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Beta diversity of diatom species and ecological guilds: Response to environmental and spatial mechanisms along the stream watercourse

Aurélien Jamoneau¹  | Sophia I. Passy² | Janne Soininen³ | Thibault Leboucher¹ | Juliette Tison-Rosebery¹

¹Aquatic Ecosystems and Global Changes Research Unit, IRSTEA, Cestas, France

²Department of Biology, University of Texas at Arlington, Arlington, TX, U.S.A.

³Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

Correspondence

Aurélien Jamoneau, Aquatic Ecosystems and Global Changes Research Unit, IRSTEA, Cestas, France.

Email: aurelien.jamoneau@irstea.fr

Abstract

1. Understanding the mechanisms that drive beta diversity (i.e. β -diversity), an important aspect of regional biodiversity, remains a priority for ecological research. β -diversity and its components can provide insights into the processes generating regional biodiversity patterns. We tested whether environmental filtering or dispersal related processes predominated along the stream watercourse by analysing the responses of taxonomic and functional diatom β -diversity to environmental and spatial factors.
2. We examined the variation in total β -diversity and its components (turnover and nestedness) in benthic diatom species and ecological guilds (motile, planktonic, low- and high profile) with respect to watercourse position (up-, mid- and downstream) in 2,182 sites throughout France. We tested the effects of pure environmental and pure spatial factors on β -diversity with partial Mantel tests. Environmental factors included eight physicochemical variables, while geographical distances between sites were used as spatial factors. We also correlated α and γ -diversity, and the degree of nestedness (NODF metric) with environmental variables.
3. Total β -diversity and its turnover component displayed higher values upstream than mid- and downstream. The nestedness component exhibited low values, even when NODF values increased from up- to downstream. Pure environmental factors were highly significant for explaining total β -diversity and turnover regardless of watercourse position, but pure spatial factors were mostly significant mid- and downstream, with geographical distance being positively correlated with β -diversity. Across sites, nutrient enrichment decreased turnover but increased the degree of nestedness. Motile and low profile diatoms comprised the most abundant guilds, but their β -diversity patterns varied in an opposite way. The lowest guild β -diversity was observed upstream for low profile species, and downstream for motile species.
4. In conclusion, environmental filtering seemed to play a major role in structuring metacommunities irrespective of site watercourse position. Filtering promoted strong turnover patterns, especially in disconnected upstream sites. The greater role of spatial factors mid- and downstream was consistent with mass effects

rather than neutral processes because these sites had lower total β -diversity than upstream sites. Motile species were most strongly affected by mass effects processes, whereas low profile species were primarily influenced by environmental conditions. Collectively, these findings suggest that partitioning of total β -diversity into its components and the use of diatom ecological guilds provide a useful framework for assessing the mechanisms underlying metacommunity patterns along the stream watercourse.

KEYWORDS

dispersal, environmental filtering, mass effects, metacommunities, species assemblages

1 | INTRODUCTION

β -diversity, defined as spatial or temporal variability in species composition among samples, provides a useful measure of regional biodiversity with implications for conservation (Socolar, Gilroy, Kunin, & Edwards, 2016) and ecosystem functioning (van der Plas et al., 2016). As biodiversity has been sharply declining during the Anthropocene, understanding the drivers of β -diversity has moved to the forefront of ecological research. Both deterministic processes (e.g. species sorting) and stochastic factors, such as dispersal or ecological drift, have been identified as mechanisms behind observed β -diversity patterns (Condit et al., 2002; Legendre, Borcard, & Peres-Neto, 2005; Lindström & Langenheder, 2012). Species sorting includes both environmental filtering (selection of well-adapted species) and species interactions, such as competition, facilitation, grazing or predation (Chase & Leibold, 2003). Dispersal mechanisms include mass effects and dispersal limitation. Mass effect processes allow species to persist in unfavourable habitats, due to high levels of dispersal from source locations where environmental conditions enable high population densities (Mouquet & Loreau, 2003; Shmida & Wilson, 1985). In contrast, limited dispersal prevents species from reaching all suitable habitats and weakens the strength of species sorting (Heino, Melo, & Bini, 2015; Hubbell, 2001). Both mechanisms affect β -diversity but generally in opposite ways: dispersal limitation increases β -diversity (Nekola & White, 1999; Qian, 2009; Soininen, 2007), whereas mass effects homogenise communities and decrease β -diversity (Mouquet & Loreau, 2003; Shmida & Wilson, 1985). However, it is still unclear how habitat filtering, dispersal limitation and mass effects control β -diversity of freshwater communities along the watercourse of rivers.

To gain further insight into the mechanisms behind spatial and temporal variation in communities, β -diversity can be partitioned into turnover (species replacement) and nestedness (species loss) components (Baselga, 2010). Despite some criticism (Carvalho, Cardoso, & Gomes, 2012; Podani & Schmera, 2011), Baselga's (2010) approach has been successfully implemented to account for spatial (Viana et al., 2016), climatic (Dobrovolski, Melo, Cassemiro, & Diniz-Filho, 2012; Hortal et al., 2011; Svenning, Fløjgaard, & Baselga, 2011; Tisseuil, Leprieur, Grenouillet, Vrac, & Lek, 2012) and temporal effects

on species communities (Angeler, 2013; Baeten et al., 2012; Hautekète et al., 2015). Therefore, it remains an important methodological framework for β -diversity analyses.

Research on freshwater β -diversity has concluded that turnover is typically the dominant component of β -diversity and that β -diversity due to nestedness is generally low (Angeler, 2013; Tisseuil et al., 2012; Viana et al., 2016; Wetzel et al., 2012), although significant nestedness has been reported as well (Heino, 2011; Karthick, Mahesh, & Ramachandra, 2011; Leprieur, Olden, Lek, & Brosse, 2009; Soininen, 2008; Tornés & Ruhí, 2013). Nevertheless, the factors governing the patterns of nestedness remain poorly understood. Gutiérrez-Cánovas, Millán, Velasco, Vaughan, and Ormerod (2013) argued that long-established natural stress gradients have led to selection of taxa with distinct preferences along these gradients, and consequently, to predominance of turnover patterns. In contrast, anthropogenic stress, which is comparatively recent at a geological time scale, should allow generalist taxa to occupy disturbed sites as speciation and specialisation of these taxa have not yet occurred. As a consequence, such conditions tend to generate nestedness patterns. However, there is still a need for large-scale systematic studies examining how deterministic (i.e. resources and natural or anthropogenic stress) versus stochastic processes (i.e. dispersal and ecological drift) control the nestedness and turnover patterns, as currently no consensus exists on their importance in different ecosystems and environmental conditions.

Diatoms are important primary producers in stream ecosystems and their metacommunity patterns could influence higher trophic levels in the stream food web (Verreydt et al., 2012), emphasising the need for better understanding of diatom assemblage distribution. Diatom species composition has long been recognised to be structured by environmental filtering (Finlay, 2002; van Dam, Mertens, & Sinkeldam, 1994), although more recently, dispersal limitation and mass effects were also evoked as controlling mechanisms (Bottin, Soininen, Alard, & Rosebery, 2016; Dong et al., 2016; Soininen, Jamoneau, Rosebery, & Passy, 2016). While earlier studies have examined how spatial processes structure freshwater species assemblages (Astorga et al., 2012; Göthe, Angeler, Gottschalk, Löfgren, & Sandin, 2013; Heino, Melo, Siqueira, et al., 2015; Rouquette et al., 2013), the variability in nestedness and turnover components of

β -diversity along the stream watercourse remains under investigated. The few investigations to examine the variation in spatial processes along the stream watercourse have found an increased influence of these processes in downstream locations for benthic invertebrate communities (Brown & Swan, 2010; Göthe, Angeler, & Sandin, 2013; Tonkin, Sundermann, Jähnig, & Haase, 2015). However, the pattern appears to be less clear for other taxa, including diatoms, fish and macrophytes, and requires further investigation (Schmera et al., in this issue). For instance, Rusanov and Khromov (2016) examined the importance of spatial processes for structuring diatom communities along the watercourse, but only at a very small scale and associated the low spatial effect to patch dynamics processes.

The dendritic structure of river networks can exert strong controls on the structuring of metapopulations and metacommunities (Altermatt & Fronhofer, 2017). Recent literature suggests that upstream diatom communities are subjected to limited dispersal (Bottin, Soininen, Ferrol, & Tison-Rosebery, 2014; Dong et al., 2016) because sites are disconnected and aerial pathways or animal vectors, which are less efficient than direct hydrological connection, become the main dispersal avenues (Liu, Soininen, Han, & Declerck, 2013). The restricted flow of immigrants may then enhance the role of species sorting (only well-adapted species can maintain populations) and stochastic extinctions. These processes are likely to result in distinct turnover patterns, strongly related to environmental heterogeneity and limited dispersal. Conversely, midstream and downstream reaches have an extensive network of tributaries and receive continuous influx of immigrants via aquatic and non-aquatic pathways. Additionally, due to their larger size, they may experience an increased target effect. In these reaches, total β and γ -diversity should be lower than in headwaters, because mass effects may prevail and homogenise the metacommunity by decreasing turnover and increasing competitive exclusion (Heino, 2011; Mouquet & Loreau, 2003). The increasing importance of mass effects should increase the strength of the correlation between spatial factors and community composition. Thus, the influence of environmental filtering should be the highest upstream and that spatial processes should be important along the entire watercourse: upstream due to dispersal limitation and downstream due to mass effects.

For diatoms, the longitudinal shifts in taxonomical β -diversity patterns should be associated with corresponding changes in guild composition, given that guilds have distinct responses to local factors, such as current velocity and resource supply (Goldenberg Vilar, van Dam, Vonk, van der Geest, & Admiraal, 2014; Passy, 2007), and geographical connectivity (Dong et al., 2016). Indeed, a higher proportion of low profile species (i.e. species of short stature, adnate to the substratum) should be observed in environments with high current velocity and low nutrient availability (i.e. upstream). Motile (i.e. fast moving species) and planktonic species (i.e. species originating from the plankton) should be most abundant downstream (Goldenberg Vilar, van Dam, van Loon, et al., 2014; Passy, 2007; Rusanov & Khromov, 2016), in conditions of lower current velocity, higher nutrient levels, and deeper water column (for phytoplankton). On the other hand, high profile species (i.e. species of tall stature erect in

the biofilm) may reach maximum abundance midstream, because there, current velocities and siltation, which adversely affect this guild, are typically comparatively low (Rusanov & Khromov, 2016). Assuming that a higher abundance leads to a higher probability of dispersal and establishment, and consequently, to lower β -diversity (due to mass effects), we would expect the guilds to show the lowest β -diversity as follows: midstream for high profile and downstream for both motile and planktonic. Although low profile species are most prevalent upstream, the low connectivity of this environment may result in particular distributions of this guild.

In this study, we examined the extent to which environmental and spatial variables influenced β -diversity and its components in benthic diatom metacommunities in France as a function of watercourse position (up-, mid- and downstream). We hypothesised that (H_1) β -diversity and its turnover component decrease along the watercourse; (H_2) anthropogenic stress (here, nutrient enrichment) is related to a decrease in turnover and increase in nestedness; (H_3) dispersal limitation is preponderant upstream, while mass effects prevail downstream and (H_4) β -diversity of diatom ecological guilds differs depending on watercourse position.

2 | MATERIALS AND METHODS

2.1 | Dataset description

We analysed a French national dataset encompassing benthic diatom samples from 2,182 sites throughout the country. All samples were collected in 2011 following a standardised method (NFT 90-354, AFNOR, 2007), whereby stones were scraped during the low flow period to eliminate any seasonal and substratum variability. About 400 diatom cells were counted in permanent slides of cleaned diatom frustules, digested in boiling H_2O_2 (30%) and HCl (35%) and mounted in a high refractive index medium. Taxa were identified mainly to species using Krammer and Lange-Bertalot (1986–1991) and Lange-Bertalot (1995–2015, 2000–2013). A taxonomic standardisation was performed with Omnidia 5.3 software (Lecointe, Coste, & Prygiel, 1993). A total of 1,048 species were identified, and 1,022 of these species were classified into four ecological guilds (Passy, 2007; Soininen et al., 2016): low profile, high profile, motile and planktonic (some species were not classified due to the lack of guild information).

Physicochemical variables were measured according to standardised AFNOR protocols provided by the National French Water Agencies (www.lesagencesdeleau.fr). Median values of each variable were calculated for the 30-day period before and after the diatom sampling. Water pH, temperature, conductivity and concentrations of total phosphorus, orthophosphate, ammonium, nitrate and nitrite were used in statistical analyses as these are typically among the most influential chemical variables for diatoms (Soininen, 2007). To reduce the number of explanatory variables, we performed a principal component analysis (PCA, on the correlation matrix) and used site scores along the first two axes as environmental variables in further analyses. We considered here nutrient enrichment as an

indicator for the degree of anthropogenic stress (see Section 3). Euclidean distance between samples in two-dimensional space, defined by the first two PCs, was used as a measure of environmental heterogeneity among samples. Prior to PCA, the concentrations of total phosphorus, orthophosphate, ammonium, nitrate and nitrite were log-transformed to better approximate normality of the residuals.

Using Strahler ranks (Strahler, 1957), three classes were created to assign a watercourse position for each sampling site: upstream (Strahler rank 1 and 2), midstream (Strahler rank 3) and downstream class (Strahler rank from 4 to 7). A similar classification (for upstream sites) was implemented in other studies (Finn, Bonada, Múrria, & Hughes, 2011; Göthe et al., 2015; Meyer et al., 2007). The number of up-, mid- and downstream sites in our dataset was 928, 569 and 685 respectively (Table 1). Mean values of environmental variables across watercourse positions are summarised in Table 1.

2.2 | Data analysis

As β -diversity and its components are strongly dependent on sampling effort (Baselga, 2010; Bennett & Gilbert, 2016), we randomly selected a fixed number of sites for each watercourse position ($N = 99$). We repeated this simulation 999 times to insure stability of the diversity measures (γ , β , α and NODF, see below) and corresponding environmental conditions.

For each random site \times species matrix (presence-absence), we calculated for all species and for each guild the mean pairwise β -diversity indices following Baselga (2010): β_{sor} , the Sørensen dissimilarity index (total β -diversity), β_{sim} , the Simpson dissimilarity index representing dissimilarity due to turnover, and β_{nes} , representing dissimilarity due to the occurrence of nested subsets of species or species loss without replacement. We used the mean pairwise β -diversity indices instead of the multiple site metrics as they are considered less dependent on γ -diversity according to Bennett and

Gilbert (2016). As β_{nes} does not quantify how strong the nestedness pattern is (Baselga, 2010, 2012), we also calculated a nestedness metric (from both row and column values), based on overlap and decreasing fill (NODF, Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008), to better assess nestedness in each site \times species matrix. We tested the validity of NODF against null models conserving row and column totals following the algorithms developed by Miklós and Podani (2004), and used z-scores to test if values in observed data were different than those expected by chance.

Because of a large sample size due to simulation (999 randomly assembled datasets for each watercourse position), we compared the distribution of diversity measures (β_{sor} , β_{sim} , β_{nes} , NODF, α and γ) and guild abundance between watercourse positions with the Cliff's delta statistic (Cliff, 1993). Cliff's statistic ($|d|$) is based on a probabilistic estimation that a randomly selected value in one group is higher than a randomly selected value in another group and prevents obtaining significant differences only because of large sample sizes (Tecchio et al., 2016). Romano, Kromrey, Coraggio, and Skowronek (2006) provided threshold values to interpret the magnitude of differences between groups: negligible for $|d| < 0.147$, small for $|d| < 0.33$, medium for $|d| < 0.474$ and large for higher $|d|$ values. In this study, we considered $|d| > 0.33$ as a threshold for significance.

To determine the relative contribution of pure environmental and spatial effects on taxonomic and guild β -diversity patterns, we carried out partial Mantel tests (Smouse, Long, & Sokal, 1986) with 999 permutations. We used β -diversity dissimilarity matrices as response variables and both environmental variation (distances between sites in the PCA ordination) and geographic distances as explanatory variables (each one computed from the 999 randomly assembled datasets of 99 samples). We calculated the mean r -coefficient and the mean p -values for the pure environmental and pure spatial effects to assess their strength and significance. To test how the environmental conditions influence β -diversity across watercourse positions, we used Spearman rank tests to correlate mean pairwise β -diversity measures (β_{sor} , β_{sim} , β_{nes}) with mean site scores (of the 999 random communities of 99 sites) along the first two axes of the PCA. In order to identify which guilds correlate the best with β -diversity of the whole community, we used Mantel tests between dissimilarity matrices of all species and dissimilarity matrices for each guild.

All analyses were performed with the packages *vegan* (Oksanen et al., 2016), *betapart* (Baselga & Orme, 2012) and *effsize* (Torchiano, 2016) of R Statistical software (R Development Core Team, 2016).

3 | RESULTS

The first principal component axis (PC1) explained 37% of the total variance in environmental data. This axis was positively correlated with the concentrations of ammonium, orthophosphate, total phosphorus and nitrite (Figure 1), thus representing an anthropogenic gradient of nutrient enrichment. The second principal component

TABLE 1 Number of sites and mean environmental values (\pm SE) according to the position of sites along the watercourse in the whole dataset. UP = upstream, MID = midstream and DOWN = downstream

	UP	MID	DOWN
Number of sites	928	569	685
Temperature (°C)	15.04 (0.11)	15.25 (0.15)	16.96 (0.16)
pH	7.79 (0.01)	7.79 (0.02)	7.93 (0.02)
Conductivity (μ S/cm)	474.35 (11.74)	476.20 (13.31)	478.13 (16.50)
NH ₄ (mg/L)	0.17 (0.02)	0.17 (0.03)	0.11 (0.02)
NO ₂ (mg/L)	0.12 (0.01)	0.11 (0.01)	0.09 (0.01)
NO ₃ (mg/L)	14.67 (0.45)	12.13 (0.48)	8.87 (0.35)
Total phosphorus (mg/L)	0.16 (0.01)	0.16 (0.01)	0.10 (0.00)
Orthophosphate (mg/L)	0.32 (0.02)	0.33 (0.03)	0.19 (0.01)

axis (PC2) explained 19% of the total variance and was negatively correlated with pH and to a lower extent, with conductivity. This axis represented a gradient of natural conditions as alkalinity and conductivity depend on bedrock type. Conductivity may also be influenced by anthropogenic activities, such as salinisation (Cañedo-Argüelles et al., 2013), which may explain its correlation with both axis 1 and 2. Downstream sites displayed lower nutrient levels, higher pH and conductivity, and lower environmental heterogeneity compared with up- and midstream sites (Figures 1 and S1).

β -diversity partitioning revealed that total dissimilarity (β_{SOR}) among French diatom communities was mainly related to turnover (β_{SIM}), and only to a small extent to nestedness, as indicated by low values of β_{NES} compared to β_{SIM} (Figure 2). Confirming H_1 , β_{SOR} and β_{SIM} were significantly higher at upstream sites than at mid- and downstream sites (Figure 2a–b, see Table S1). The total dissimilarity (β_{SOR}) continuously decreased along the watercourse, while turnover values (β_{SIM}) did not differ significantly between mid- and downstream. The β_{NES} component was lower downstream, but higher at, and statistically indistinguishable between, up- and midstream sites (Figure 2c).

γ -diversity was significantly higher at up- and midstream sites than at downstream sites (see Figure S2.1). α diversity, on the other hand, exhibited the lowest values upstream, with no significant difference between mid- and downstream. The nestedness degree (NODF) was significantly different from the null model in only 19%, 22% and 19% of random matrices up-, mid- and downstream respectively. Accordingly, z-scores exhibited low values (around 0), and

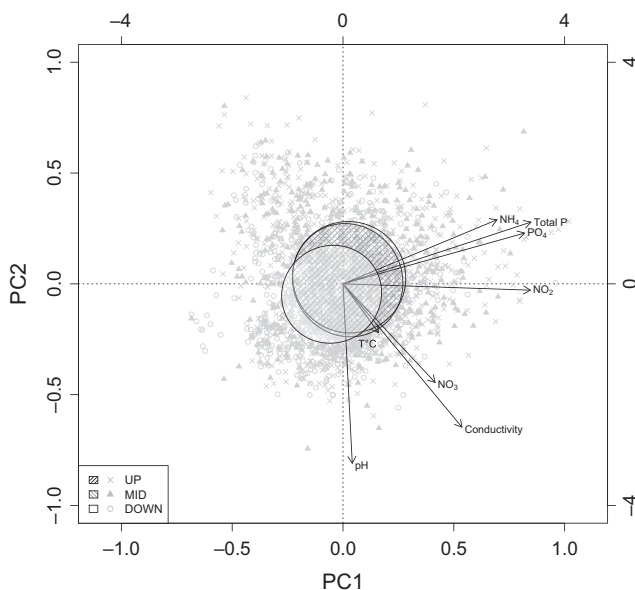


FIGURE 1 Sampling site scores and environmental variable position along the first two axes of the principal component analysis ordination. Symbols and ellipses represent respectively, the position of sites and their standard deviations (up-, mid- and downstream). The first and second axis explain 37% and 19% of the total variance respectively. $T^{\circ}\text{C}$ is the temperature in degree Celsius, NH_4 , total phosphorus (total P), PO_4 , NO_2 and NO_3 were measured in mg/L (axis scales for environmental vectors are displayed above and right)

tended to be more negative for downstream sites (see Figure S2.1), indicating lower NODF values than expected by chance. Even so, NODF significantly increased from up to downstream (Figure S2.1) and similar results were obtained when regarding only NODF values significantly higher than a null model (results not shown).

The influence of environmental heterogeneity on β -diversity did not vary along the watercourse, unlike spatial distance, which tended to increase downstream (Figure 3). The metrics β_{SOR} and β_{SIM} were significantly correlated with pure environmental and pure spatial factors across all positions (except upstream for β_{SIM} and space). The nestedness component (β_{NES}) exhibited non-significant correlations with both environmental and geographical distances (Figure 3).

Correlations between β -diversity measures and the first two PCA axes revealed significant relationships (Figure 4). Across all positions, the correlation between site scores on PC1 and β_{SOR} and β_{SIM} was negative, confirming our hypothesis H_2 and suggesting that nutrient enrichment tended to decrease both overall β -diversity and its turnover component. Along PC2, the correlation between site scores and β_{SOR} and β_{SIM} were all positive and significant, indicating that overall β -diversity and turnover decreased with increasing pH. In accordance with our hypothesis H_2 , nutrients had a positive, but weak effect on β_{NES} at up- and midstream sites, suggesting that the higher nutrients at these positions might have resulted in a higher nestedness component (Figure 4a). The correlation between β_{NES} and PC2 was significant only downstream, indicating that β_{NES} increased with increasing pH.

γ -diversity was negatively correlated with both the nutrient (PC1) and pH (inversely correlated with PC2 values) gradient (only the gamma-PC2 correlation in downstream sites was non-significant). NODF was positively correlated with these gradients (except in midstream sites for pH, see Figure S2.2). Alpha diversity tended to increase along the nutrient gradient (except upstream) but decrease along the pH gradient (see Figure S2.2).

Along the watercourse, motile and low profile species were the most abundant (see Figure S3) and contributed the most to the overall β -diversity (see Figure S4). Consistent with H_4 , β_{SOR} and β_{SIM} decreased significantly and monotonically along the watercourse for motile species and to a lower degree for planktonic species, but increased for low profile species (Figure 5). In these guilds, β_{NES} exhibited the opposite patterns to β_{SOR} and β_{SIM} with respect to watercourse position. For high profile species, β_{SOR} tended to be the lowest midstream, whereas β_{NES} showed the lowest values mid- and downstream.

Across catchment positions, environmental heterogeneity had a strong influence on β_{SOR} and β_{SIM} in all guilds except for planktonic species (Figure 6). In the high profile guild, the correlation of the environment with β_{SIM} was significant only mid- and downstream. The correlation of pure spatial factors with β -diversity metrics was never significant upstream. The pure spatial effect on β_{SOR} was significant mid- and downstream for all guilds (Figure 6). The spatial distance- β_{SIM} correlation was significant only in the low profile guild at mid- and downstream sites. In all guilds, neither the environmental nor the spatial correlations with β_{NES} were significant.

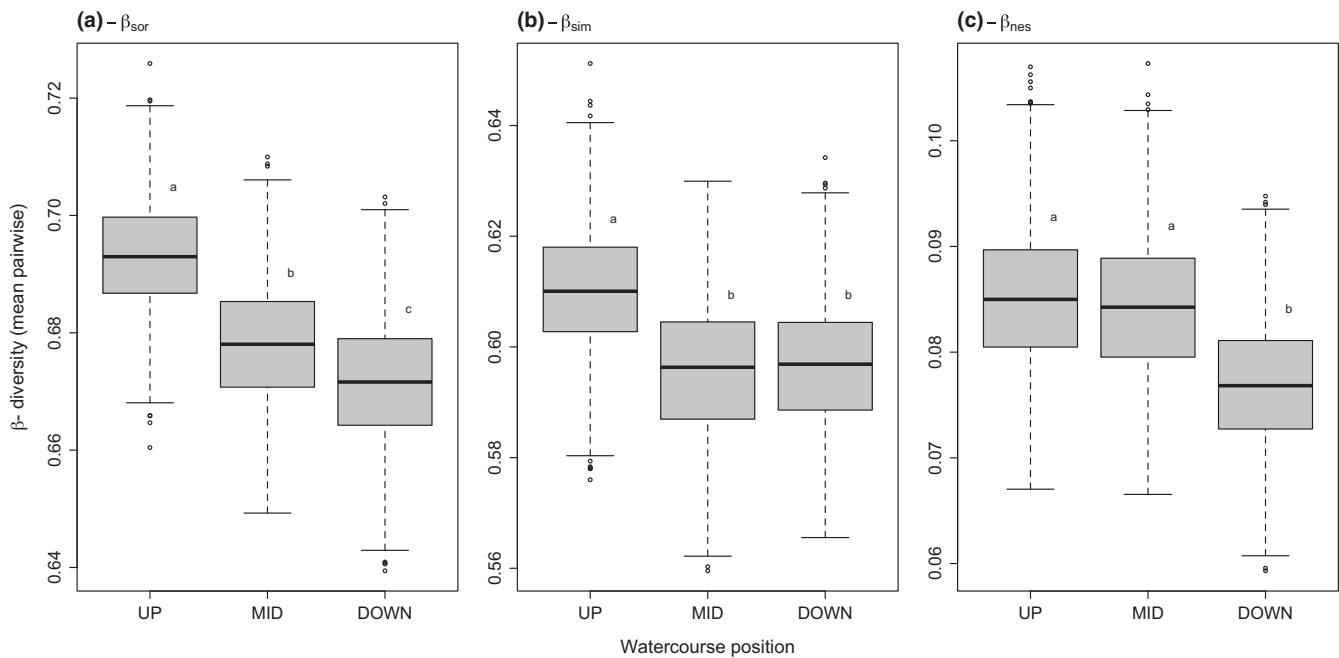


FIGURE 2 Boxplots of the mean pairwise β -diversity measures for each random matrix of 99 sites, simulated 999 times, according to site watercourse position (UP = upstream, MID = midstream and DOWN = downstream). β_{sor} , Sørensen dissimilarity index; β_{sim} , Simpson dissimilarity index (turnover) and β_{nes} , dissimilarity due to nestedness. Different letters represent significant differences between groups according to the delta Cliff statistic (see Table S1)

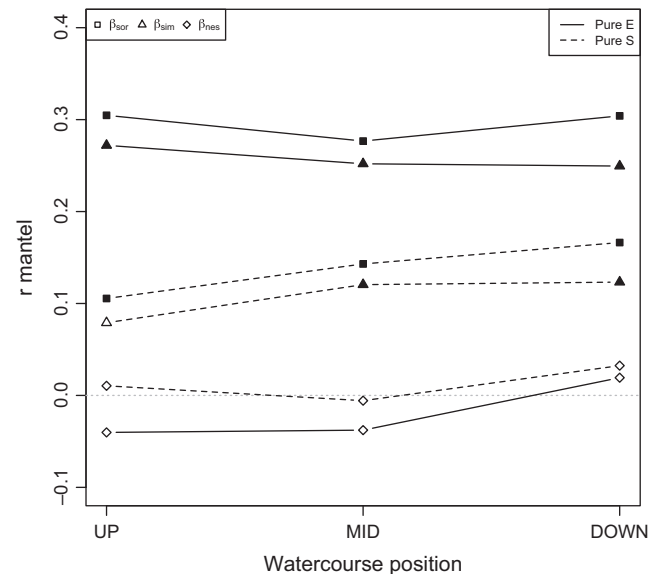


FIGURE 3 Mean partial Mantel coefficients of the pure effect of environment (pure E, solid lines) and space (pure S, dashed lines) (measured for each random matrix of 99 sites simulated 999 times) on β -diversity, according to site watercourse position (UP = upstream, MID = midstream and DOWN = downstream). β_{sor} , Sørensen dissimilarity index; β_{sim} , Simpson dissimilarity index (turnover) and β_{nes} , dissimilarity due to nestedness. Filled symbols represent significant ($p \leq .05$) relationships and open symbols, non-significant ones based on the mean p -values for all randomly sampled communities

4 | DISCUSSION

This is the first study to document the dependence of diatom taxonomic and guild β -diversity and its components on watercourse position and associated environmental and spatial factors at a large spatial scale. We highlight the importance of stream longitudinal effects on regional diversity, and thus contribute to a better understanding of metacommunity processes in freshwater ecosystems.

4.1 | Environment as the main driver of diatom β -diversity

In agreement with our first hypothesis, we found total β -diversity and turnover to be highest upstream. In upstream sites, the strong and positive correlation of β -diversity with pure environmental heterogeneity together with the weak spatial influence (Figure 3) suggested that communities were mostly controlled by species sorting. The strong correlation between environment and γ -diversity upstream (see Figure S2.2), which was the highest in these reaches (see Figure S2.1), provided further evidence for the important role of the environment in determining different aspects of diatom biodiversity in small streams. Similar to upstream sites, environmental factors exerted a strong influence on β -diversity in mid- and downstream sites as well, emphasising the dominant role of species sorting in structuring diatom metacommunities along the entire watercourse. Similar results have been reported by other studies on stream organisms, but generally at smaller spatial scales (Göthe, Angeler, & Sandin, 2013; Rusanov & Khromov, 2016; Tonkin et al., 2015). We further revealed that the patterns of β -diversity were primarily

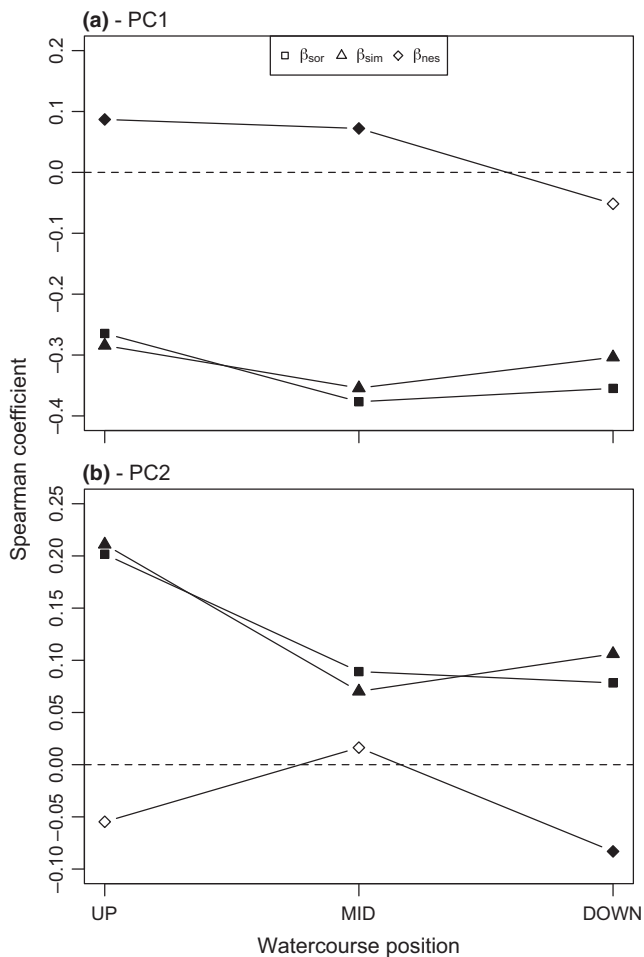


FIGURE 4 Mean Spearman rho coefficient between mean pairwise β -diversity and mean scores of 99 randomly selected sites along (a) the first axis (PC1) and (b) the second axis (PC2) of principal component analysis ordinations according to site watercourse position (based on 999 permutations). β_{sor} , Sørensen dissimilarity index; β_{sim} , Simpson dissimilarity index (turnover) and β_{nes} , dissimilarity due to nestedness. Filled symbols represent significant ($p \leq .05$) relationships and open symbols, non-significant ones based on the mean p -values for all randomly sampled communities

driven by the turnover component, in accordance with previous studies on other aquatic organisms (Angeler, 2013; Tisseuil et al., 2012; Tonkin, Heino, Sundermann, Haase, & Jähnig, 2016; Viana et al., 2016) but not shown previously for diatom communities at such a study scale (but see Wetzel et al., 2012).

Surprisingly, we found that nutrient enrichment declined downstream, a counterintuitive result according to the river continuum hypothesis (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). We explain this trend with the presence of cattle farming, usually located in headwater areas (Jamoneau, Chabrierie, Closset-Kopp, & Decocq, 2012), which may increase the phosphorus inputs locally. Nevertheless, across watercourse positions, nutrient enrichment was negatively related with β -diversity and its turnover component, which confirmed our second hypothesis (Figure 4). According to Gutiérrez-Cánovas et al. (2013), community homogenisation

associated with an increase in the nestedness component along an anthropogenic gradient should be due to the predominance of generalists. We did not test this hypothesis directly in our study, but we observed that β_{nes} and NODF were strongly positively correlated with PC1 scores (Figures 4 and S2.2).

4.2 | Importance of dispersal processes along the watercourse

Although environment appeared to be the major driver of diatom β -diversity, we also found a significant correlation of β -diversity and turnover with geographical distance at all sites, indicating that dispersal-related mechanisms may play an important role along the entire watercourse. However, the correlation between β -diversity and pure spatial factors was significant but weak upstream ($r = .11$, $p = .046$), which implies that these communities may be weakly controlled by dispersal mechanisms. A significant effect of pure spatial factors may be indicative of dispersal limitation as well as mass effects (Cottenie, 2005) and several studies found difficulties in separating these two processes using observational field data only (Bottin et al., 2014; Dong et al., 2016). Given that upstream communities are disconnected, we conclude that the upstream spatial effect may be related to limited dispersal rather than mass effects. The limited dispersal may operate at least in some regions (thus explaining the weak correlation), such as in mountainous catchments with constrained aerial dispersal. The importance of dispersal limitation in diatom communities has already been suggested by several authors for upstream sites of mountain areas (Bottin et al., 2014; Dong et al., 2016).

A set of findings let us conclude that mass effects rather than limited dispersal was the more likely process behind the pure spatial factors at mid- and downstream sites (in accordance with H_3). First, turnover at mid- and downstream sites was lower than upstream sites. Second, γ -diversity was lower at downstream sites than mid- and upstream sites. Third, nestedness degree values increased from up- to downstream sites (see Figure S2.1). Fourth, the intensity of the spatial signal increased from up- to downstream. We think all these findings point to the importance of mass effects in structuring these communities but not to limited dispersal.

Surprisingly, mass effects have been reported relatively rarely for microorganisms (De Meester, 2011; Lindström, Forslund, Algsten, & Bergström, 2006), even though microbes are generally considered good dispersers. Recent literature emphasised the importance of spatial factors for river diatom community composition (Bottin et al., 2016; Dong et al., 2016; Goldenberg Vilar, van Dam, van Loon, et al., 2014), hypothesising that mass effect dynamics rather than limited dispersal drives the observed patterns. Our results add to this knowledge by showing for the first time that mass effects could indeed be an important process in structuring diatom diversity in the mid- and downstream parts of the watercourse.

In summary, environmental filtering appeared to be the most important process in determining the β -diversity patterns of diatom communities although high rates of dispersal interacted with local

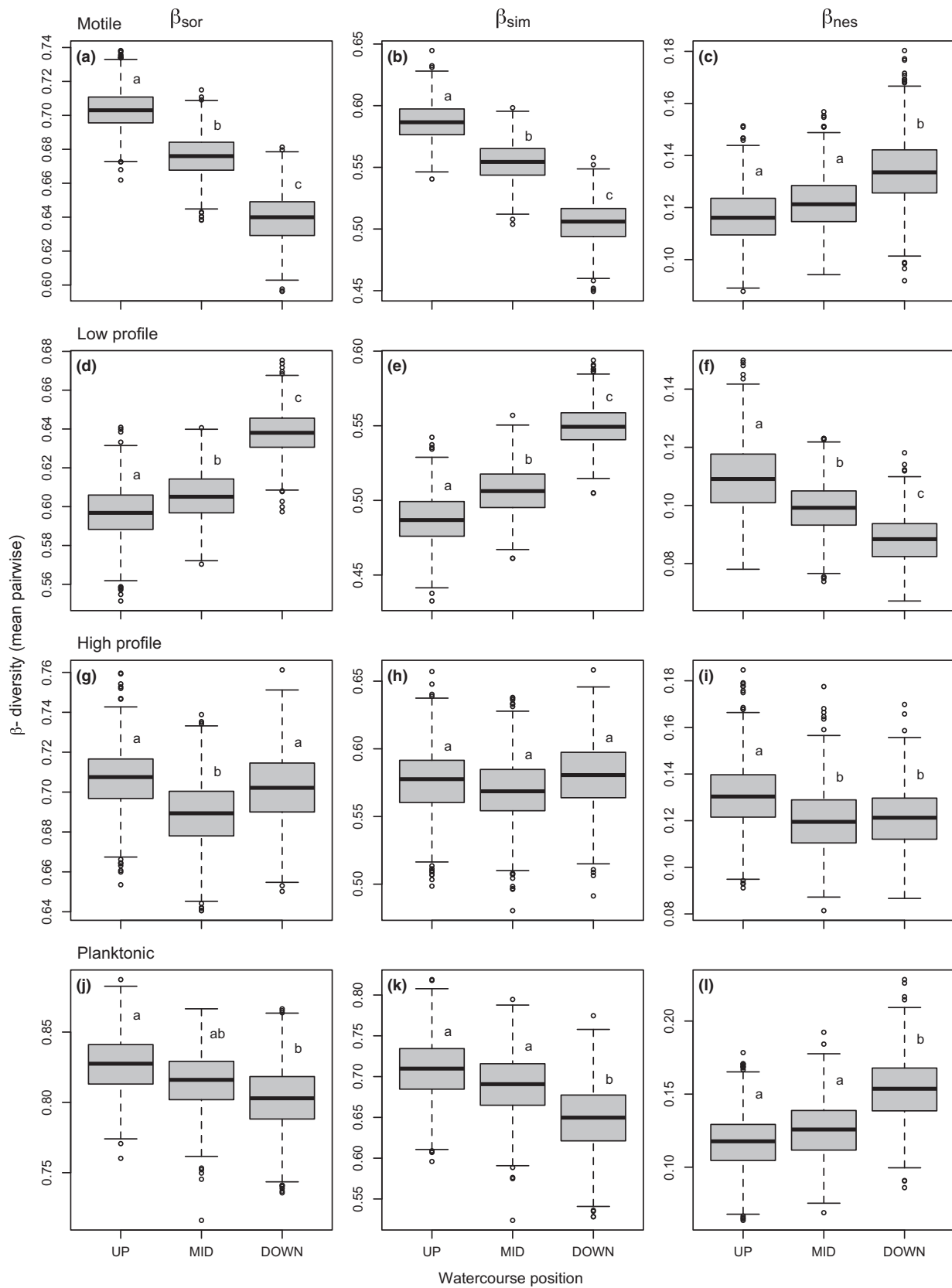


FIGURE 5 Boxplots of the mean pairwise β -diversity measures (for each random matrix of 99 sites simulated 999 times) according to site watercourse position (UP = upstream, MID = midstream and DOWN = downstream) for motile (a–c), low profile (d–f), high profile (g–i) and planktonic (j–l) species. β_{sor} , Sørensen dissimilarity index; β_{sim} , Simpson dissimilarity index (turnover) and β_{nes} , dissimilarity due to nestedness. Different letters represent significant differences between groups according to the delta Cliff statistic (see Table S1)

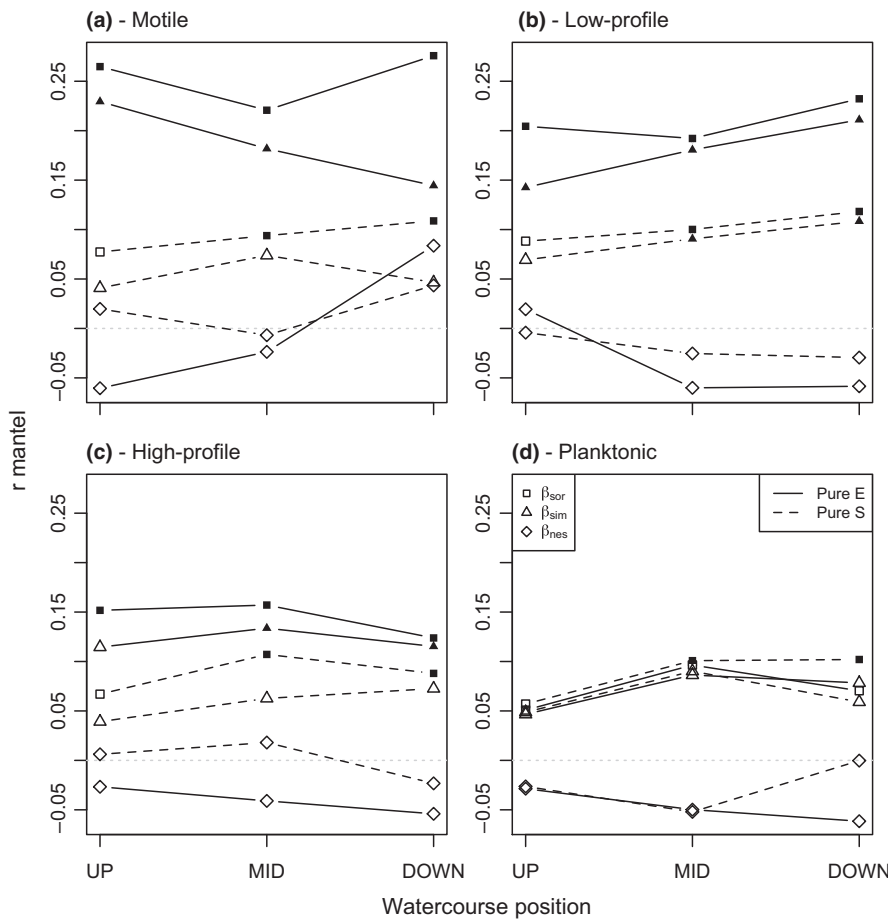


FIGURE 6 Mean partial Mantel coefficients of the pure effect of environment (pure E, solid lines) and space (pure S, dashed lines), measured for each random matrix of 99 sites simulated 999 times, according to site watercourse position for each guild: motile (a), low profile (b), high profile (c) and planktonic species (d). β_{sor} , Sørensen dissimilarity index; β_{sim} , Simpson dissimilarity index (turnover) and β_{nes} , dissimilarity due to nestedness. Filled symbols represent significant ($p \leq .05$) relationships and open symbols, non-significant ones based on the mean p -values for all randomly sampled communities

influences at lower reaches. These results partially support a more general view that different types of factors may control species communities in isolated streams *versus* larger mainstem rivers, already quantified for macroinvertebrates (Brown & Swan, 2010; Göthe, Angeler, & Sandin, 2013; Tonkin et al., 2015) and fishes (Tisseuil et al., 2012), but not for diatom communities (but see Schmera et al., in this issue).

4.3 | Diatoms guilds provide deeper insights into the metacommunity patterns

Environmental and spatial processes also had distinct effects on the ecological guilds along the watercourse, consistent with our hypothesis H₄. Motile and low profile species represented the most abundant guilds with the strongest contribution to overall β -diversity (see Figures S3 and S4). However, the β -diversity of these guilds exhibited contrasting patterns along the watercourse, suggesting that the underlying processes are likely to be different.

Generally, as predicted, the β -diversity of all guilds was the lowest in reaches where these guilds were the most abundant (see Figure S3). Motile species were more abundant mid- and downstream because of their tolerance to high siltation (Goldenberg Vilar et al., 2015; Passy, 2007; Rusanov & Khromov, 2016; Fore, 2003). The planktonic guild also had a greater abundance in lower reaches due

to greater habitat availability (greater water volume). Consequently, both guilds demonstrated similar patterns of β -diversity with the lowest total β -diversity and turnover component and the highest nestedness component downstream. Given the significant correlation between β -diversity and spatial factors mid- and downstream (Figure 6), mass effects appear to be influential for the motile and planktonic guilds. Mass effects may also explain the β -diversity patterns of high profile species midstream, where, as predicted, the lowest β -diversity was significantly associated with spatial factors (Figures 5 and 6). Spatial effects were not observed for the high profile guild upstream, despite its higher abundance there, probably due to the low connectivity among sites. It is, however, difficult to conclude what processes drive this guild downstream because of contradictory results (significant spatial effect associated with an increase in total β -diversity between mid- and downstream that may be due to a paralleled simultaneous decrease in abundance). Nonetheless, results for this guild were not straightforward, which may be due to the fact that its response to nutrient and disturbance gradients is less clear than for motile and low profile guilds (Soininen et al., 2016).

The abundance of low profile species, continuously decreasing from upstream to downstream, was paralleled by an increase in its total β -diversity and turnover. Upstream, we expected these patterns to be associated with a greater probability of dispersal and establishment due to the high abundance of low profile species in these

reaches. However, the absence of correlation between β -diversity and pure spatial factors upstream may suggest that, at low connectivity, higher guild abundance is insufficient to produce mass effects. The influence of space became significant mid- and downstream, concurrent with an increase in β -diversity. This could have been indicative of limited dispersal, but considering that low profile species are better dispersers at large scales than the other guilds (Passy, 2016), this result might be related to some spatially structured, yet unmeasured environmental variables. In particular, current velocity, river size, canopy characteristics and land use near the stream channel are recognised to strongly influence the presence of low profile species (Leland & Porter, 2000; Passy, 2007).

4.4 | Importance for water quality assessment

This study can be useful for improving water quality assessment methods based on benthic diatom communities. In particular, the two guilds with the strongest impact on β -diversity (low profile and motile, see Figure S4) seem to be controlled by distinct processes along the watercourse. Low profile species, according to our results, may be predominantly driven by environmental factors across watercourse positions, making them excellent candidates for biomonitoring. On the other hand, motile species may rather be influenced by mass effects at mid- and downstream sites. Their use as key indicator species in mid- and downstream reaches should thus be reconsidered, as they may be controlled by local environmental conditions as well as by dispersal processes. Indeed, mass effects, responsible for the presence of species in unsuitable habitats, could mask the effect of the local environment (Heino, Melo, Siqueira, et al., 2015; Leibold et al., 2004). Also, β -diversity of planktonic species was not correlated with environmental variability across watercourse positions, suggesting that this guild cannot be used for quantifying the anthropogenic pressure, at least at this study scale. As benthic diatoms are broadly used in biomonitoring, particularly in the context of the European Water Framework Directive (European Union, 2000), our findings may facilitate the development of more effective water quality assessment indices and programs, incorporating biotic responses to both environmental and dispersal related processes.

5 | CONCLUSIONS

These results suggest that different processes probably govern diatom β -diversity at species and guild levels along the watercourse in stream ecosystems. Environmental filtering played a major role in structuring species assemblages along the river course, while dispersal-related processes, most likely mass effects, exerted a significant influence mid- and downstream. However, the relative influence of environmental and spatial factors along the watercourse appears to be guild dependent. This new information on the diversity patterns of diatom ecological guilds in response to environmental and dispersal processes can be very useful for future stream bioassessment and management efforts.

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SUPPORTING INFORMATION

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