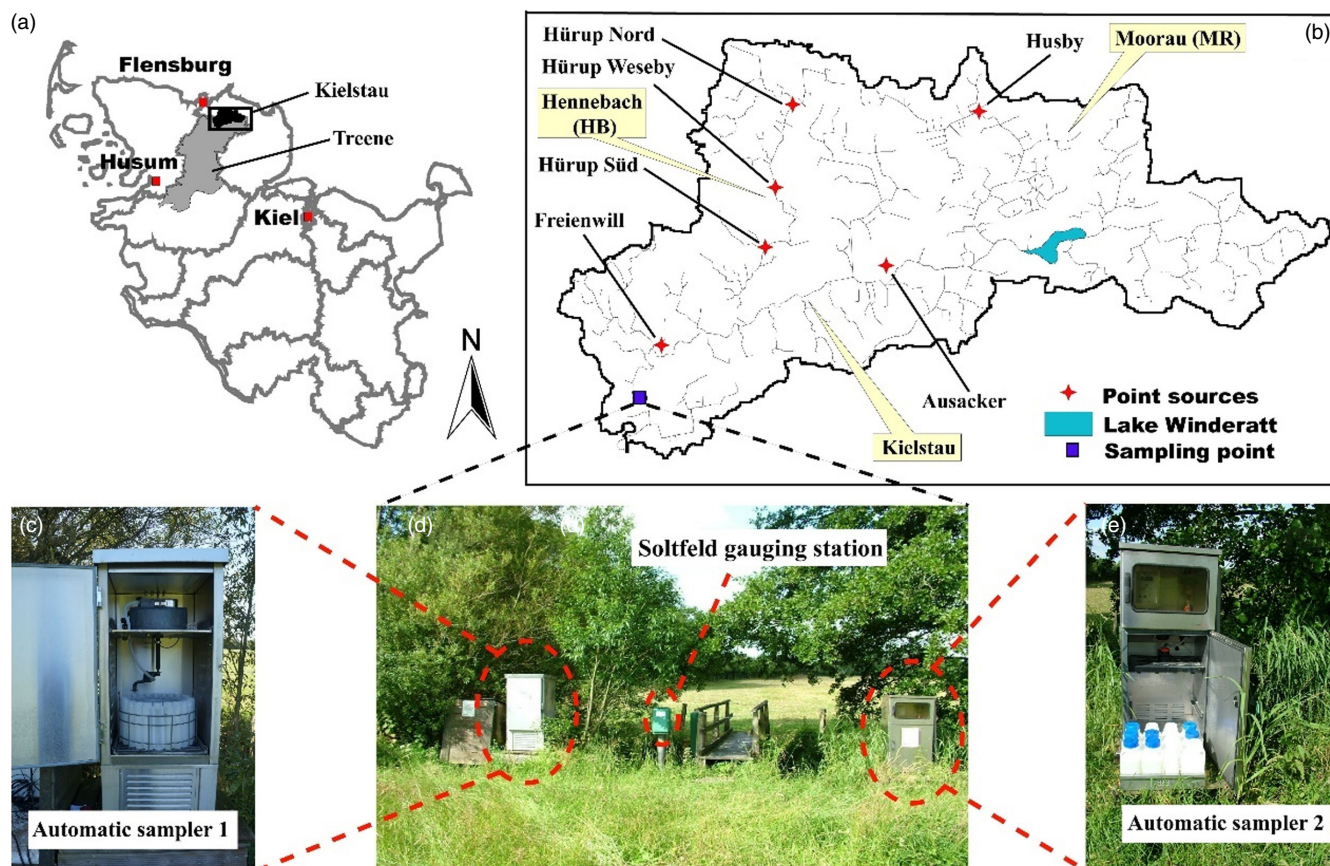


FIGURE 1 The location of Kielstau catchment at Schleswig-Holstein state, Germany (a) and the sampling site (b). Photos of the Soltfeld gauging station and two automatic samplers (c–e) were taken by Sun (2015)

(Qu et al., 2018, 2019; Sun et al., 2018; Wu et al., 2011a, 2011b, 2016). However, few studies have examined the diversity patterns of riverine algal communities (e.g. Wu et al., 2018), with no studies examining the temporal beta diversity and its main drivers within the Kielstau River.

## 2.2 | Field sampling and processing

The collection of daily mixed water samples was conducted at the outlet of the catchment from 25 April 2013 to 30 April 2014. Using two automatic samplers (Figure 1c,e), daily mixed water samples were collected and kept in the refrigerators at 4°C. They were picked once a week (normally on Monday) and taken back to the laboratory of the Department of Hydrology and Water Resources Management of Kiel University. Since diatoms are the predominant algal group in this region (Wu et al., 2011a, 2011b), we focused on diatoms in the following analyses. The diatoms present here are a mix of suspended benthic diatoms, and any planktonic communities from upstream wetlands and lakes, or communities developing in the river (Wu et al., 2016). In the laboratory, Hydrogen Peroxide Method (30% H<sub>2</sub>O<sub>2</sub> solution) and Naphrax (Northern Biological supplies Ltd., UK, R1 = 1.74) were used to prepare permanent diatom slides. We counted a minimum of 300 valves for each sample using a

Zeiss Axioskop microscope at 1000× under oil immersion. Diatoms were identified to the lowest taxonomic level possible (mainly species level). The detailed laboratory procedures including diatom sedimentation, preservation and identification have been described in previous articles (Sun et al., 2018, 2022; Wu et al., 2016). Since samples on 32 dates were missing due to technical problems or low temperatures, a total of 338 samples were gathered finally.

Water chemical parameters, including metal ions (Cl<sup>-</sup>, K<sup>+</sup>, Ca<sup>+</sup>, Na<sup>+</sup>, Mg<sup>2+</sup> and Si<sup>2+</sup>), ammonium-nitrogen (NH<sub>4</sub>-N), nitrate-nitrogen (NO<sub>3</sub>-N), orthophosphate (PO<sub>4</sub>-P) and sulphate (SO<sub>4</sub><sup>2-</sup>), were measured in the laboratory (for methods, see Appendix S1). We also collected hydrological variables included daily discharge (Q), discharge skewness (Sk), precipitation (Prec) and antecedent precipitation index (API) (more details have been given in Wu et al. (2016)). We computed both flow (using Q) and nutrient (using NH<sub>4</sub>-N, NO<sub>3</sub>-N and PO<sub>4</sub>-P) regimes with R package SER (Guo et al., 2019). Unlike traditional indices, the environment regimes focused on a short-period event (i.e. 3, 7 and 14 days) prior to the sampling date. Therefore, we have short-period environment regime indices elucidating three aspects: magnitude, frequency and change rate of environment variables at three temporal scales (Appendix S2).

The abiotic factors were split into three categories: (a) hydrological variables (Hydrology), which included Q, Prec, Skewness and API (Appendix S3), and hydrological variables + flow regimes

(Hydrology+), which included both Hydrology and flow regime indices of Q; (b) metal ions (Metal), which included six parameters ( $\text{Cl}^-$ ,  $\text{K}^+$ ,  $\text{Ca}^+$ ,  $\text{Na}^+$ ,  $\text{Mg}^{2+}$  and  $\text{Si}^{2+}$ ); and (c) nutrients (Nutrient), which included  $\text{NH}_4\text{-N}$ ,  $\text{NO}_3\text{-N}$ ,  $\text{PO}_4\text{-P}$ ,  $\text{SO}_4^{2-}$  and nutrients + nutrient regimes (Nutrient+), which contained both Nutrient variables and their regime indices.

### 2.3 | Diatom traits

To obtain trait-based temporal beta diversity and its decomposition, we assigned diatom species into three categories (i.e. biovolume, ecological guild and life-form) including 15 traits based on trait information from literature (Biggs et al., 1998; Lange et al., 2016; Passy, 2007; Wagenhoff et al., 2013; Witteveen et al., 2020; Wu et al., 2017) (Table 1).

### 2.4 | Data analysis

At first, we calculated beta diversity and its components (i.e. total, turnover and nestedness) for both facets: (a) taxonomy-based temporal beta diversity and its components were generated based on presence-absence data (using Sørensen distance); (b) trait-based temporal beta diversity and its turnover and nestedness components were produced using the 15 traits (using Sørensen distance), following the approach in previous studies (Perez Rocha et al., 2019; Wu et al., 2021). The decomposition of temporal beta diversity allowed us to explore the relative roles of turnover and nestedness components to total trait- and taxonomy-based temporal beta diversity (question i).

TABLE 1 Three categories of diatom traits, and their codes in this study

Categories	Traits	Codes
1. Biovolume	Nano (0–100 $\mu\text{m}^3$ )	CellSize01
	Micro (100–300 $\mu\text{m}^3$ )	CellSize02
	Meso (300–600 $\mu\text{m}^3$ )	CellSize03
	Macro (600–1500 $\mu\text{m}^3$ )	CellSize04
	Large ( $\geq 1500 \mu\text{m}^3$ )	CellSize05
2. Ecological guild	Low profile	LowPro
	High profile	HigPro
	Motile taxa	MotTax
	Planktonic taxa	PlaTax
3. Life-form	Unicellular life-form	LF_Uni
	Filamentous life-form	LF_Fil
	Colonial life-form	LF_Col
	Weak attachment	ATT_Wea
	Medium attachment	ATT_Med
	Strong attachment	ATT_Str

To answer question ii and test the relationship between trait- and taxonomy-based temporal beta diversity components, Mantel tests were run with 999 permutations. Mantel test is a statistical test of the linear or monotonic independence between two dissimilarity or distance matrices (Legendre & Fortin, 2010) and has been widely used in ecological studies. The correlation strength is represented by the Mantel statistic  $r$  (–1 to 1), and a higher Mantel  $r$  value demonstrates a stronger correlation.

Distance-based redundancy analysis (db-RDA) (Legendre & Anderson, 1999) was conducted to examine the relationships between biotic matrices (i.e. temporal beta diversity and its components) and three abiotic matrices (i.e. hydrology, metal ions and nutrients). We selected db-RDA with two main reasons. First, this method can be based on any dissimilarity or distance matrices, although it is similar to redundancy analysis (Legendre & Legendre, 2012). Second, many previous similar studies (e.g. Branco et al., 2020; Ding et al., 2021; López-Delgado et al., 2020; Perez Rocha et al., 2018; Pozzobom et al., 2021; Wu et al., 2021) have employed db-RDA, with which our results can be comparable. Therefore, we followed the step-by-step procedures devised in previous studies (see also the work flow chart in Appendices S4 and S5). In all db-RDA analyses, 'bray' distance was used, while  $\text{sqrt.dist}$  correction for negative eigenvalues was added (Legendre, 2014).

First, we excluded the variables with strong multicollinearity (i.e. variance inflation factor  $\geq 3$ ). Second, stepwise selection of abiotic factors: to avoid highly inflated type I error and overestimation of explained variance, we used a two-step procedure as recommended by Blanchet et al. (2008). (a) A global test using all explanatory variables was tested by ANOVA at a significance level of  $\alpha = 0.05$ . (b) Only if the global test was significant, a stepwise selection was conducted to obtain a final set of three abiotic datasets with two stopping criteria: significance level and the adjusted coefficient of determination ( $\text{Adj } R^2$ ). Third, variation partitioning analysis (VPA) (Borcard et al., 1992): to quantify the relative roles of Hydrology, Metal and Nutrient to each facet of temporal beta diversity and its components (question iii), VPA was applied using the variables retained after stepwise selection procedure. This method was routinely employed to evaluate the relative importance of different abiotic datasets on metacommunities and detect the ecological processes. Results from VPA were shown by Venn diagrams, which is a standard way to show the fractions explained purely by each dataset as well as by their intersections (e.g. López-Delgado et al., 2020; Perez Rocha et al., 2018; Wu et al., 2021).

Furthermore, to check whether inclusion of environment regimes increase the explained variation of temporal beta diversity and its components (question iv), we ran db-RDA and VPA again with flow and nutrient regimes (i.e. Hydrology+, Metal and Nutrient+) according to the same procedures above.

All analyses were performed with R (version 4.0.2) (R Core Team, 2020): temporal beta diversity decomposition was done using functions *beta.pair* and *functional.beta.pair* respectively in R package BETAPART (Baselga & Orme, 2012); multicollinearity test was performed with *vifstep* function in R package USDM (Naimi et al., 2014);

Mantel test, ANOVA test, stepwise selection, db-RDA and VPA were conducted with *mantel*, *anova*, *ordistep*, *capscale* and *varpart* functions, respectively, in R package *VEGAN* (Oksanen et al., 2019).

### 3 | RESULTS

#### 3.1 | Temporal beta diversity decomposition

We observed a total of 113 diatom species (for detailed taxonomic composition and diversity see Sun et al. (2018, 2022), Wu et al. (2016)) in this study and the average species richness was 20.64 (range: 7–36). Trait-based total temporal beta diversity (mean  $\pm$  SD:  $0.130 \pm 0.095$ ) was dominated by nestedness ( $0.111 \pm 0.095$ ) with a small contribution from turnover ( $0.019 \pm 0.036$ ) (Figure 2). For taxonomy-based temporal beta diversity, as expected by H1, mean values of the three components (i.e. total temporal beta diversity, turnover and nestedness) were much higher ( $0.460 \pm 0.114$ ,  $0.338 \pm 0.132$  and  $0.123 \pm 0.105$  respectively), and the turnover contributed more than nestedness component (Figure 2). The correlations between trait- and taxonomy-based temporal beta diversity components were relatively weak, although significant as indicated by the Mantel test ( $p < 0.001$ ; Figure 3), which supported our second hypothesis (H2). The highest Mantel correlation coefficient was found between total temporal beta diversity (Mantel  $r = 0.460$ ), followed by nestedness ( $r = 0.400$ ) and turnover ( $r = 0.187$ ).

#### 3.2 | Main driving forces of trait- and taxonomy-based beta diversity components

Overall, the selected variables in the db-RDA models differed for both facets of temporal beta diversity components (Appendices S6 and S7). For taxonomy-based beta diversity components, the multicollinearity test and stepwise selection procedure selected two Hydrology, six Metal and four Nutrient variables for total temporal beta diversity; one Hydrology, five Metal and three Nutrient variables for turnover; and two Hydrology, three Metal and two Nutrient variables for nestedness (Appendix S6). For trait-based

temporal beta diversity components, only two Hydrology, three Metal and two Nutrient variables were picked by stepwise selection for total temporal beta diversity; no Hydrology, one Metal and one Nutrient variable were picked for turnover; and two Hydrology, two Metal and two Nutrient variables were picked for nestedness (Appendix S7).

When environment regimes were added, more variables were selected. For taxonomy-based beta diversity components, we selected 3 Hydrology+, 3 Metal, and 20 Nutrient+ variables for total temporal beta diversity; 3 Hydrology+, 2 Metal, and 20 Nutrient+ variables for turnover; and 3 Hydrology+, 2 Metal, and 10 Nutrient+ variables for nestedness (Appendix S8). For trait-based temporal beta diversity components, 5 Hydrology+, 2 Metal and 7 Nutrient+ variables were taken by stepwise selection for total temporal beta diversity; 1 Hydrology+, no Metal and 3 Nutrient+ variables were taken for turnover; and 3 Hydrology+, 2 Metal and 7 Nutrient+ variables were taken for nestedness (Appendix S9).

VPA results indicated that the pure and shared fractions of Hydrology, Metal and Nutrient were different among the components of each facet of temporal beta diversity (Figure 4). Generally, the pure contributions of Hydrology to taxonomy-based beta diversity (3.1%–4.8%) were much higher than those to trait-based beta diversity (i.e. 0). Metal (except for turnover) and Nutrient (except for nestedness) showed similar trends. Their joint effects were 4.8%, 1.9% and 2.9% for taxonomy-based nestedness, trait-based total temporal beta diversity and nestedness respectively (Figure 4). This finding demonstrated a clear interaction among the three abiotic datasets. For taxonomy-based temporal beta diversity, the total explained variations were 21.4% for total temporal beta diversity, 20.1% for turnover and 21.2% for nestedness (Figure 4). In contrast, for trait-based temporal beta diversity, models explained only 8.8%, 7.1% and 14.8% of total temporal beta diversity, turnover and nestedness respectively.

When we added environment regime indices, as expected by H3, the explained variations were dramatically increased not only for taxonomy-based but also for trait-based temporal beta diversity and its components (Figures 4 and 5). In particular, taxonomy-based total temporal beta diversity, turnover and nestedness increased by 3.0%, 4.9% and 15.5%, respectively, while trait-based temporal beta

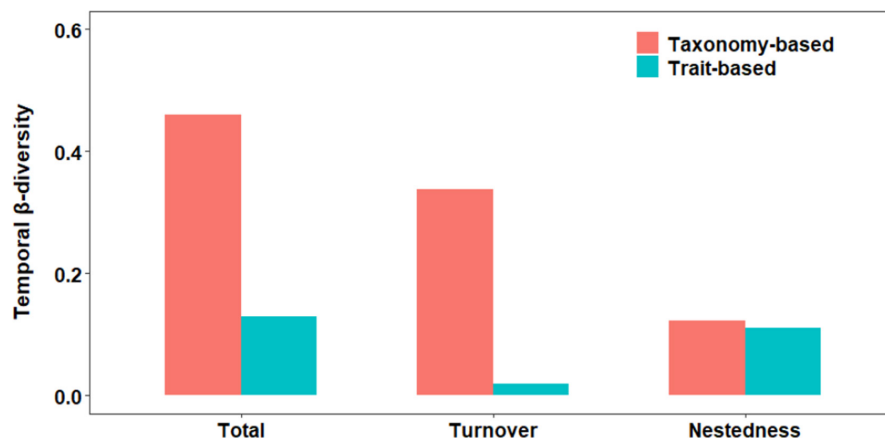


FIGURE 2 The decomposition of temporal beta diversity for riverine diatoms in the Kielstau catchment

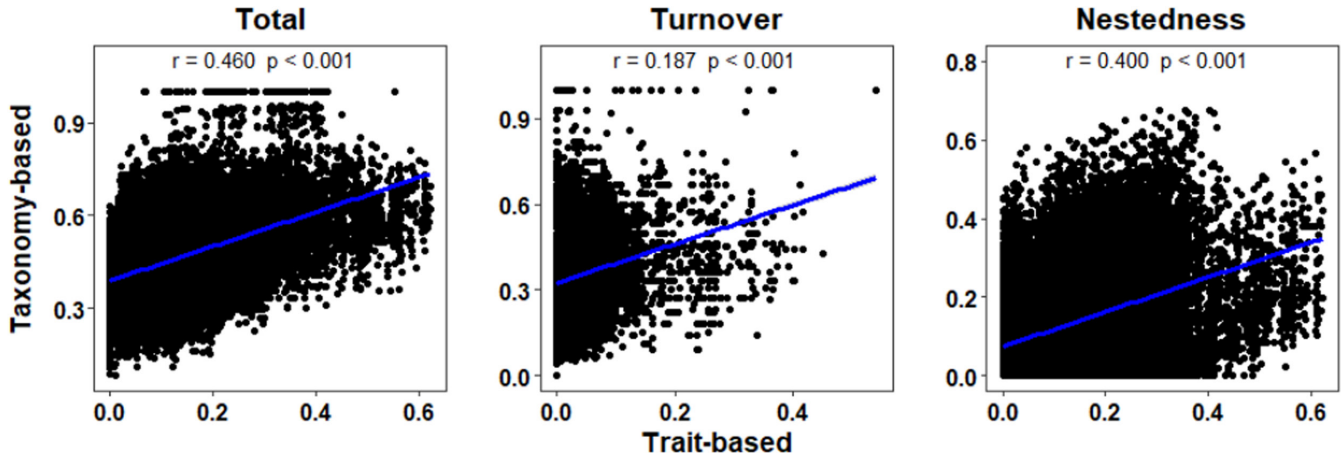


FIGURE 3 Relationships between trait- and taxonomy-based temporal beta diversity components. Mantel tests were used to test their relationships. The linear regression was shown by solid blue lines with 95% confidence interval (i.e. shaded grey area)

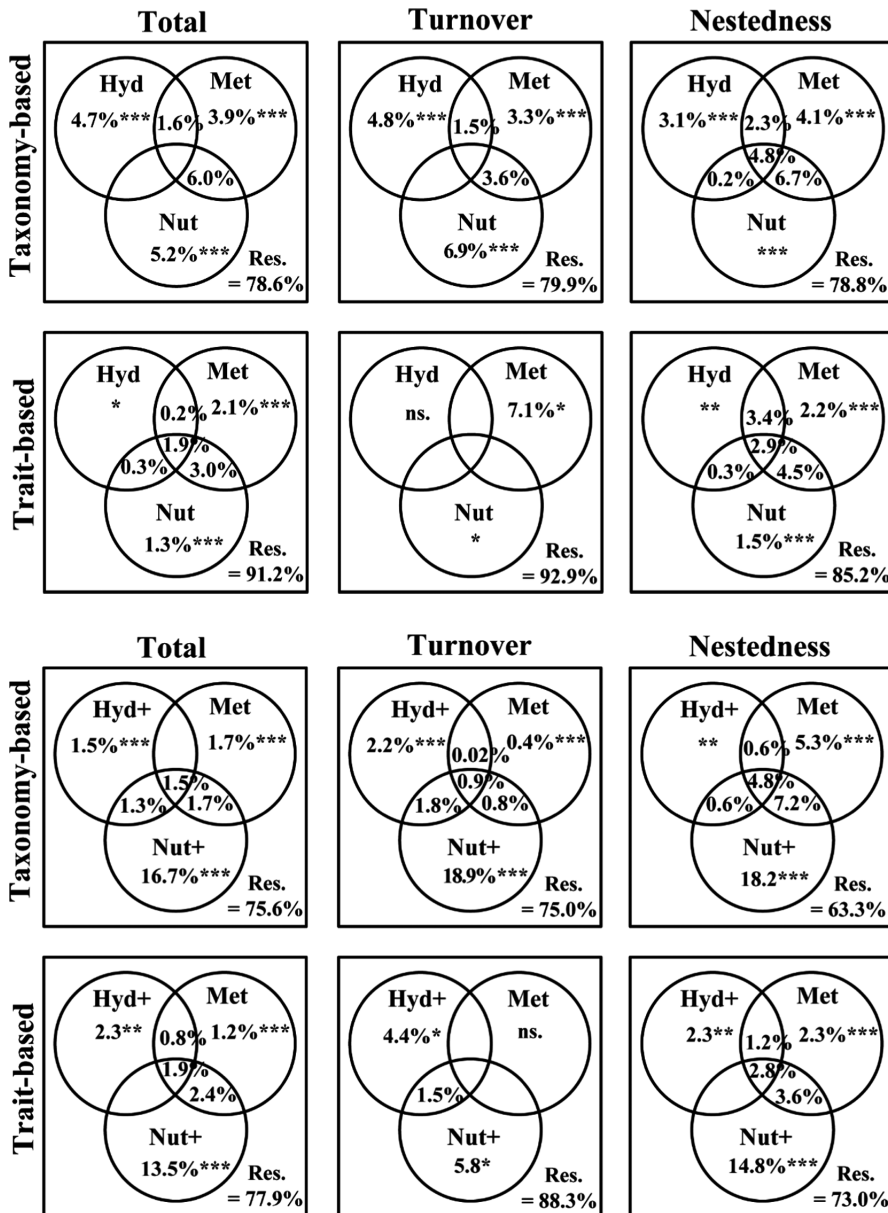


FIGURE 4 Contributions of hydrological variables (Hyd), metal ions (Met) and nutrients (Nut) to trait- and taxonomy-based temporal beta diversity components of riverine diatoms. The adjusted  $R^2$  is shown, while ns. represents no significant value for trait-based turnover component. \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$

FIGURE 5 Contributions of hydrological variables + flow regime (Hyd+), metal ions (Met) and nutrients + nutrient regime (Nut+) to trait- and taxonomy-based temporal beta diversity components of riverine diatoms. The adjusted  $R^2$  is shown, while ns. represents no significant value for trait-based turnover component. \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$

diversity and its components increased by 13.3%, 4.6% and 12.2% respectively. Interestingly, inclusion of flow regimes (i.e. Hydrology+) played a less important role in taxonomy-based temporal beta diversity than trait-based temporal beta diversity. In contrast, Nutrient+ (nutrient variables + nutrient regimes) explained more variations in taxonomy-based temporal beta diversity than trait-based temporal beta diversity (Figure 5). Compared with VPA without environment regimes (Figure 4), the pure fractions of Metal have declined in VPA with flow and nutrient regimes (except for nestedness; Figure 5).

## 4 | DISCUSSION

In this observational study with 1-year daily samples, for the first time, we examined the temporal beta diversity of riverine diatoms and its components in relation to three abiotic groups (i.e. hydrology + flow regime, metal ions and nutrients + nutrient regime). Our first hypothesis (H1) that taxonomy-based temporal beta diversity is relatively higher, particularly a higher turnover, than trait-based temporal beta diversity received support. Besides, we found that there was a weak correlation between the two facets of temporal beta diversity, especially the turnover component (as indicated by Mantel  $r$  correlations), thus supporting our second hypothesis (H2). The third hypothesis (H3) was confirmed as VPA results demonstrated that inclusion of environment regimes (e.g. flow and nutrient regimes) has clearly increased their explained variation of temporal beta diversity and its components.

### 4.1 | Relative roles of turnover and nestedness

After decomposition of the trait- and taxonomy-based temporal beta diversity of riverine diatom assemblages, we found that turnover was more important than nestedness (i.e. net loss of species) in taxonomy-based total temporal beta diversity. Since we did not find studies about temporal beta diversity of riverine diatoms and its decomposition, we compared our results with previous surveys concerning spatial beta diversity, which observed similar patterns (e.g. Branco et al., 2020; Perez Rocha et al., 2019; Soininen et al., 2018; Wu et al., 2021). The high rates of species turnover in the Kielstau Basin can be explained by several factors. A potential reason is that this basin location at northern Germany with a clear physicochemical and hydrological variation over the 1-year study period. For example, discharge varied from 0.036 to 1.798 m<sup>3</sup>/s, NH<sub>4</sub>-N ranged from 0.008 to 2.216 mg/L, PO<sub>4</sub>-P (0–0.501 mg/L) and NO<sub>3</sub>-N (1.406–8.474 mg/L) changed strongly. The big temporal environmental changes favour rapid species turnover (Heino & Tolonen, 2017). It is possible that the variation in riverine diatoms was caused by distinct adaptive and evolutionary strategies, which resulted in a higher temporal species turnover.

In contrast to taxonomy-based temporal beta diversity, trait-based total temporal beta diversity and turnover were much lower, which supported our first hypothesis (H1). Furthermore, nestedness

contributed more than turnover to the trait-based temporal beta diversity in our study, which was in line with previous observations in spatial beta diversity of stream algae communities (e.g. Perez Rocha et al., 2019; Wu et al., 2021). Selective extinction could be a potential reason for the dominance of nestedness in trait-based temporal beta diversity, namely, due to environmental filtering, some traits become dominant than others. Another possible reason for the high nestedness and low turnover was the variation in habitat heterogeneity among sampling dates. For instance, some dates with a high level of homogeneous habitats favoured only species of certain traits, while heterogeneous habitats harboured species of various traits (Goldenberg Vilar et al., 2014). The communities with low trait diversity were thus a subset of high trait-diversity assemblages (Heino & Tolonen, 2017). Overall, a higher trait-based nestedness and a lower trait-based turnover implied that more uniform diatom traits have been developed in our study period.

### 4.2 | Relationships between trait- and taxonomy-based temporal beta diversity

We observed weak correlations between trait- and taxonomy-based temporal beta diversity components (Mantel  $r$  ranged from 0.187 to 0.460), which were consistent with previous reports that carried out in spatial beta diversity patterns of riverine algae (e.g. Branco et al., 2020; Perez Rocha et al., 2019; Wu et al., 2021). This indicated that components of both trait- and taxonomy-based temporal beta diversity provided complementary ecological information, which has been confirmed in various habitats (e.g. lowland rivers, ponds, and lentic water bodies) and organisms (e.g. benthic algae, plankton, fish, macroinvertebrates and aquatic plants) (Gianuca et al., 2018; Heino & Tolonen, 2017; Hill et al., 2019; Pozzobom et al., 2021; Villéger et al., 2013; Wu et al., 2021). This finding also highlighted the necessity to incorporate these different facets of beta diversity with the aim of a deep understanding towards the variation and maintenance of biological assemblages.

We found that trait-based total beta diversity was much lower than taxonomy-based total beta diversity (0.130 vs. 0.460); as expected, taxonomy-based total beta diversity had a high contribution by turnover component (0.338), whereas trait-based total beta diversity was largely driven by nestedness component (0.111). This was because taxonomic variation was not necessarily associated with functional differences. Our result indicated that there was a relatively high temporal trait convergence (i.e. species turnover with similar biological traits) occurring during our study period, although a high temporal taxonomic divergence (i.e. a high degree of species turnover) was detected. This result implied a lower functional complementarity between dates due to adaptation of distinct species to similar habitat or environmental conditions (Villéger et al., 2013). As a consequence, most functional traits were shared by species in different sampling dates leading to a low trait-based beta diversity (Heino & Tolonen, 2017; Perez Rocha et al., 2019). Indeed, this result was in line with those obtained by recent studies (e.g. Heino &



Tolonen, 2017; Perez Rocha et al., 2019; Villéger et al., 2013; Wu et al., 2021).

### 4.3 | Temporal beta diversity patterns relative to abiotic factors

VPA results (Figures 4 and 5) showed that our abiotic factors explained 7.1%–27.0% and 20.1%–36.7% variations of trait- and taxonomy-based temporal beta diversity components respectively. Although the explained proportions of our VPAs were similar to those of previous studies with spatial beta diversity (~ 20%–40% is common; e.g. Branco et al., 2020, López-Delgado et al., 2020, Perez Rocha et al., 2018, Wu et al., 2021, Pozzobom et al., 2021), the residuals were still high (~63%–93%) (Figures 4 and 5). A common problem when assessing the underlying mechanisms that drive community dynamic and biodiversity change is the lack of comprehensive and appropriate abiotic dataset. This was well-known because it is difficult to obtain all aspects of an organism's environmental condition. We realize that the observed temporal beta diversity dynamics could be affected by other ecological processes that were not covered in present study, such as in situ parameters (e.g. pH, conductivity, oxygen), light intensity, pollutants (e.g. pesticides) (Wijewardene et al., 2021), biotic (e.g. interspecific interactions, predation, competition) factors, due to the unmeasured data (e.g. some dates with diatom samples do not have total phosphorus data). Hence, inclusion of aforementioned variables in future investigations may strengthen our understanding of the relationship between temporal beta diversity and environment.

We assume that 'species–trait–environment' relationships might be scale and catchment dependent (Lansac-Tôha et al., 2021; Leboucher et al., 2019). Thus, the relationships between temporal beta diversity and their surrounding environment in the present study may also be scale dependent. Nevertheless, since there are only a limited number of studies that have described the decomposition of spatial beta diversity (none for temporal beta diversity) for riverine algae community, further investigations at different temporal scales (e.g. year, decade, month) are highly needed to understand the scale-dependent temporal beta diversity decomposition and guide the biodiversity conservation of aquatic ecosystems.

Another impressive finding was that environment regimes, especially the nutrient regimes, accounted for big fractions of trait- and taxonomy-based temporal beta diversity components (Figures 4 and 5), supporting our third hypothesis. Environment regime was defined as the environmental dynamic characteristics during a given (either long or short) period, such as change rate, magnitude and frequency of extreme events, which might be masked by using only simple median or average values (Guo et al., 2019). Several recent studies have proved the importance of flow regimes in structuring the distribution and biodiversity of riverine algae communities (Guo et al., 2020, 2021; Qu et al., 2019; Wu et al., 2018, 2019). For example, short-period flow regimes (e.g. skewness, change rate in flow events) played an important role in riverine biofilm community. Guo et al. (2020) calculated short-period hydrological regime indices

(14 and ~28 days before sampling date), and found that these indices override physicochemical variables in structuring riverine diatom traits and community functions. Using structural equation models, Qu et al. (2019) observed that the flow regimes (i.e. skewness of 7 days discharge before sampling date) were considered as a key driver for riverine phytoplankton community during two hydrological periods.

In contrast, although the influence of nutrients on riverine algae communities has been widely recognized (e.g. Wijewardene et al., 2021; Wu et al., 2011b, 2018), nutrient regime indices as done in the current study have not been considered yet, to our best knowledge. One of the reasons might be the lack of appropriate, high quality and long-term monitoring data that enable us to calculate the nutrient regime indices. However, given the ability of continuous monitoring, progress in modelling as well as modern technology (e.g. remote sensing), we envisage that nutrient regime indices based on long-term data will be more and more frequently available in the future. Interestingly, we found that the contribution of nutrient regimes to both trait- and taxonomy-based temporal beta diversity and its components was higher than that of flow regimes, which was beyond our expectation. A possible reason was that the gradient of discharge data was smaller than nutrients factors (Appendix S10) that they were not sufficiently large to be reflected in the temporal beta diversity. Nevertheless, inclusion of environment regimes can increase the explained variations of temporal beta diversity and its components, which warrants further investigation at different temporal ecoregions and scales.

### 4.4 | Implications for biomonitoring and management

The strength of community analysis is highly depended on its ability to integrate biotic interaction and abiotic factors over time, and difficulty may arise when the influential factors for the sampled community are not observable (Cook et al., 2018). Our findings imply that treating temporally shifting assemblages as a relatively static community is too simple that may be inadequate to examine temporally biotic–abiotic relationships (Heino et al., 2015). Indeed, field samplings that are conducted only annually might fail to capture the community composition at the regional level for different aquatic organisms with active dispersal capabilities, for example, macroinvertebrates (Cook et al., 2018) and fish (Fernandes et al., 2014). Thus, taking appropriate temporal scales into biomonitoring protocols is important to address ecological questions that may be affected by temporal variables (Wu et al., 2016). However, the majority of investigations so far have either addressed on a temporal extent too fine to reflect seasonality (e.g. ~1 month duration; Brown, 2003), or a temporal scale with the aim of assessing long-term community variation (e.g. repeated at the same time over multiple years; Lindholm et al., 2021, Sinclair et al., 2021).

Compared with few studies of taxonomy-based temporal beta diversity (e.g. Passy & Blanchet, 2007), studies on trait-based temporal

beta diversity of riverine diatoms are still missing. Therefore, examining whether patterns of taxonomy-based temporal beta diversity are consistent with trait-based temporal beta diversity could help assess restoration progress and prioritize protection effort, particularly in the era of the Anthropocene (Crutzen, 2002). For instance, freshwater eutrophication stemming from anthropogenic nutrient inputs was shown to lead to more temporally homogenous communities (Dunck et al., 2019) and drive sharp decline in temporal beta diversity of stream benthic macroinvertebrates (Cook et al., 2018). Flow regime changes resulting from human activities could filter species traits and modify the functional features of riverine algae communities (Wu et al., 2019). Our findings concerning a high temporal trait convergence among riverine diatoms could be a result of past human influences in the catchment (e.g. habitat homogenization, nutrient enrichment by intensive agriculture activities), supporting the previous studies. Furthermore, since riverine algae communities, as an important primary producer, occupy a key role in stream food webs, decline in temporal beta diversity could exert a bottom-up processing that contributes to decreased ecosystem functions. Hence, the current prevalence and projected increase in human disturbances may have profound impacts on the whole aquatic ecosystems that are dramatically underestimated by examining only (either spatial or temporal) taxonomy-based beta diversity alone. More studies concerning both trait- and taxonomy-based beta diversity are greatly needed for a sound understanding of community dynamics and its responses to human disturbances.

To a broad extent, the decomposing temporal beta diversity at a large temporal and spatial scale might be crucial for a more holistic biodiversity protection and conservation, because this approach provides complementary ecological information. We hereby advocate that environmental biomonitoring and assessments should take different facets into consideration. The experience gained by this study can be beneficial for exploring temporal beta diversity of other aquatic organisms, such as aquatic plants, macroinvertebrates and fish, so that other ecological processes (e.g. community assembly, species interactions) can be further extensively examined. Due to the complexity of lowland river ecosystems and environmental changes caused by either anthropogenic (e.g. morphological change, land use, pollution) or natural factors (e.g. flooding, climate change), examination of spatial and temporal beta diversities in term of different facets and components may offer a new understanding into the mechanisms that structure the community assembly of aquatic and even terrestrial communities. Besides, a sound understanding of between beta diversities and abiotic factors at local and regional scales may provide solid basis for sustainable management as well as biodiversity protection. In addition, given the importance of environment regimes on biotic indices, it has important implications on both basic and applied ecology. On one hand, inclusion of environment regimes (e.g. thermal, nutrient, flow regimes), particularly short-term environment regimes, can be robust variables in ecological studies of different organisms in various ecosystems. On the other hand, studying biological responses to changes of environment regimes can be used for policy making and environmental management. For example, by

exploring the relationships between water-level regimes and the occurrence of cyanobacterial blooms, water-level management has a potential to mitigate cyanobacterial blooms (Bakker & Hilt, 2016).

## 5 | CONCLUSIONS

In summary, our results emphasized the advantage of the decomposition of trait- and taxonomy-based temporal beta diversity for understanding diversity patterns of riverine diatoms in relation to abiotic variables. More specifically, the relatively low correlations between trait- and taxonomy-based temporal beta diversity indicated their complementary ecological information. The taxonomy-based total beta diversity had a high contribution by turnover component, whereas trait-based total beta diversity was largely driven by nestedness component. This demonstrated a relatively high temporal trait convergence among riverine diatom communities (Carvalho et al., 2020). Abiotic factors including hydrology, metal ions and nutrient affected the both facets of temporal beta diversity of riverine diatoms. However, other factors (e.g. biotic interaction, local environmental parameters, pollutants) seem also to be important to overall temporal beta diversity of diatoms. Additionally, exploring different facets and components of temporal beta diversity provided a trait-based insight into temporal dynamics of riverine diatoms, which have been largely neglected in previous studies (Magurran et al., 2019). Furthermore, this study highlighted the importance of environment regimes in explaining the variation of temporal beta diversity as well as its decomposition and should be incorporated in future ecological studies.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

N.W. and N.F. conceived the ideas; N.W. performed the data analyses and led the writing; N.W., X.S. and C.F. collected the samples and analysed the data; Ya.W. and Yi.W. helped with data organization, analysis and partial writing. All authors contributed to writing the manuscript and gave final approval for publication.

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## DATA AVAILABILITY STATEMENT

The data used in this study are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.6q573n612> (Wu et al., 2022).

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