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Diatom β -diversity in streams increases with spatial scale and decreases with nutrient enrichment across regional to sub-continental scales

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Abstract

Aim: To quantify the relative contributions of local community assembly processes versus γ -diversity to β -diversity, and to assess how spatial scale and anthropogenic disturbance (i.e. nutrient enrichment) interact to dictate which driver dominates.

Location: France and the United States.

Time period: 1993–2011.

Major taxa studied: Freshwater stream diatoms.

Methods: β -diversity along a nutrient enrichment gradient was examined across multiple spatial scales. β -diversity was estimated using multi-site Sørensen dissimilarity. We assessed the relative importance of specialists versus generalists using Friedley coefficient, and the contribution of local community assembly versus γ -diversity to β -diversity across spatial scales, with a null model. Finally, we estimated the response of β -diversity to environmental and spatial factors by testing the correlations between community, environmental and geographical distance matrices with partial Mantel tests.

Results: β -diversity generally increased with spatial scale but the rate of increase depended on nutrient enrichment level. β -diversity decreased significantly with increasing nutrient enrichment level due to the loss of specialist species. Local assembly was an important driver of β -diversity especially under low nutrient enrichment. Significant partial Mantel correlations were observed between diatom β -diversity and pure environmental distances under these conditions, highlighting the role of species sorting in local assembly processes. Conversely, in heavily enriched sites, only spatial distances were significantly correlated with β -diversity, which indicated a substantial role of dispersal processes.

Main conclusions: Nutrient concentration mediated the expected increase in β -diversity with spatial scales. Across spatial scales, β -diversity was more influenced by local assembly processes rather than by γ -diversity. Nutrient enrichment was associated with an overall decline in diatom β -diversity and a shift in assembly processes from species sorting to dispersal, notably due to the elimination of some specialists and their subsequent replacement by generalists.

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KEYWORDS

β -diversity, γ -diversity, community assembly, diatom communities, dispersal processes, landscape windows approach, multi-scale, null model, species sorting

1 | INTRODUCTION

One of the most interesting facets in the study of biodiversity is the consistent shift in species membership as one samples biological communities across space and time. The pattern of variation in local community composition (α -diversity), given a regional species pool (γ -diversity), was dubbed β -diversity by Whittaker (1960, 1972) more than 50 years ago, and was originally defined in his work as 'the extent of change in community composition in relation to a complex-gradient of environment, or a pattern of environments'. The concept of β -diversity has since morphed from a simple scalar (*i.e.* $\beta = \gamma / \alpha$), into numerous mathematical definitions, which now include similarity/distance and variance-based measures (Tuomisto, 2010a,b; Tuomisto & Ruokolainen, 2006). The development of new β -diversity indices has thus given researchers powerful tools to study different aspects of Whittaker's concept of community variation (Socolar, Gilroy, Kunin, & Edwards, 2016). Consequently, β -diversity has a recent surge of interest because differences in many widely studied macroecological patterns (*e.g.* species–area relationships and species abundance distributions) are associated with variation in β -diversity among different metacommunities and regions.

β -diversity is generally caused by an interplay of biogeographic, environmental and spatial gradients (Jamoneau, Passy, Soininen, Leboucher, & Tison-Rosebery, 2018; Tonkin, Sundermann, Jähnig, & Haase, 2015; Viana et al., 2016). Species sorting (*i.e.* environmental filtering coupled with biological interactions), and dispersal processes are particularly important drivers of β -diversity (Chase & Leibold, 2003; Soininen, 2007), however, their relative influence are scale-dependent (local vs. regional). Scale effects on measures of β -diversity, and their drivers, have been of particular interest because research has shown that the average distance between sampling units, their spatial configuration, and the spatial extent of the sampling region all confound comparisons of β -diversity between study areas (Conroy & Noon, 1996; Mac Nally, Fleishman, Bulluck, & Betrus, 2004; Noss, 1983; Wilson & Shmida, 1984). Quantitative multi-scales approaches are thus recommended to better understand how local and regional processes affect β -diversity (Huston, 1999; Mac Nally et al., 2004), and to also identify the appropriate spatial scales for studying mechanisms that structure communities (Mac Nally et al., 2004; Underwood & Chapman, 1996; Willis & Whittaker, 2002). However, few studies have actually implemented quantitative scale-explicit frameworks to explore such relationships.

β -diversity tends to vary with spatial scale through different deterministic and stochastic processes. Species sorting, in particular, shapes community composition along environmental gradients (Lack, 1976; Leibold et al., 2004) and thus along spatial gradients when

environmental heterogeneity increases with scale. Where environmental gradients persist at geological time scales (*i.e.* under natural conditions), local specialization leads to high regional-level community dissimilarity (Gutiérrez-Cánovas, Millán, Velasco, Vaughan, & Ormerod, 2013), and thus β -diversity tends to increase with spatial scale. Dispersal processes may also influence community dissimilarity by compositional homogenization (lower β -diversity) or differentiation (higher β -diversity) as a function of the rate of dispersal (Bottin, Soininen, Alard, & Rosebery, 2016; Dong et al., 2016; Jamoneau et al., 2018; Soininen, 2007). However, it remains poorly understood how species sorting and dispersal processes interact to influence community variation across scales, given that their relative contributions are clearly dependent on the spatial context in which they are measured.

A further complication in the study of β -diversity drivers is that β -diversity itself is constrained by variation in α -diversity and γ -diversity along the same environmental and spatial gradients (Kraft et al., 2011). Consequently, to assess the impact of local assembly processes (*i.e.* α -diversity pattern) on β -diversity, one must account for the influence of the regional species pool (*i.e.* γ -diversity). Null models have proven to be useful in this regard, and have seen widespread application in the analysis of β -diversity pattern and its drivers (*e.g.* Chase, Kraft, Smith, Vellend, & Inouye, 2011; Kraft et al., 2011; Myers et al., 2013), but have not been widely adopted into quantitative multi-scale frameworks.

Scale dependence of β -diversity drivers (*i.e.* species sorting, local assembly processes, dispersal and the regional species pool) are further influenced by anthropogenic disturbance, causing extensive impairment of terrestrial and freshwater ecosystems (Vörösmarty et al., 2010). Anthropogenic disturbances have been associated with taxonomic homogenization (loss of β -diversity), but it remains unclear which are the key mechanisms and processes contributing to such homogenization. One general pattern often reported is the elimination of sensitive species (McKinney & Lockwood, 1999; Olden & Poff, 2003, 2004; Socolar et al., 2016) and subsequent replacement by a few generalist species, usually sharing similar traits (Gutiérrez-Cánovas et al., 2013). Under natural conditions, β -diversity increases with spatial scale owing to increased environmental heterogeneity and habitat specialization (Chase, 2014). However, when anthropogenic disturbances eliminate sensitive species, the species pool may contract and become dominated by generalist species with traits for tolerance. Nevertheless, it remains unclear whether anthropogenic disturbance, by impoverishing the species pool of specialists and increasing the prevalence of generalists, would attenuate the increase in β -diversity with spatial scale.

The replacement of specialists by generalists is likely the result of differential interactions of anthropogenic disturbance with the

underlying deterministic and stochastic processes operating on β -diversity. If anthropogenic disturbances eliminate specialists and promote generalists with broader niches, one consequence is that the effect of species sorting might weaken and species composition would be mostly affected by stochastic processes, including dispersal. However, deterministic (e.g. species sorting) and stochastic processes (e.g. dispersal) are scale dependent, and it remains unknown whether anthropogenic disturbance may shift the dominant processes with changing spatial scale.

Our goal was to assess the relative contributions of local community assembly processes versus γ -diversity, and species sorting versus stochastic processes, in driving β -diversity, and whether spatial scale and anthropogenic disturbance interact to determine which processes dominate. Diatoms represent an appropriate biological model for such research since their communities exhibit biogeographical patterns (Soininen, Jamoneau, Rosebery, & Passy, 2016; Vanormelingen, Verleyen, & Vyverman, 2008; Vyverman et al., 2007), subject to both local and regional processes. We first explored how stream diatom β -diversity responded to different levels of agricultural nutrient enrichment from local to sub-continental scales. We then quantified how β -diversity was driven by local processes versus γ -diversity and by spatial versus environmental effects. We tested the following three hypotheses.

1. β -diversity in diatom communities should generally increase with scale due to greater environmental heterogeneity but such increase would be weak in nutrient-impacted sites if sensitive species are lost and the species pool becomes impoverished.
2. In conditions of impoverished species pool, the influence of γ -diversity on β -diversity would increase at the expense of local assembly processes.
3. If anthropogenic disturbances eliminate specialists and promote generalists, species sorting would have a weaker effect on communities under nutrient-impacted conditions and species composition would be mainly constrained by spatial processes, including dispersal.

2 | MATERIALS AND METHODS

2.1 | Diatoms and environmental datasets

Diatom datasets from France and the United States included a total of 3,391 spatially distinct localities (Table 1). Samples were collected

TABLE 1 Stream diatom datasets from France and the United States

	No. of unimpacted sites	No. of slightly impacted sites	No. of heavily impacted sites	No. of species	Years of sampling
France	636	1,163	413	901	2011
United States	555	358	165	946	1993–2011

primarily between May and October in order to reduce seasonal variability in species assemblages. All community and physico-chemical data were gathered in 2011 by the Water Agencies for the French sites and between 1993 and 2011 by the US Geological Survey's National Water-Quality Assessment (NAWQA) Program for the US sites. In both countries, coordinates for all samples were calculated with WGS84 datum and projected using a Robinson projection (EPSG: 54030). Environmental variables included water pH, conductivity (at 20°C, mS/cm), dissolved oxygen saturation (%), concentrations of total phosphorous (mg/L of $_{15}P$), orthophosphate (mg/L of $_{15}P$), ammonia (mg/L of $_{7}N$), nitrate (mg/L of $_{7}N$) and nitrite (mg/L of $_{7}N$). Environmental data were not recorded at the time of community sampling; therefore, we used the median values of all environmental variable measurements obtained during the 60 days before and the 15 days after the diatom sampling date. We also included altitude (m, 1 arc-second) and river slope (%), drawn from the Shuttle Radar Topography Mission (Farr et al., 2007) and climatic variables, that is annual precipitations (mm) and annual air temperature (°C), drawn from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Climate data covered the years 1950–2000 and the average values were included in the analyses.

In France, diatoms were sampled with a standardized protocol, in line with the European standards (EN 13946, European Commission). In the United States, diatoms were sampled following standardized NAWQA protocols. In both countries, cells were identified at 1,000 \times magnification by examining permanent slides of cleaned diatom frustules (400 valves per slide in France and 600 valves per slide in the United States). The French and the US diatom datasets were taxonomically homogenized at the species level using Omnidia 5.3 and different databases (<http://www.algaebase.org/>, <https://westerndiatoms.colorado.edu/>).

2.2 | Level of nutrient enrichment

To classify the sampling stations along a eutrophication gradient, we first performed principal components analysis (PCA) on power-transformed nutrient concentrations (nitrate, nitrite, ammonia, orthophosphate and total phosphorous). We used Box-Cox maximum likelihood estimation (Box & Cox, 1964) to decide the best power-transformation for approximating normality. We retained only the components with eigenvalues greater than those randomly generated by a broken-stick model (Jackson, 1993; Legendre & Legendre, 2012). Following this procedure, we found that only the first principal component axis (PC1) was significant. PC1 explained 55% of the total variance and represented a gradient of nutrient enrichment (Figure 1). We used an ascending hierarchical classification (AHC, Lebart, Morineau, & Piron, 2000) of the PC1 scores to classify sites into classes of nutrient enrichment based on their Euclidean distances. AHC identified three homogeneous classes optimizing the average silhouette width (Rousseeuw, 1987), that is unimpacted, slightly impacted and heavily impacted sites (Table 1).

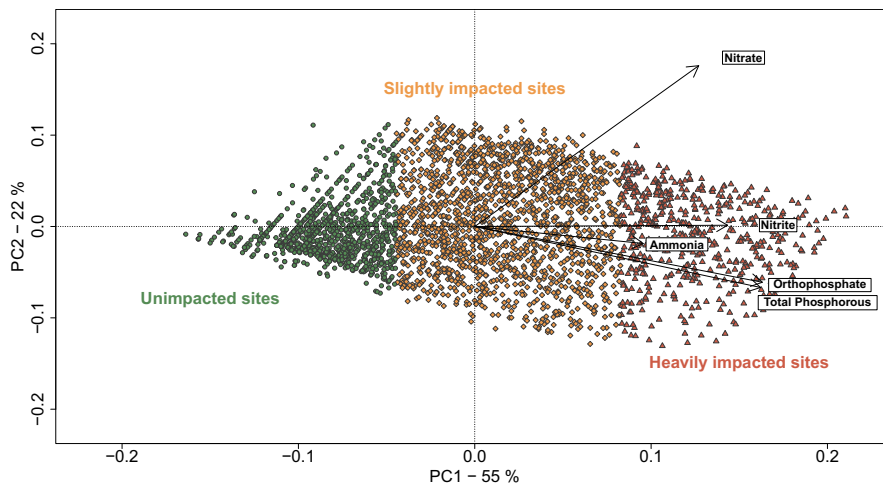


FIGURE 1 Principal component analysis plot for axes 1 and 2 using nitrate, nitrite, ammonia, total phosphorous and orthophosphate concentrations. Environmental variables are shown with arrows and colours represented the nutrient enrichment level

2.3 | Generalist and specialist species

To achieve a classification of species along a generalist-specialist gradient, we implemented the approach by Fridley, Vandermaet, Kuppinger, Manthey, and Peet (2007), which is based on species co-occurrences and allows species characterization without measuring an N-dimensional niche for each species. This approach derives from a β -diversity statistic and relies on the assumption that generalists should co-occur with many species, whereas specialists should co-occur with relatively few species (Fridley et al., 2007), independently of the species pool size (Zelený, 2009). The continuous metric (θ -value or Fridley coefficient) obtained for each species reflects the relative species niche width: low θ -values denote a confined niche (specialist species), whereas high θ -values denote a broader niche (generalist species). We measured the mean θ -value at each site, weighted by the abundance of each species present at that site, to estimate the relative importance of specialists versus generalists both in France and in the United States, following the equation:

$$\theta_{\text{site}} = \sum_1^n \theta_i \cdot \frac{Ab_i}{Ab_{\text{tot}}}$$

where n is the number of species in the site, θ_i is the θ -value of species i , Ab_i is the abundance of species i in the site and Ab_{tot} is the total abundance of all species in the site.

2.4 | Landscape windows approach

β -diversity among sites was examined across multiple spatial scales with square polygons (*i.e.* landscape windows), using R 3.4.2 (R Core Team, 2017). Spatial scales are defined by the size of the landscape windows and varied between 200×200 km and $2,000 \times 2,000$ km (0.4×10^5 and 40×10^5 square km respectively). Latitudinal transects at 50 km intervals were used to place the centre of each window. Windows were aligned along these transects at 50 km distances between their centres, resulting in 9,006 possible and potentially overlapping windows at each scale (Figure 2). We selected windows that contained at least 25 unimpacted, 25 slightly impacted and 25 heavily impacted sites distributed over at least 80% of the window's area to

ensure equal sampling effort across categories (see Appendix S1). Among 9,006 possible landscape windows, 2,514 in both France and the United States met our selection criteria. There were no landscape windows below 6.4×10^5 square km in the United States because of the low density of sampling localities. For simplicity, each spatial scale was denoted by the width of its corresponding window, for example the 200×200 km window (0.4×10^5 square km) was denoted as '200 km window'. The creation of landscape windows in R 3.4.2 (R Core Team, 2017) is provided in Appendix S3. In contrast to a simple distance-decay approach, our landscape windows approach explicitly accounts for community dissimilarities and spatial distribution of sites and thus renders the spatial-scaling pattern of β -diversity more informative, robust and comparable among studies.

2.5 | β -diversity calculations

We estimated the β -diversity of each window using the multi-site total β -diversity of Baselga-family decomposition of the Sørensen dissimilarity coefficient for species presence-absence data (Baselga, 2010) obtained with the `beta.div.comp` function (R-package: 'adespatial', Dray et al., 2018) using the equation:

$$\beta = \frac{[\sum_{i < j} \min(b_{ij}, b_{ji})] + [\sum_{i < j} \max(b_{ij}, b_{ji})]}{2 \cdot [\sum_i S_i - S_T] + [\sum_{i < j} \min(b_{ij}, b_{ji})] + [\sum_{i < j} \max(b_{ij}, b_{ji})]}$$

where S_i is the total number of species present in site i , S_T is the total number of species in all sites, and b_{ij} and b_{ji} are the number of species exclusive to sites i and j .

Because total β -diversity can be influenced by sampling effort, we followed the recommendation by Bennett and Gilbert (2016) and randomly sampled 25 sites per window for each impact category to measure β -diversity. We conducted a sensitivity analysis varying sample size from two sites to 250 sites to validate the choice of 25 sites (Appendix S4). We resampled the data 999 times for each window and calculated the corresponding mean β -diversity. Using the `beta.div.comp` function, the maximum value of the total β -diversity is 0.5 when sites contain no shared species, and the minimum value is 0 when all sites share the same species (Legendre & De Cáceres, 2013).

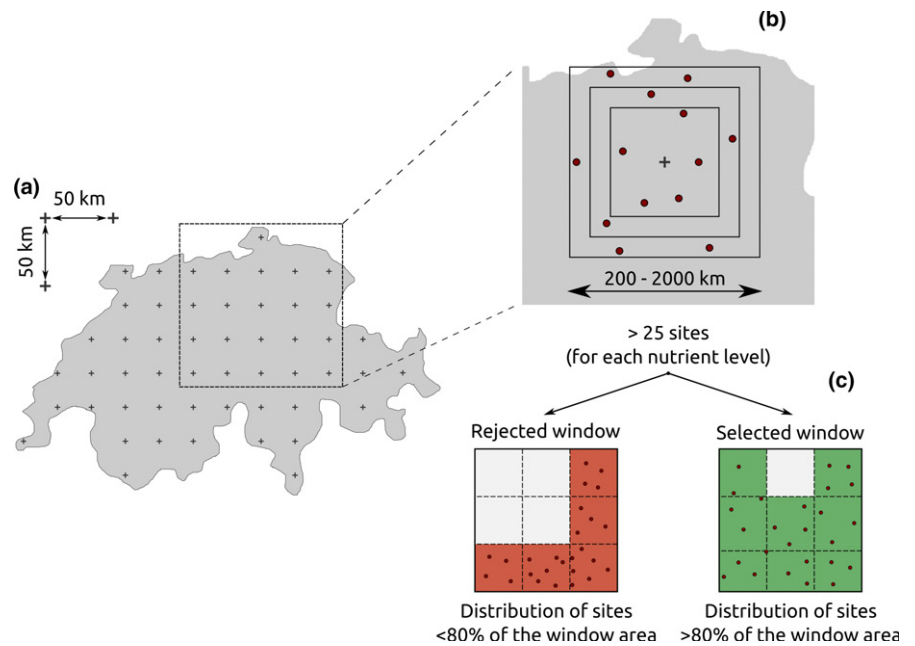


FIGURE 2 Schematic representation of the landscape windows approach. (a) The centres of the windows were aligned every 50 km along latitudinal transects in the study area. (b) We selected windows that contained at least 25 sites for each nutrient level. (c) For each nutrient level, sites must be distributed over at least 80% of the window's area

2.6 | Relative influence of local community assembly processes versus γ -diversity

We estimated the contributions of the local community assembly processes versus γ -diversity on β -diversity, across spatial scales, with a null model (Chase & Myers, 2011; Kraft et al., 2011). This procedure randomizes individuals among sites, while preserving γ -diversity, the total number of individuals per site and the species abundance distributions within each window. After randomizing individuals, we built new presence/absence tables to calculate β -diversity as explained above. We modified this method to be compatible with the Baselga-family decomposition of the Sørensen dissimilarity coefficient for species presence-absence data by transforming each randomized null matrix into a total β -diversity matrix (999 matrices total). Then, we calculated β -deviation (β_{dev}) with the following equation:

$$\beta_{\text{dev}} = \frac{\beta_{\text{obs}} - \beta_{\text{null}}}{SD_{\text{null}}}$$

where β_{obs} is the β -diversity of the original sample, β_{null} , the mean β -diversity of the 999 random samples (null model) and SD_{null} , the standard deviation of β -diversity of the 999 random samples.

Positive values indicate that observed β -diversity is greater than expected if β -diversity were driven solely by γ -diversity, thus highlighting the importance of local community assembly processes.

2.7 | Characterization of local community assembly processes

To estimate the relative response of β -diversity to environmental and spatial factors, we tested the correlations between community, environmental and geographical distance matrices with partial Mantel tests in each window for each resampling (999 times) and calculated the mean value for each window (p -values calculated with 999

permutations). Although partial Mantel tests have some limitations in capturing spatial effects, they were shown to perform comparably to other commonly used methods, such as variance partitioning (Gilbert & Bennett, 2010).

To determine if communities were significantly structured by pure environmental or spatial factors at each scale, we compared the proportion of significant and non-significant partial Mantel tests by chi-squared tests (Greenwood & Nikulin, 1996). The partial Mantel tests revealed significant correlations between spatial distances (pure spatial processes) or environmental distances (pure niche/habitat processes) and community distances (*i.e.* Sørensen dissimilarities) after partialling out the effects of the other explanatory matrix. To characterize the environment, we used all the variables listed earlier, nutrients included. Latitude and longitude were used as spatial predictors.

2.8 | Statistical analyses

Given that simulation and permutation procedures generated an artificially large sample size, we analysed the distributions of β -diversity, β -deviation and partial Mantel statistics with the Cliff's delta statistic (Cliff, 1993) which accounts for large sample size (Tecchio et al., 2016). This statistic estimates the probability that a randomly selected value in one group is higher, or lower, than a randomly selected value in a second group, that is $\delta = p(x_1 > x_2) - p(x_1 < x_2)$. Comparing the degree of overlap between the two groups indicates whether a significant difference is due to an effective ecological process or to sample size alone. Romano, Kromrey, Coraggio, and Skowronek (2006) interpreted the magnitude of differences between groups as follows: negligible for $|d| < 0.147$, small for $0.147 < |d| < 0.33$, medium for $0.33 < |d| < 0.474$ and large for higher $|d|$ values. In this study, we considered $|d| > 0.33$ as a threshold for significance (see Appendix S2). All data analyses were performed with R 3.4.2 (R Core

Team, 2017), using the 'vegan' and 'adespatial' packages (Dray et al., 2018; Oksanen et al., 2018).

3 | RESULTS

3.1 | The effect of scale on β -diversity values

Sørensen dissimilarities ranged between 0.27 (heavily impacted sites) and 0.37 (unimpacted sites) in France and between 0.30 (heavily impacted sites) and 0.38 (unimpacted sites) in the United States. Although the minimum and maximum values were similar between the two countries, β -diversity patterns across spatial scales were different. β -diversity increased with spatial scale regardless of enrichment level (Figure 3), however, the rate of increase differed across nutrient enrichment levels in both France and the United States. In France, β -diversity values in unimpacted sites increased significantly with spatial scale, whereas in slightly and heavily impacted sites, β -diversity increased to about 400 km. In the United States, β -diversity increased significantly with scale to about 1,500 km across enrichment levels, but tapered off between 1,500 and 2,000 km. Only the 800 km scale was common to France and the United States, and it is notable that the corresponding β -diversity values were clearly distinct, especially for unimpacted sites.

3.2 | Impact of nutrient enrichment on β -diversity and specialist species

β -diversity decreased significantly with nutrient enrichment and even a slight impact had a strong effect on communities (Figure 3). Moreover, in France β -diversity tended to plateau at 400 km in impacted sites (slightly and heavily), but continued to increase in unimpacted ones. In the United States, β -diversity differences were even more pronounced. For unimpacted sites, β -diversity increased steeply between 800 and 1,200 km, whereas at the same scales, β -diversity in impacted sites increased only slightly. As in France, β -diversity in the United States significantly declined with the level of impact,

except at 1,100 and 1,200 km where there was no difference between slightly and heavily impacted sites.

The proportion of specialist species declined among heavily impacted sites, given the significant increase in θ -values with nutrient enrichment level in both France and the United States (Figure 4). Although we observed that for the French data, there was a significant difference between unimpacted sites and slightly impacted sites, such a difference was absent for the US data.

3.3 | Relative contributions of local community assembly processes versus γ -diversity on β -deviations

The sign and magnitude of β -deviation indicated that β -diversity among diatom communities was driven primarily by local community assembly processes rather than by γ -diversity, regardless of enrichment level and spatial scale (Figure 5). Similar to β -diversity, β -deviation varied with scale. In France, β -deviation in unimpacted sites increased significantly to 500 km. In slightly impacted sites, no difference in β -deviation was observed across scales, and in heavily impacted sites, only the first two scales exhibited lower β -deviation values than the larger scales. In the United States, across enrichment levels, β -deviation values increased significantly to 1,500 km (impacted sites) or 1,600 km (unimpacted sites).

Nutrient enrichment had a strong negative effect on β -deviation, especially at large spatial scales (Figure 5). In France, β -deviation significantly decreased from unimpacted to heavily impacted sites. In the United States, β -deviation in unimpacted sites was always significantly higher than in impacted sites (both slightly and heavily). However, except for the 800 km scale, there were no differences between β -deviation values in slightly impacted and heavily impacted sites.

3.4 | Characterization of the local community assembly processes

Partial Mantel test results diverged according to impact level (Figure 6). However, there were only very few significant differences between spatial scales and we have not considered them further (see

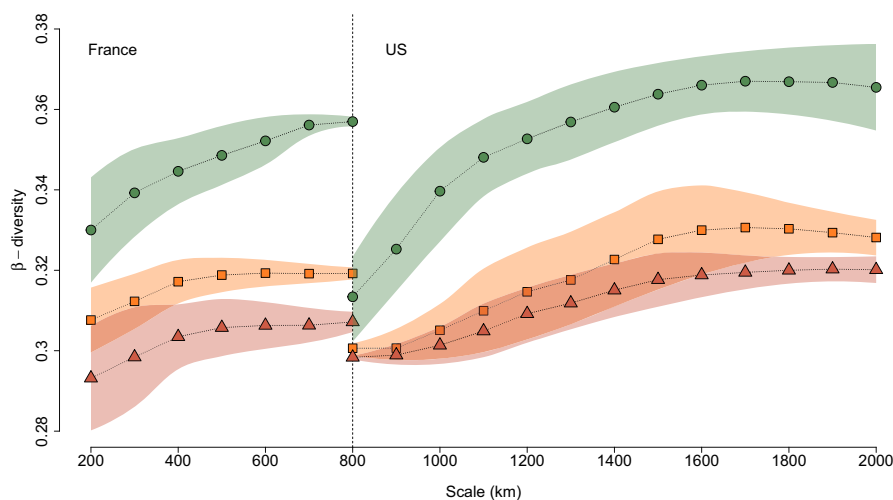


FIGURE 3 Mean β -diversity values (symbols) and SD (bands) measured in unimpacted conditions (round symbols), slightly impacted conditions (square symbols) and heavily impacted conditions (triangle symbols) across spatial scales



FIGURE 4 Boxplot of the mean θ -values (Fridley coefficient) measured in unimpacted, slightly impacted and heavily impacted conditions. Differences between nutrient levels were tested with Kruskal–Wallis tests followed up by Nemenyi post hoc tests. Stars represent significant differences between nutrient levels ($p < 0.001$: ‘***’; and $p < 0.05$: ‘*’)

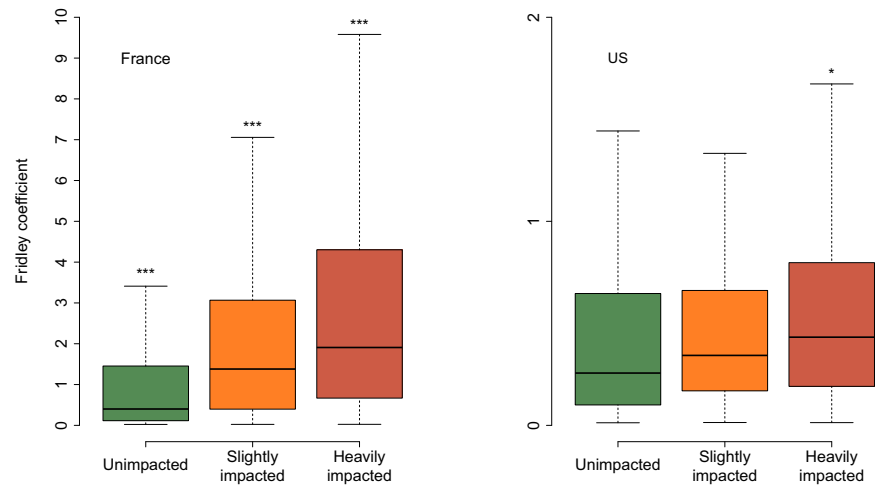


FIGURE 5 Mean β -diversity values (symbols) and SD (bands) measured in unimpacted conditions (round symbols), slightly impacted conditions (square symbols) and heavily impacted conditions (triangle symbols) across spatial scales

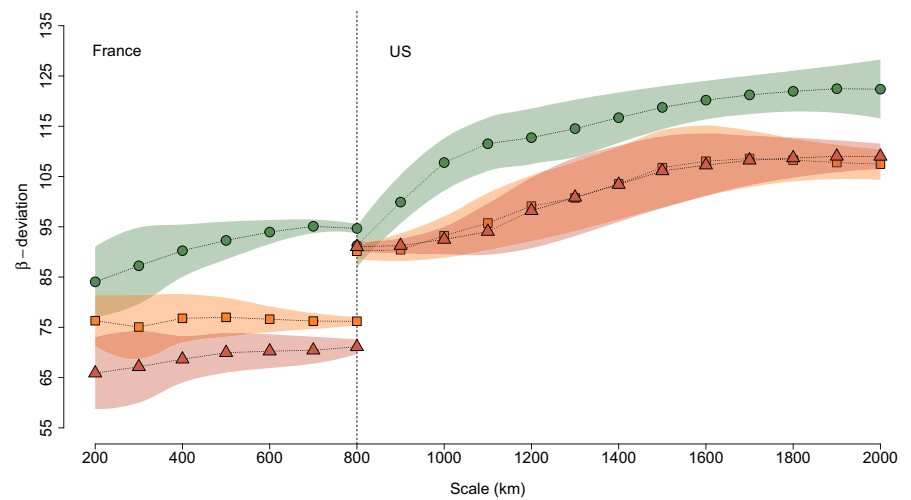
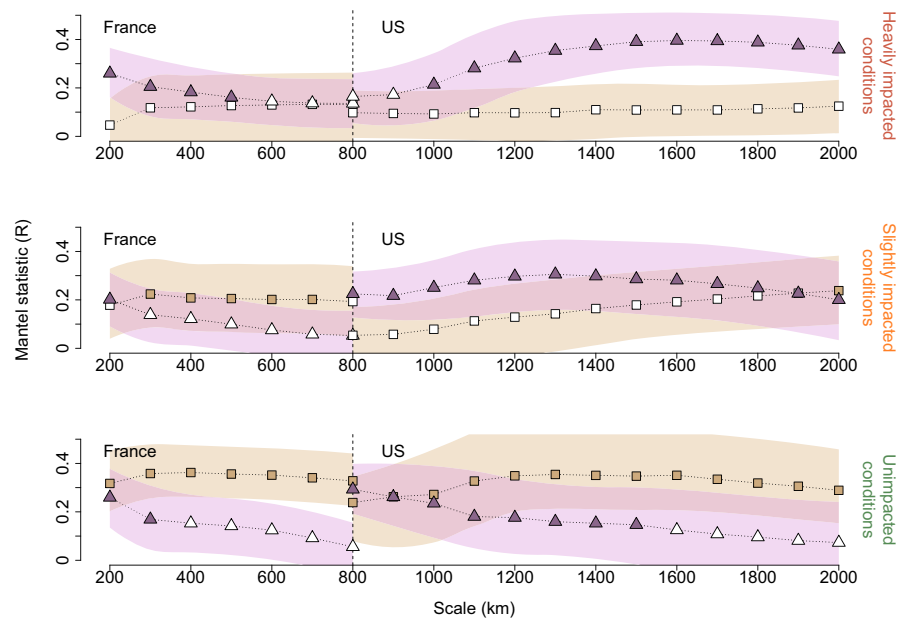


FIGURE 6 Mean partial Mantel coefficients (symbols) and SD (bands) of pure environmental (square symbols) and pure spatial effect (triangle symbols) on β -diversity along a spatial gradient. Filled symbols represent significant relationships (Cliff's $|d| > 0.33$) and open symbols, non-significant ones (Cliff's $|d| \leq 0.33$)



Appendix S2). In unimpacted sites, there was a significant correlation between diatom β -diversity and pure environmental distance. The pure spatial influence was significant in France at 200 and 300 km scales,

and in the United States between 800 and 1,500 km. In contrast, in heavily impacted sites, only pure spatial effect was significant at small and intermediate scales (200–500 km) in France, and between 1,000

and 2,000 km in the United States. Pure environmental effect, on the other hand, was non-significant in both France and the United States.

Results for slightly impacted sites differed between France and the United States. In France, we observed significant correlations between diatom β -diversity and pure environmental distances between 300 and 700 km. Notably, the pure environmental effect in France was significantly greater in unimpacted sites than in slightly impacted sites regardless of the scale. A pure spatial influence was significant at the 200 km scale only. In the United States, pure environmental effect was not significant in slightly impacted sites except at the 2,000 km scale, whereas pure spatial influence was significant across all scales.

4 | DISCUSSION

This work provided information on diatom β -diversity patterns and drivers along a nutrient enrichment gradient and across multiple spatial scales. First, we confirmed that β -diversity increases with spatial scale, but nutrient enrichment clearly modulated this increase. Second, in both continents, local assembly processes had a stronger contribution to β -diversity than γ -diversity regardless of scale and nutrient enrichment level. However, nutrient enrichment played a clear role in determining whether species sorting and/or dispersal dominated assembly processes along the spatial gradient. We discuss the implications of these findings below.

4.1 | β -diversity across scales and nutrient levels

We confirmed our first prediction that β -diversity of diatom communities increases with spatial scale, which is generally consistent with prior literature (Gabriel, Roschewitz, Tschantke, & Thies, 2006; Martiny, Eisen, Penn, Allison, & Horner-Devine, 2011). We also revealed that regardless of spatial scale, β -diversity was dependent on nutrient level and that greater enrichment more strongly depressed β -diversity. Anthropogenic and natural stress gradients differ in type and variability, which ultimately drive richness and spatial distribution patterns of sensitive and tolerant species across scales (Clavel, Julliard, & Devictor, 2011). Acute and persistent anthropogenic stress, such as eutrophication, may offer insufficient time for adaptation by specialists and potentially eliminate them from the species pool (Gutiérrez-Cánovas et al., 2013; Kaspari, Stevenson, Shik, & Kerekes, 2010). The loss of specialists benefits subsequent colonization by more physiologically plastic generalists, which are normally poor competitors for resources and niche space compared to specialists (Bolnick, Svanbäck, Araújo, & Persson, 2007; Olden & Rooney, 2006). Our data thus showed that the strength of spatial dependence of β -diversity was likely regulated by how strongly anthropogenic gradients shifted the species pool towards greater prevalence of species with generalist versus specialist traits. Analyses of the Fridley coefficient, θ , indeed indicated that these patterns were attributable to the fact that among impacted streams, relatively fewer new species (particularly those with specialist traits) were added to the pool compared to unimpacted streams. Our results thus

support widely reported observations that agriculture-driven nutrient enrichment is a major driver biotic homogenization (Blüthgen et al., 2016; Ekroos, Heliölä, & Kuussaari, 2010; Karp et al., 2012; Vallejos, Padiál, & Vitule, 2016) but further demonstrate that the mechanism of this homogenization is through changes in trait composition.

However, these findings run counter to studies that reported a positive correlation of β -diversity with productivity (e.g. Chase, 2010). Nutrient levels in our study systems were substantially high (i.e. max TN ~50 mg/L and max TP ~2 mg/L versus max TN ~2 mg/L and max TP ~0.2 mg/L in Chase's study), and might have exceeded the physiological thresholds of oligotrophic and mesotrophic species, thus resulting in diminished species pool and low β -diversity.

4.2 | Roles of local assembly versus γ -diversity in driving β -diversity

The role of γ -diversity compared to local assembly in driving β -diversity generally increased with impact, given the lower β -deviation values at higher nutrients levels in both datasets. Species pools tended to be more impoverished with increased impact, and dominated by generalists, thus smaller β -deviation at higher impact was likely indicative of increased stochastic sampling of generalists from the regional species pool (Karp et al., 2012; Kraft et al., 2011). Therefore, under stressful conditions, β -diversity was more strongly constrained by regional processes, affecting the distribution of specialists and the size of the regional species pool. A similar finding was reported for diatoms in an acid-impacted region, where acid stress increased the importance of the regional species pool for β -diversity due to the elimination of acid-sensitive species (Pound, Lawrence, & Passy, 2018). Furthermore, we generally observed weak scale dependence of β -deviation in heavily impacted sites. This suggested that the relative roles of γ -diversity and local assembly processes may be decoupled from spatial scale if anthropogenic disturbance is high. Our results disagree to a certain extent with prior research, reporting that the relative importance of community assembly processes in wood plant communities is strongly scale dependent along elevational gradients (Tello et al., 2015). It is thus possible that the scale dependence of the mechanisms underlying β -diversity may vary along natural (e.g. elevation) versus anthropogenic gradients (here, eutrophication).

4.3 | Relative influence of species sorting versus dispersal processes

With heavy nutrient enrichment, the correlation between community dissimilarity and pure environmental distance virtually disappeared whereas the correlation between community dissimilarity and spatial distance increased. This suggested that nutrient enrichment weakened the influence of species sorting and dispersal processes became a more important driver of community composition. Mass effects and dispersal limitation are the two principal dispersal processes that can generate spatial structure of community dissimilarity, with mass effects treated as a community homogenizer (Mouquet & Loreau, 2003; Shmida & Wilson, 1985) and dispersal limitation, as a

community differentiator (Heino et al., 2015; Hubbell, 2001; Jaconeau et al., 2018). However, it is difficult to disentangle these two processes with Partial Mantel tests because they both can be inferred from correlations between spatial variables and community composition. It is also possible that the spatial effects are due to unmeasured environmental factors, but this may be less of a problem in our study, given that we measured dominant environmental gradients.

The results of the partial Mantel tests indicated that species sorting was the dominant mechanism of local assembly in unimpacted sites. In the United States, the strength of species sorting increased with spatial scale. Özkan, Svenning, Jeppesen, and Webb (2013), working with bird communities, also documented stronger species sorting compared to dispersal processes across spatial scales. Interestingly, local assembly and species sorting increased only weakly with spatial scale in the French data. A likely reason for this difference can be the biogeographical context of the two datasets, with longer latitudinal and longitudinal gradients (i.e. study extent) and greater total richness in the US dataset.

In sum, the increase in β -diversity with spatial scale was apparently stronger when species sorting processes dominated but weaker when dispersal processes prevailed. Severity of anthropogenic impact was also important in determining whether species sorting (unimpacted conditions) or dispersal processes (heavily impacted) dominated across spatial scales. However, under slightly enriched conditions, spatial correlations were significant only among US sites regardless of spatial scale whereas environmental correlations were significant for French sites. Thus, the severity of nutrient enrichment, along with biogeographical context, may influence the roles of environmental and dispersal processes in structuring community dissimilarity and ultimately how fast β -diversity increases with scale.

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DATA ACCESSIBILITY

All environmental and diatom data for the United States are available: <https://water.usgs.gov/nawqa/>. All environmental and diatom data for France are the property of the French Water Agencies.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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