Environmental Research 285 (2025) 122284

Contents lists available at ScienceDirect

Environmental Research

journal homepage: www.elsevier.com/locate/envres

Beyond the flow: ecological insights from diatom communities of a Mediterranean intermittent river

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ARTICLE INFO

Keywords:
Temporary streams
Intermittent water flow
Diatom taxonomic diversity
Physicochemical parameters
Climate change

ABSTRACT

Intermittent rivers (IR) are among the most widespread watercourses globally, characterized by alternating dry and wet phases. Despite these fluctuations, IRs support diverse ecosystems and considerable biodiversity. Among their biotic communities found in these rivers, diatoms serve as key primary producers and bioindicators. Due to the limited knowledge of how droughts affect IR biodiversity, this study investigates diatom responses to seasonal hydrological changes and water flow. Specifically, it focuses on taxonomic and functional composition and community structure of diatoms in a naturally occurring Mediterranean IR. Overall, species richness appeared to be unaffected by droughts and water flow, with similar values observed at both lentic and lotic sites. Taxonomic and functional α-diversity were generally higher in lotic waters (TRic $= 12.9$; Fric $= 9.79$) compared to lentic (TRic $= 8.7$; Fric $= 3.23$) sites across all diversity indices, though no significant differences were found in α-diversity between sites. While the environmental variables considered did not significantly affect variability between sampling sites, permutational analysis identified temperature ($F = 1.49$, $p = 0.09$) and dissolved oxygen ($F = 2.11$, $p = 0.01$) as important predictors for taxonomic and functional α-diversity. However, seasonality significantly influenced taxonomic ($F = 2.28$, $p = 0.009$) and functional ($F = 8.86$, $p < 0.01$) β-diversity, with greater variability (1.33 times) observed in August. Findings also indicate significant differences in taxonomic dispersion between site types ($F = 2.21$, $p = 0.04$) but no significant differences in functional dispersion. These results suggest that whereas IR conditions may not definitely influence diatom α-diversity, seasonal changes play a key role for community turnover, highlighting the importance of the hydroperiod for shaping IR biodiversity. In the context of ongoing climate change, these findings are particularly relevant, as shifts in hydrological regimes may increasingly affect ecological dynamics and community structure in IR systems.

1. Introduction

Intermittent rivers (IR) are the most common type of watercourse worldwide (Sarremejane et al., 2022) and are now believed to outnumber perennial rivers—a trend that is expected to intensify with climate change (Cottet et al., 2023). Unlike perennial rivers, IR do not flow continuously throughout the year; they typically dry out during droughts or dry seasons and resume flow in response to rainfall, snowmelt, or periodic groundwater recharge (Cottet et al., 2023; Fovet et al., 2021). Due to increasing temperatures from global climate change and the rising need for water resources for civil and industrial purposes, it is expected that both the number of IR and the length of dry periods will rise, with several perennial rivers turning into temporary ones (Tramblay et al., 2021; Leigh et al., 2016). Typical of arid and semi-arid regions, IR gained attention by scientific literature in the 1970s and 1980s; however, although their increasing awareness, these ecosystems has been largely overlooked by aquatic ecologists and water managers until recently (Steward et al., 2022).

During rainy seasons, IR can reconnect isolated aquatic habitats, promoting gene flow and species dispersal across the landscape. During dry periods, refugia such as hyporheic zones and groundwater-fed ponds become critical for the persistence of many aquatic organisms (DelVecchia et al., 2022). Beyond their role in maintaining ecological connectivity and providing essential ecosystem services, IR also host distinct biotic communities (Larned et al., 2010). These communities are often composed of organisms with high ecological plasticity and functional adaptations that enable them to survive and reproduce under highly variable hydrological conditions (Grgić et al., 2022; Sabater

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https://doi.org/10.1016/j.envres.2025.122284
Received 18 May 2025; Received in revised form 13 June 2025; Accepted 1 July 2025

et al., 2017; Williams, 2012). The alternation between water flowing, isolated ponds, and completely dry phases creates dynamic habitat mosaics that support both aquatic and semi-aquatic species (Magand et al., 2020; Datry, 2017). Invertebrates, amphibians, and algal communities can show a wide range of adaptation strategies, such as dormancy (e.g., diapausing eggs in invertebrates), burrowing (amphibians and some fish), rapid development, and dispersal abilities, which allow them to exploit temporary water availability while enduring adverse dry periods (Kerezsy et al., 2017; Stubbington et al., 2017; Datry et al., 2014).

Among the different biotic communities residing in IR, diatoms constitute an essential category of primary producers and bioindicators (Biswas et al., 2025; Yang et al., 2015). These single-celled, silica-based algae can rapidly react to alterations in water levels, substrate conditions, nutrient accessibility, and disturbances, making them especially suitable for identifying ecological changes in fluctuating environments like IR (Agarwal, 2025; Hamed, 2023; Novais et al., 2020). The Water Framework Directive (WFD) (Directive, 2000/60/EC) adopted diatoms as key biological indicators to be used in monitoring studies, in order to achieve good qualitative and quantitative status of all (ground and surface) water bodies according to a set of standard criteria (Moss et al., 2020; Poulier et al., 2014). Nonetheless, the ecology of diatoms in IR is still inadequately studied, as most biomonitoring frameworks continue to depend on assumptions based on perennial systems (Tornés et al., 2021; Novais et al., 2020; Stenger-Kovács et al., 2013). Flow intermittence can modify habitat conditions at both micro- and macro-scales, affecting for example moisture retention, light exposure, and nutrient fluxes—factors that directly influence diatom composition and photosynthetic activity, especially in the Mediterranean region (B-Béres et al., 2022; Timoner et al., 2014). During dry phases, benthic diatom communities can persist in biofilms within moist sediments or generate resistance forms (resting stages or spores), while others recolonize from aerial dispersal or upstream refugia once flow resumes (Quevedo-Ortiz et al., 2024; Novais et al., 2020). This cyclical disturbance regime selects for taxa with high ecological tolerance, rapid growth, or flexible life-history traits, often resulting in communities that are functionally distinct from those in permanent rivers (Novais and Morais, 2024; Falasco et al., 2021).

Despite these peculiar adaptations, the functional and taxonomic diversity of diatoms in IR is still inadequately integrated into ecological monitoring programs. Expanding our knowledge of how diatom assemblages respond to different water flow regimes is critical for refining water quality indicators and understanding ecosystem resilience under increasingly intermittent flow conditions. The present research aims at investigating the effects of flow intermittency, caused by the combined effect of climatic and seasonal variables, on benthic diatom communities in a Mediterranean region of Central Italy (namely Latium). Specifically, we explored the response of diatom communities to hydrologic seasonal changes in a naturally IR at the level of taxonomic composition, structure, and functional diversity.

We hypothesized that cumulative effects of non-flow events, determined by the seasonal climate fluctuations, would result in: (H1) α-diversity increase from lentic to lotic sites, with no effects of seasonality; (H2) taxonomic and functional α-diversity (and their components) would show different responses to the physicochemical gradients; (H3) β-diversity and its turnover component should be mostly influenced by seasonality compared to water flow. In particular, following Falasco et al. (2021), we expected pioneer diatom communities, composed of smaller sized taxa and thus likely adapted to unstable environments (i.e. low-profile diatoms, characterized by adnate growth form) in the months following flow resumption after dry periods.

2. Materials and methods

2.1. Study area

The research was conducted along the Licenza River, a right-bank tributary of the Aniene River located within the Lucretili Mountains Regional Park in the province of Rome, Central Italy. The stream spans 14.5 km in length and drains a catchment area of approximately 52 km^2 (Fig. 1a).

From a climatic point of view, which includes the Licenza River catchment area, experiences a warm temperate Mediterranean climate, characterized by prolonged, dry summers and mild, wet winters. Average monthly temperatures consistently remain above 2 °C throughout the year. Land use within the watershed includes pastures (40 %), forests (30 %), and permanent crops (30 %).

The Licenza River exhibits an intermittent flow regime, alternating between flowing (lotic or lentic) and dry conditions. Between July and October, some segments of the streambed dry out completely, while others retain isolated ponds, and a few maintain perennial flow with lentic characteristics during the dry season. During winter and spring, the stream resumes a more torrential flow regime, with rapid variations in discharge and velocity driven primarily by rainfall events.

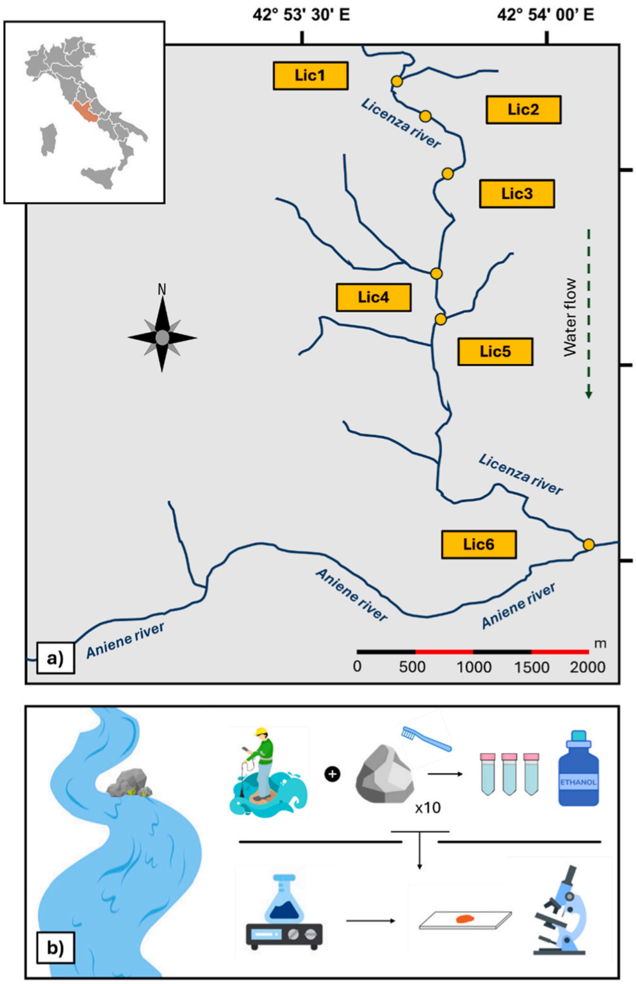

Fig. 1. Location of sampling sites in the Latium region, Italy. The inset map (a) shows the location of Latium within Italy and the distribution of the six sampling sites along the Licenza River, with yellow dots indicating their precise locations. The panel b) displays the field sampling activities and the following laboratory activities for the oxidation and subsequent identification of diatoms. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.2. Sampling design

Sampling was performed in 6 stream sites 1–1.5 km apart (Fig. 1), during August and October 2018. These months were selected as they represent contrasting hydrological phases typical of Mediterranean climates: August corresponds to the peak of the dry season, often characterized by low or no flow conditions, while October follows the first autumn rains, marking the onset of rewetting and flow resumption. Diatom sampling activities were performed following ISPRA (2014a): for each sample, at least 10 stones (dimensions between 64 mm and 256 mm) were scraped using a commercial toothbrush (taking care to use a different toothbrush for each sampling site); then, the toothbrush was immersed in a 50 ml Falcon containing 70 % diluted ethanol and distilled water. The falcons, properly labeled, were then stored in cooler bags and kept in the dark to prevent further cell division. In this way the diatomic component was also made suitable to be carried out in the laboratory for oxidation operations. For each site, three different replicates were performed as suggested by Maitland et al. (2020) and Kelly et al. (1998) (Fig. 1b).

Diatom samples were processed and analyzed in the laboratory by following the oxidation method explained in Taurozzi et al. (2023) and Marcheggiani et al. (2019) for inland waters: through the use of hydrogen peroxide, the organic matter was digested, and diatoms were mounted on permanent slides using Naphrax® (high resin power of refraction) to fix the coverslip. The morphological identification of diatom species was conducted under a microscope at 100 × magnification (Leica), using taxonomic guides (DREAL Languedoc Roussillon, 2021; Bahls et al., 2018; ISPRA, 2014b; Ector and Hlúbiková, 2010; Taylor et al., 2007; Krammer, 2002; Krammer and Lange-bertalot, 1991b; Krammer and Lange-bertalot, 1991a; Krammer and Lange-bertalot, 1988; Krammer and Lange-bertalot, 1986). For each slide, the analysis was considered completed when identification at the species level of at least 400 valves was achieved (ISPRA, 2014a).

2.3. Environmental variables

To assess water physicochemical variables through the months, water temperature (°C), electrical conductivity (μS/cm), oxygen concentration (ml/l; %), salinity (‰) and pH were measured in each site during the two samplings. These parameters were recorded in the field using a multiparametric probe Hannah® HI98194. Collected water samples were returned to the laboratory to measure Chemical Oxygen Demand (COD) and concentration of phosphates (PO_4^{3-} mg/l) and nitrates (NO_3^- mg/l) using special kits of cuvette (Hach, LCK 448 0.5–5.0 mg/L PO_4^{3-}; LCK 339 0.23–13.50 NO_3^- mg/L; LCK 114 150–1000 mg/L O_2) and a spectrophotometer (Hach, DR1900). Nutrients (PO_4^{3-} and NO_3^-) were measured following Ma et al. (2021, 2023): 1L of water samples was taken from each sampling sites and filtered glass microfibers filter papers (Lab Logistic Group GmbH, VWRI516-08882, binder free, 0.7 μm, 47 mm, 100, 516–0882). 70 mL of the filtered sample was added with chloroform for fixation, and then stored at −20 °C. The PO_4^{3-} and NO_3^- were analyzed using a nutrient analyzer (SEAL Analytical AA100 AutoAnalyzer).

2.4. Data analysis

Normality, homogeneity of variance, and independence were assessed prior to statistical analyses. Based on the results of these preliminary checks, both parametric and non-parametric tests were applied where appropriate.

Sites were categorized as either lentic or lotic based on water flow conditions, with particular attention given to the variable “current velocity,” considered the most indicative parameter of structural and compositional changes in the two communities under study. Recorded current velocities across sampling months were classified as follows.

a. Class 0 – dry sites, completely desiccated;
b. Class 1 – lentic water, confined in isolated ponds;
c. Class 2 – no perceptible flow;
d. Class 3 – low flow velocity;
e. Class 4 – intermediate flow velocity;
f. Class 5 – high flow velocity.

For statistical analyses, two broader categories of “site types” were created: lentic sites, encompassing classes 0 to 2, and lotic sites, including Classes 3 to 5.

A two-tiered analysis was performed. The first phase focused on taxonomic and functional α-diversity and the influence of environmental variables. Taxonomic α-diversity was calculated using the diversity function from the *vegan* package (Oksanen et al., 2019) in R (version 4.4.2; R Core Team, 2024), based on five indices: species richness (TRic), Shannon-Wiener (TSha), Simpson (TSim), Evenness (TEve), and Margalef (TMar). Functional α-diversity was assessed using the dbFD function in the *FD* package (Laliberté and Legendre, 2010), based on a diatom matrix incorporating species composition and 15 binary-coded functional traits (e.g., cell size, ecological guild, and life form) following Wu et al. (2024). Five functional diversity indices were computed: Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), Functional Dispersion (FDis), and Rao’s Quadratic Entropy (RaoQ).

The second phase of the analysis focused on taxonomic and functional β-diversity, evaluating the effects of seasonality and hydrological conditions on community dissimilarities.

To test the first hypothesis (H1), that whether α-diversity changed among different sites and sampling dates, the non-parametric Kruskal–Wallis tests among the two site types and months were performed.

To test the second hypothesis (H2) and evaluate the key physicochemical factors determining spatial patterns of taxonomic and functional α-diversity, a distance-based redundancy analysis (db-RDA) (Legendre and Anderson, 1999) was conducted. Distance-based Redundancy Analysis (db-RDA) is a multivariate statistical technique that allows for non-Euclidean distances, commonly used in community ecology to examine the relationships between species composition or guild-based community and environmental variables. Following Wu et al. (2024), first the *findCorrelation* function from the *caret* package in R was used to remove the physicochemical variables exhibiting high intercorrelation (i.e., Spearman’s rank $|r| > 0.8$), thereby reducing multicollinearity. Subsequently, a global test was conducted for each taxonomic and functional α-diversity index using the *capscale* function in the *vegan* package, with significance assessed via ANOVA ($p < 0.05$).

To test the third hypothesis (H3), taxonomic and functional β diversities were calculated based on the presence–absence matrix, utilizing the Sørensen dissimilarity index. Functional matrix was generated using the *pco* function from the vegan package. The decomposition of taxonomic β-diversity into turnover and nestedness components was achieved using the *beta.pair* function from the R package *betapart* (Baselga and Orme, 2012). Concurrently, the computation of functional turnover and nestedness components followed the methodology proposed by Wu et al. (2024), using the *functional.beta.pair* function in the R package *betapart*. Subsequently, ANOVA tests were then performed looking for significant differences in β diversities among different seasons and water flows. Principal Coordinate Analysis (PCoA) and the Euclidean distance were used to characterize seasonal and water flow-dependent β-diversity variations in species-based and guild-based communities, which were statistically assessed by permutational multivariate analysis of variance (PERMANOVA).

Statistical tests were considered significant when p-value was <0.05. Statistical analyses were computed in PAST 4.17c software (Hammer et al., 2001) and R software (R Core Team, 2024). Figures were drawn using R software and GraphPad Prism 8.0 software (GraphPad).

3. Results

3.1. Site hydrology and physicochemical variables

Across the sampling sites of the Licenza River, environmental variables exhibited spatial and temporal variability between August and October (Table S1). The hydrological characteristics of sampling sites in different seasons were shown in Table 1. Phosphate concentrations (PO_4^{3-}) ranged from 0.010 mg/L (LIC3, August) to 0.740 mg/L (LIC5, August), while nitrate (NO_3^-) values varied from 0.207 to 1.03 mg/L, with higher values generally recorded in August. Chemical oxygen demand (COD) was highly variable, with maximum values observed in lentic sites LIC1 and LIC6 (38.1 and 54.6 mg/L, respectively) and minimum values in LIC3 (8.05 mg/L). Dissolved oxygen (O_2) levels ranged from 7.13 to 10.02 mg/L, with corresponding oxygen saturation percentages between 74.8 % and 106.3 %. The water temperature declined from summer to autumn across all sites, with the highest values in August (up to 21.6 °C) and lower values in October (down to 10.6 °C). Electrical conductivity (Cond) was highest in LIC6 (575 μS/cm) and lowest in LIC3 (292 μS/cm), reflecting variations in ion concentration among the stations. Salinity remained generally low (0.19–0.32 ‰), consistent with freshwater conditions. pH values were slightly alkaline across sites, ranging from 7.84 to 8.49.

3.2. Diatom community overview

A total of 60 diatom taxa were recorded across the six sites (LIC1–LIC6) in August and October (Table S2). Species composition varied notably among sites and between sampling periods. LIC6 had the highest species richness, with 22 different taxa observed across the two sampling periods. Overall, 12 dominant species were identified (abundance >2 %) (Fig. 2). *Cocconeis placentula* and *Gomphonema elegantissimum* were the most abundant and widespread taxa, occurring in multiple sites and both samplings, with particularly high occurrences in LIC1, LIC4, and LIC5. Several species, including *Cymbella excisa, Cymbella compacta*, and *Fragilaria ulna*, were also frequently observed but showed marked fluctuations in abundance over time. Site-specific taxa were also evident; for example, *Navicula capitatoradiata* and *Navicula cryptotenella* were only found at LIC6, while *Gomphonema calcareum* was restricted to LIC3. Temporal differences were observed in many sites, with some taxa appearing only in August (Fig. 2a) or October (Fig. 2b): for instance, in LIC2, *Amphora copulata*, *Cymbella cistula*, and *Eolimna subminuscola* were recorded only in October, whereas *Amphora ovalis*, *Cymbella helvetica*, and *Denticula tenuis* were detected only in August. Overall, October samples exhibited higher species abundances, and a broader representation of taxa compared to August. Several species, such as *Cocconeis placentula, Cymbella excisa,* and *Gomphonema elegantissimum*, were notably more abundant or exclusively recorded in October, while others like *Gomphonema olivaceum* and *Navicula tripunctata*, were more prevalent in August. However, no statistically significant differences emerged in the number of species between sampling months (H = 0.02, p = 0.87).

Table 1

Characterization of the sampling sites according to the proposed classification system based on water velocity: Class 0 – dry sites, completely desiccated; Class 1 – lentic water confined to isolated ponds; Class 2 – no perceptible flow; Class 3 – low flow velocity; Class 4 – intermediate flow velocity; Class 5 – high flow velocity.

Site	Month	Water velocity	Code	Site type
LIC1	AUG	0	2	Lentic
LIC1	OCT	0	2	Lentic
LIC2	AUG	0.17	3	Lotic
LIC2	OCT	0.62	4	Lotic
LIC3	AUG	0.60	4	Lotic
LIC3	OCT	0.45	4	Lotic
LIC4	AUG	0	2	Lentic
LIC4	OCT	0	2	Lentic
LIC5	AUG	1.20	5	Lotic
LIC5	OCT	1.10	5	Lotic
LIC6	AUG	0	2	Lentic
LIC6	OCT	0.22	3	Lentic

Similarly, the analysis of diatom species distribution across lentic and lotic environments revealed notable compositional differences, while no statistically significant differences emerged in the number of species between site types (H = 0.77, p = 0.36). Overall, the dataset indicates distinct assemblages between lentic and lotic habitats, with several species occurring exclusively in one or the other; some species were widespread and recorded on multiple sites, while others were restricted to specific habitats or sampling periods. *Gomphonema elegantissimum* was highly abundant in lentic sites LIC1 and LIC4 in October but was absent from lotic sites. In contrast, *Gomphonema pumilum* was found exclusively in lotic environments, particularly in LIC2 and LIC3 during August. Species such as *Cymbella compacta* were present in both habitat types, though with differing abundances. A few species, including *Rhopalodia gibba* and *Stauroneis smithii*, had a very limited distribution, occurring in only two samples.

3.3. α-diversity fluctuations in diatom communities of lotic and lentic sites and physicochemical factors

Taxonomic α-diversity of diatom communities showed average TRic values of 8.7 in lentic waters and 12.5 in lotic waters, with no significant variations across water flows for all the indices considered: TRic (H = 0.78, p = 0.36), TSha (H = 1.25, p = 0.26) and TSim (H = 1.64, p = 0.20), TEve (H = 1.25, p = 0.26) and TMar (H = 0.77, p = 0.36) (Fig. 3a) (Table S3).

Similarly, functional α-diversity showed average higher values for FRic in lotic waters (9.79) rather than lentic (3.23) and for all the others indices considered; however, Kruskal-Wallis test highlighted no significant differences in functional α-diversity values between sites: FRic (H = 3.1, p = 0.07), FEve (H = 1.64, p = 0.2), FDiv (H = 2.56, p = 0.1), FDis (H = 1.25, p = 0.26), RaOQ (F = 1.26, p = 0.26) (Fig. 3b) (Table S4).

The results of the db-RDA (Redundancy Analysis) on environmental data and the taxonomic distance matrix between sites show that the model explains 68.32 % of the total variance in the data. The variability explained by the environmental variables (PO_4^{3-}, NO_3, COD, O_2, Sal, T, pH) is distributed across the first seven principal components (RDA1-RDA7), with the first two components (RDA1 and RDA2) together explaining 35.28 % of the variance (Fig. 3c). Although the model explains a significant portion of the variance (67.32 %), the permutation test (999 permutations) did not detect a statistically significant relationship (p-value = 0.178), suggesting that the environmental variables considered do not have a significant impact on the variability between sampling sites. Permutational analysis highlighted that T (F = 1.49, p = 0.09) and O_2 (F = 2.11, p = 0.01) can be considered important predictors for taxonomic α-diversity variation, while pH (F = 1.94, p = 0.03), PO_4^{3-} (F = 0.88, p = 0.57), NO_3 (F = 1.21, p = 0.23), COD (F = 1.14, p = 0.29) and Sal. (F = 1.14, p = 0.27) did not show statistically significant influences. Therefore, while suggesting some relationship between environmental variables and ecological distances between sites, the model does not support a strong significant link to explain the functional diversity among the sampled sites.

Similarly, the results of the db-RDA on functional trait data show that the model explains 68.06 % of the total variance in the data. The constrained part of the variance (related to the environmental variables PO_4^{3-}, NO3, COD, O2, Sal, T, pH) accounts for 68.06 %, while the remaining 31.94 % is unexplained (unconstrained variance) (Fig. 3d). The first two principal components (RDA1 and RDA2) together explain 58.58 % of the constrained variance, with RDA1 contributing 33.12 % and RDA2 contributing 25.46 % to the overall variability in the functional composition. The results of the permutation test (999 permutations) indicate that the model is not statistically significant (p-value =

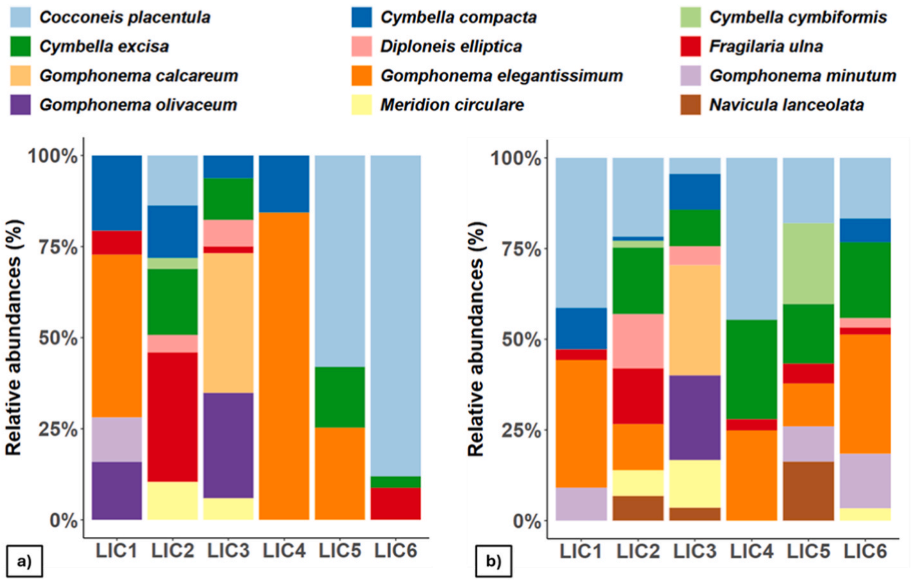

Fig. 2. Temporal and spatial fluctuations in the proportion of the most abundant (>2 %) diatom species found in a) August (or dry period) and b) October (or flow regime).

0.373), suggesting that the environmental variables considered do not significantly explain the functional diversity among the sites. The eigenvalue distribution supports this finding, as RDA1 and RDA2 have the largest contributions to the variance, but the remaining components contribute only marginally. Permutational analysis highlighted that O_2 ($F = 3.43$, $p = 0.02$) can be considered important predictors for taxonomic α-diversity variation, while T ($F = 1.42$, $p = 0.25$), pH ($F = 0.99$, $p = 0.4$), PO_4^{3-} ($F = 0.38$, $p = 0.8$), NO_3 ($F = 1.07$, $p = 0.35$), COD ($F = 1.70$, $p = 0.16$) and Sal. ($F = 0.73$, $p = 0.54$) did not show statistically significant influences. The variance partitioning analysis further confirms that the total contribution of the environmental variables is relatively modest in explaining the functional diversity, with a substantial portion of the variance remaining unexplained. Therefore, while there is some explanatory power in the model, it does not strongly support a significant relationship between the environmental factors and the functional diversity at the studied sites.

3.4. *β-diversity of diatom communities*

The total taxonomic β-diversity among the studied sites was found to be high (0.861), with turnover (0.767) being the dominant component, compared to nestedness (0.095) (Fig. 4a). When comparing lentic and lotic sites, the multivariate dispersion analysis (*betadisper*) showed no significant differences in the variability of taxonomic composition between the two site types ($F = 0.006$, $p = 0.939$) (Fig. 4b). This indicates that the diatom communities exhibit similar species composition in both lentic and lotic habitats.

The analysis of the taxonomic β-diversity between August and October revealed a significant difference in dispersion (Fig. 4b). The ANOVA results showed that the group factor (month) significantly influenced the distances ($F = 5.08$, $p = 0.04$), indicating that the β-diversity differed between the two months. The average distance to the median was slightly higher in August (0.5025) compared to October (0.3773), suggesting greater variability in the β-diversity in August and the less dispersion in October.

The Principal Coordinates Analysis (PCoA) based on the Bray–Curtis dissimilarity matrix revealed that the first two axes (PCoA1 and PCoA2) accounted for approximately 54.4 % of the total variation in community composition, with PCoA1 explaining 31.0 % and PCoA2 23.4 % (Fig. 4c). The cumulative variation explained by the first four axes reached nearly 80 %, indicating a relatively strong structuring of the data in the reduced dimensional space. A PERMANOVA test confirmed that there were significant differences in taxonomic community composition among sites ($R^2 = 0.65$, $F = 2.28$, $p = 0.009$), suggesting that over 65 % of the variation in dissimilarity could be attributed to seasonal differences. This supports the hypothesis that site-level factors play a major role in shaping community structure. Similarly, PERMANOVA test confirmed that there were significant differences in taxonomic community composition among site types ($R^2 = 0.18$, $F = 2.21$, $p = 0.04$).

Regarding functional diversity, PCoA showed that β-diversity in the trait-based diatom community exhibited substantial fluctuations between sites (PERMANOVA, $F = 8.86$, $p < 0.01$): the first two axes (PCoA1 and PCoA2) together explain 89.91 % of the variation in functional β-diversity between sites (Fig. 4d). Differently, PCoA showed that β-diversity in the trait-based diatom community did not exhibit substantial fluctuations between site type (PERMANOVA, $F = 1.01$, $p = 0.33$). Our results highlighted that, in terms of the variability of community composition across these groups, there is evidence of significant differences in dispersions between sites but not between site types.

4. Discussions

Our research aimed to determine taxonomic and functional differences of diatom communities of IR investigating the effects of physicochemical parameters in shaping diatom diversity. In particular, this study represents the first attempts to identify the relative influence of water flows and seasonality for shaping diatom communities in IR, involving even physicochemical parameters as determinant factors.

4.1. *Diatom community characterization*

Our analysis highlighted variability in the composition of diatom communities across the six studied sites, both spatially and temporally, despite the absence of statistically significant differences in taxonomic richness between sampling months and site types. Our results suggested that, although the total number of species was relatively homogeneous, the composition of diatom communities, expressed as species, was influenced by environmental variables and site characteristics (Weckström and Korhola, 2001). The higher species abundance observed in October compared to August could be addressed to the more favorable ecological conditions typical of autumn: moderate

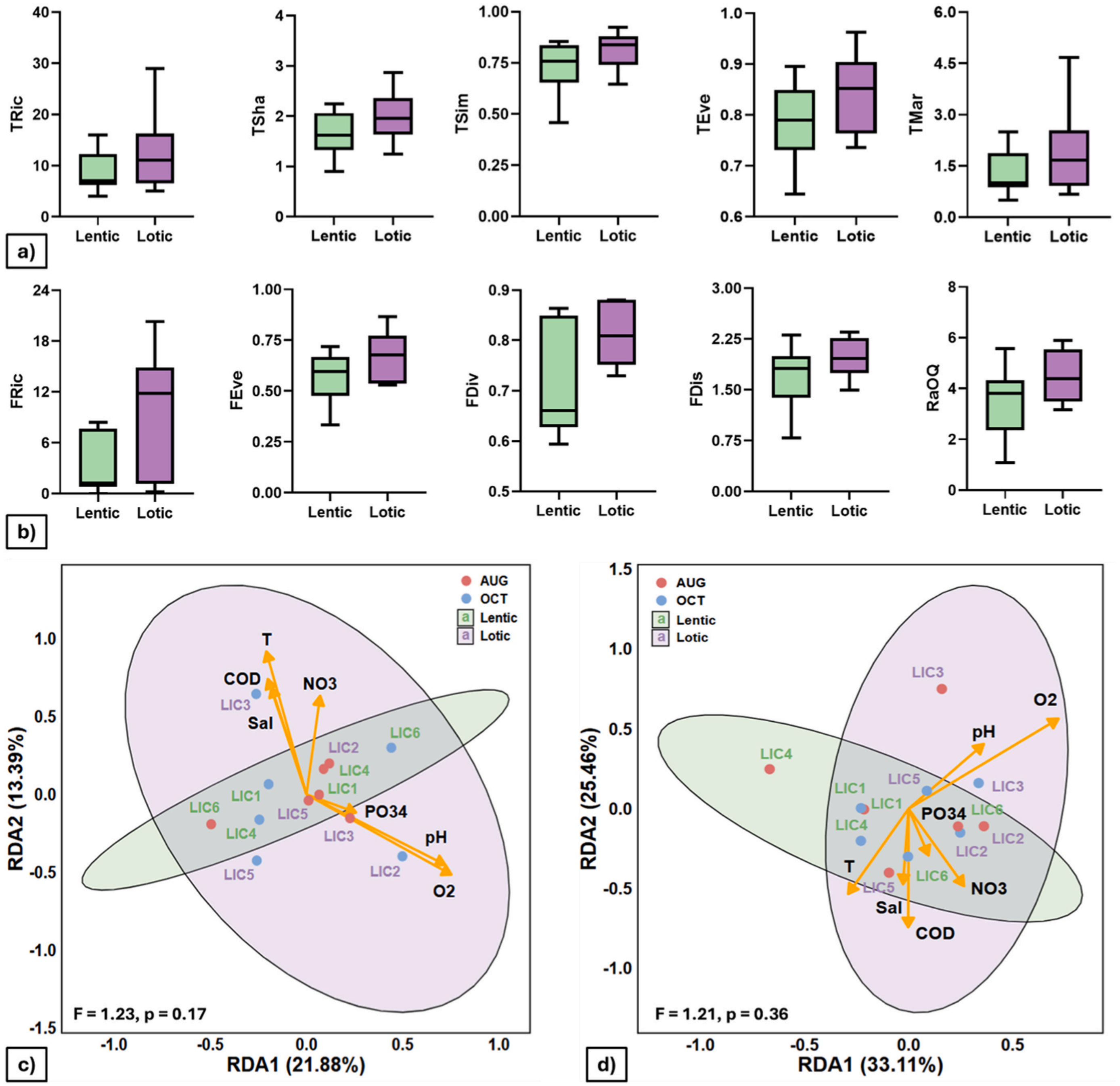

Fig. 3. Taxonomic a) and functional b) α-diversity values for lentic and lotic sites, calculated using five α-diversity indices (species richness = TRic, Shannon-Wiener = TSha, Simpson = TSim, Evenness = TEve, Margalef = TMar) No statistically significant differences from the Kruskal-Wallis tests were observed for the selected variables. Plots of Redundancy Analysis for c) taxonomic and d) functional α-diversity.

temperatures and higher dissolved oxygen levels may support greater diatom diversity and favor cell growth (Taurozzi et al., 2024a; Liu et al., 2022; Soininen and Eloranta, 2004). Previous studies have already demonstrated that seasonal variations significantly influenced diatom communities, with intra-annual fluctuations playing a key role in shaping the temporal dynamics of benthic communities (Falasco et al., 2021; Guo et al., 2020). Differently from Müllner and Schager (2003), where pool habitats hold a higher number of taxa than riffle sites, in this research species richness was similar among sites. Although the observed similar species richness, the important differences in community composition between lentic and lotic sites could be related to ecological specialization of certain diatom species in response to specific habitat characteristics (Lindholm et al., 2018). For example, the presence of *Gomphonema elegantissimum* and *Gomphonema pumilum*, found respectively in lentic and lotic sites, may be associated with environmental variations among the sampling sites, primarily based on abiotic elements like water flow and nutrient availability. Our findings are in accordance with previous research where diatoms were reported to be strongly variable through different habitat gradients, with large variations in composition and β-diversity among lentic and lotic environments (Soininen and Weckstrom, 2009). The observed variability in diatom composition between August and October underscores the significance of seasonal dynamics in shaping diatom communities in IR (Tan et al., 2014; Soininen and Eloranta, 2004). The greater variability in August may also highlight unfavorable environmental conditions, including higher temperatures or fluctuating water levels, that could

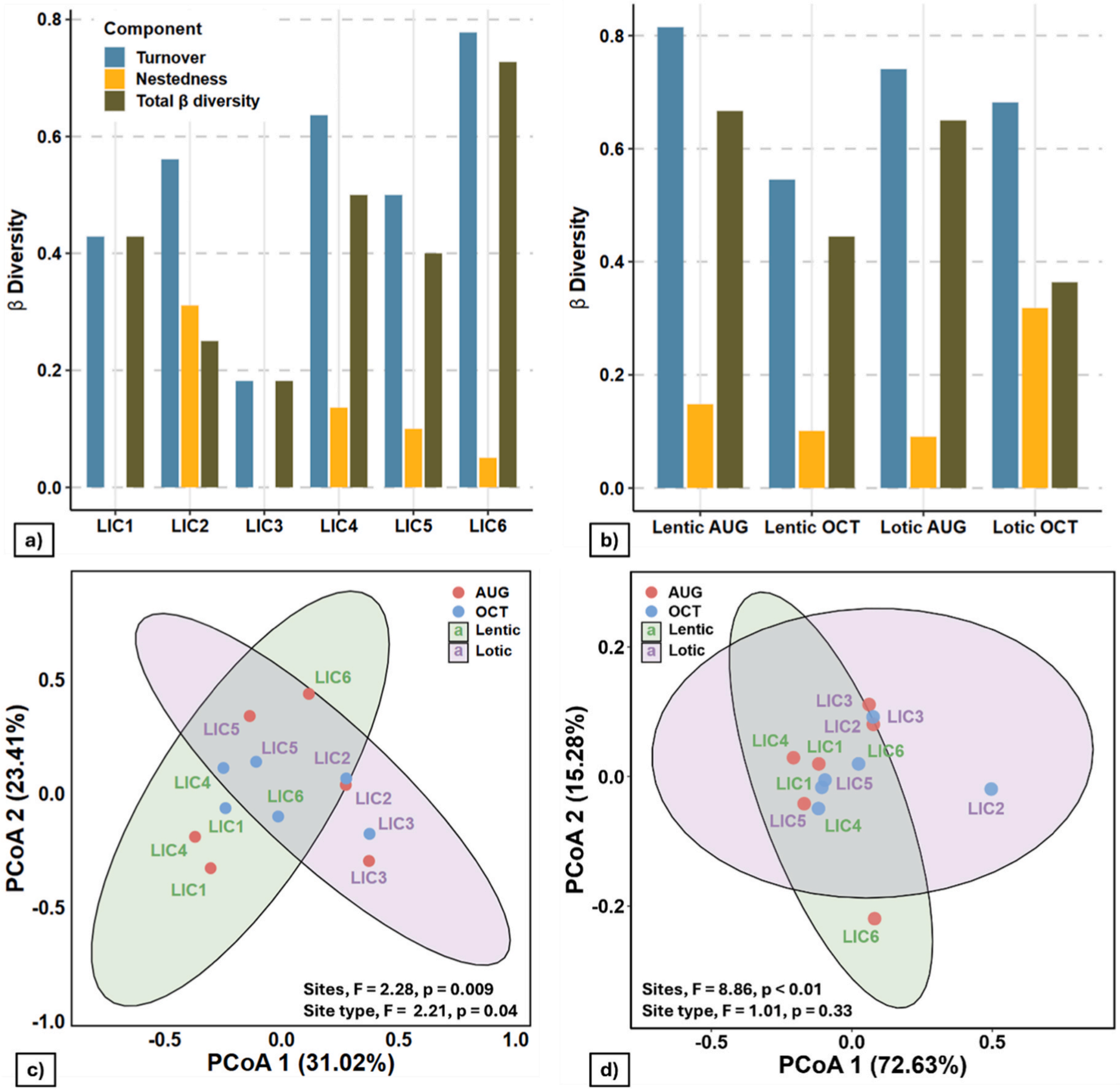

Fig. 4. β-diversity components (Turnover, Nestedness, and Total β-diversity) for a) different sites and b) site types (Lentic and Lotic) and sampling months (August and October). The bar chart shows the variation in beta diversity for each combination of site type and month. PCoA of c) taxonomic and d) functional β-diversity of diatom communities.

influence habitat availability and community structure (Virta et al., 2020). Seasonal dynamics were then recognized as key drivers for structuring diatom communities, with numerous implications for the management and conservation of IR ecosystems.

The diatom species composition was very different among the sites along the river continuum, forming three distinct assemblages. Our findings are in line with previous research, where the distribution of diatom species is generally characterized by oligotrophic species found in the upstream sections and eutrophic species found in the downstream sections (Mao et al., 2018; Centis et al., 2010). Specifically, in the upstream sites, species such as *Amphora ovalis*, sensitive to organic pollution but tolerant of salinity, and *Cymbella helvetica*, typical of oligotrophic freshwaters with moderate conductivity, were predominant. Midstream sites were characterized by the presence of *Gomphonema calcareum* and *Gomphonema elegantissimum*, oligosaprobic species indicative of low-nutrient conditions and commonly found across a range of freshwater environments. In contrast, downstream sites were dominated by tolerant, pioneer taxa like *Cocconeis placentula* and *Navicula tripunctata*, commonly inhabiting benthic substrates (e.g., epiphytic surfaces, wood and pebbles), and associated with moderate organic pollution levels.

In addition, the highest diatom species richness was observed at LIC6, located at the confluence with the Aniene River. Generally, confluence zones often support increased biodiversity due to ecological mechanisms such as enhanced nutrient input, disturbance-regulated diversity, and higher oxygenation (Rice et al., 2001). Moreover, abiotic and anthropogenic factors, including nutrient enrichment and pollution, have also been linked to higher benthic diatom richness (Xing et al., 2024). Interestingly, this contrast with the findings of Tornés et al. (2018), who reported reduced diversity at similar confluence sites. However, in our case, the presence of species, indicators of eutrophic waters, such as *Navicula capitatoradiata* and *Navicula cryptotenella*, suggested that LIC6 is a meso- and eutrophic site. Although not all the possible variables were considered here, we could hypothesize that the high species richness observed may result from the combined effects of nutrient loading and physical mixing dynamics at the confluence (Benda et al., 2004; Dodds and Welch, 2000).

4.2. *α-diversity and physicochemical variables*

The analysis of diatom α-diversity across lentic and lotic sites highlighted a general higher mean taxonomic and functional richness in lotic systems compared to lentic ones. However, these differences were not statistically significant, indicating a general similarity in α-diversity across water flow regimes. These findings partially confirmed our H1. However, these results are not in line with previous research which documented higher relationships between habitat type and α-diversity in microbial and algal communities, particularly in systems with high environmental heterogeneity or where dispersal limitation is reduced (Dalkıran et al., 2021; Thrush et al., 2011). Although lotic sites showed higher average FRic and TRic values, i.e. greater functional and taxonomic niche space occupied, the statistical analysis conducted did not confirm significant differences. Our findings could even reflect the relative influence of environmental filtering, being lower than expected, or the possible presence of generalist species which are able to survive under diverse hydrological conditions (Baattrup-Pedersen et al., 2013; Konar et al., 2013). Moreover, the low variability observed between sites and the potential overlap in trait composition between lentic and lotic sites might reduce the observable differences.

In addition, the results emerged from the db-RDA analysis supported this interpretation. In fact, whereas the environmental variables explained an important portion of the variance of the taxonomic and functional community composition, the observed differences were not statistically significant. This could suggest that the results found might be driven by different variables not considered in this research. Furthermore, dissolved oxygen emerged as the most important factor for both taxonomic and functional communities, supporting previous studies that highlighted the importance of dissolved oxygen as main driver of diatom communities (Bhatt et al., 2025; Shibabaw et al., 2021). Although temperature and pH are commonly reported as key drivers of diatom assemblage composition (Soininen et al., 2016; Teittinen et al., 2016), they showed minor and negligible effects, respectively, in our study. Consequently, hypothesis H2 was not supported. This lack of influence may be attributed to seasonal homogenization, limited environmental gradients, or the dominance of environmentally tolerant taxa. Furthermore, nutrient concentrations such as PO_4^{3-} and NO_3^-, despite their ecological importance, did not explain significant portions of the variance, maybe due to the rapid uptake of cycling of nutrients in dynamic freshwater systems (Atkinson et al., 2017).

Our findings highlight the need to explore, in further studies, additional environmental variables which could be involved in diatom community structuring. For instance, factors like microhabitat structure, hydrological connectivity, and biotic interactions (e.g., grazing pressure, competition), which are known to influence diatom assemblages, could account for some of the unexplained variation (Taurozzi et al., 2024b; Medeiros et al., 2022). However, overall, our findings highlight the complexity of the ecological processes behind diatom diversity in IR (Falasco et al., 2016). Although environmental filtering through physicochemical variables, particularly via dissolved oxygen, emerged as important for diatom community structuring, its role seems relatively limited. This highlights the need to consider both biotic and abiotic factors, but also temporal turnover and spatial succession for understanding patterns of diatom biodiversity across ephemeral lentic and lotic systems.

4.3. *β-diversity patterns*

The analysis of diatom β-diversity revealed substantial shifts in community composition among the investigated variables. In particular, seasonal variation in taxonomic β-diversity between late summer and early autumn was statistically significant, confirming the hypothesis H3. The increased dispersion community observed in August supports the hypothesis of high environmental heterogeneity or higher biotic interactions under warmer conditions. This aligns with findings by Lepori and Malmqvist (2009), who reported elevated β-diversity during hydrologically unstable periods. The predominance of species turnover over nestedness further indicates that seasonal shifts are mainly driven by species replacement across sites, rather than by species loss or gain (Baselga, 2012). Such patterns are commonly attributed to environmental gradients, biotic interactions, and dispersal limitations (Pellissier et al., 2018; Tylianakis and Morris, 2017). Diatoms are known to dominate the spring bloom, often followed by a secondary growth phase in summer (Reynolds, 1973). However, contrary to the findings of Fontaine and Rynearson (2023), no consistent summer–autumn assemblages were identified in our study. Instead, notable taxonomic differences emerged between these two seasons. These findings suggest that in lotic systems, diatoms undergo significant seasonal taxonomic shifts characterized by species replacement, likely driven by differential adaptation to both small- and large-scale climatic variations. Such adaptations manifest through changes in the biotic and abiotic parameters of the watercourse (Jin and Agustí, 2018; Anderson, 2000), reinforcing the role of environmental filtering and temporal dynamics in shaping diatom community structure.

Differently, the absence of significant differences in community structure between lotic and lentic sites could depend on several ecological and hydrological factors. For instance, lotic systems are often characterized by high connectivity, in particular during flood events: this can favor diatom dispersion, allowing similar species to colonize different habitats, from the river to the nearby lentic habitats like pools (Qu et al., 2018). Moreover, since lentic pools are generally formed within or adjacent to the river, they are not completely isolated. Periodic hydrological events, like rain or fluctuating river levels, can reconnect these habitats, reducing β-diversity across lentic and lotic sites (McDonough et al., 2011). In addition, it is important to consider the relative effect of environmental and physicochemical variables on diatom assemblages. However, although water velocity and flows differ, other environmental factors (e.g., temperature, light, nutrient levels, substrate type) could not vary drastically between sites: diatoms are sensitive to such variables (Passow and Laws, 2015; Shi et al., 2015), and if the conditions are similar, the species filtering process may select for similar communities across both habitat types.

PCoA analysis also reflected spatial heterogeneity as a key factor for community assembly processes. Furthermore, site type explained a comparatively smaller portion of compositional variance, suggesting that the categorical distinctions based on water velocity adopted in this research, (lotic vs lentic) could oversimplify, underlying ecological complexity. In contrast, functional β-diversity exhibited a statistically significant response to water flow. Trait-based analysis highlighted a significant degree of variation among sites, supporting the hypothesis that functional diversity is mostly influenced by localized environmental filters rather than broad habitat classifications (Chapman and McEwan, 2018). Indeed, the absence of significant differences across site types highlighted the potential for ecological redundancy in trait composition between lentic and lotic systems, despite taxonomic dissimilarities. Our findings support the growing consensus that taxonomic and functional diversity, while interrelated, are shaped by distinct ecological processes (Mouchet et al., 2010), with temporal and spatial factors differently influencing community assembly mechanisms (Menéndez-Serra et al., 2023; Gizachew, 2021). In this sense, the use functional analysis can provide critical insights about ecosystem-level responses to environmental shifts that the taxonomic approaches alone may fail to capture (Inkpen et al., 2017; Hevia et al., 2016; Villéger et al., 2010).

5. Conclusions

Our analysis provides valuable insights into the ecological dynamics of IR systems. Although the overall species richness appeared relatively homogeneous across sites, diatom community composition was clearly shaped by environmental variables and site-specific characteristics. Notably, autumn supported higher diatom biodiversity, with no significant differences detected between lotic and lentic sites. Furthermore, a consistent spatial pattern emerged in IR: oligotrophic species predominated in upstream sections, while eutrophic taxa were more common downstream. These findings highlight the influence of longitudinal gradients and seasonal dynamics in structuring diatom assemblages in IR systems.

A general uncertainty remains regarding the influence of water flow on diatom communities. In this study, we provide initial evidence suggesting slightly higher taxonomic and functional richness in lotic systems compared to lentic ones. Although these differences were not statistically significant, the results may reflect the influence of local environmental factors or the presence of generalist species capable of adapting to varying hydrological conditions. In particular, while the relative influence of dissolved oxygen and temperature was demonstrated here, especially for taxonomic diversity, further investigations are therefore needed, involving several abiotic factors, including hydrological variations throughout the year. Beta diversity analyses also revealed no clear distinction between lentic and lotic sites, supporting the idea of ecological similarity in terms of water flow. Overall, seasonality appeared to be the dominant factor influencing diatom diversity, likely linked to rainfall and weather patterns that can alter river connectivity and flow regimes.

In this sense, diatom patterns, together with their associations with environmental variables in Mediterranean IR systems may be used to guide management practices and conservation activities. In a changing world subject to climate change, diatoms can serve as valuable bioindicator: sensitive species and tolerant taxa can provide valuable insights on the real threats of IR. Effective conservation and management strategies should integrate climate projections to monitor diatom communities, implement adaptive measures to mitigate habitat degradation, and protect biodiversity. Understanding diatom responses to climate change can inform the development of robust monitoring programs and conservation actions aimed at preserving freshwater ecosystem health in a rapidly changing climate scenario.

CRediT authorship contribution statement

Davide Taurozzi: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Giulia Cesarini:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Carmela Di Santo:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Massimiliano Scalici:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Consent to participate

Not applicable.

Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval

Not applicable.

Funding

This research was supported by the Grant of Excellence Departments, MIUR-Italy (ARTICOLO1, COMMI 314–337 LEGGE 232/2016). In addition, this study was also supported by the NBFC to University of Roma Tre funded by National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4—Call for Tender No. 3138 of 16 December 2021, rectified by Decree No. 3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union —NextGenerationEU. Project Code CN00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP F83C22000730006, Project title ‘National Biodi versity Future Center—NBFC.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors acknowledge the support of NBFC to University of Roma Tre, funded by the Italian Ministry of University and Research, PNRR, Missione 4 Componente 2, “Dalla ricerca all’impresa”, Investimento 1.4, Project CN00000033. We are grateful to the Reviewers who implemented our manuscript quality.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envres.2025.122284.

Data availability

Data will be made available on request.

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