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Ecological drivers of rarity and commonness in freshwater benthic diatoms

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ABSTRACT

Natural communities are generally composed of many rare species constituting the major part of species richness. Despite the ecological importance and vulnerability of rare species, our knowledge about them is very limited, particularly concerning the environmental factors influencing them. This gap is largely due to their exclusion from ecological analyses. Benthic diatoms have crucial importance in aquatic ecosystems making it vital to enhance our understanding of their ecological drivers. In the present research, the niche- and neutral-based ecological processes governing common and rare benthic diatoms were analysed. For this purpose, a total of 100 sampling sites in the Danube catchment (Hungary and Croatia) were investigated in spring and autumn 2022. The study (i) analysed the extent of environmental and spatial processes contributing to the distribution of rare (small population size, habitat specialist, geographical restricted, and absolute rare encompassing all the three types) and common species; moreover (ii) identified the constraining variables. Our findings revealed that the distribution patterns of rare species characterized by small population sizes are generally more distinct from other types of rarities, and are similar to that of the common species. All types of rare species exhibited marginal environmental optima and narrow tolerances, yet both environmental and spatial processes determine their distributions at similar extents. The explanatory power of the background variables was lower for rare species, and notable differences were found in the key parameters

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affecting them (fine to large spatial scales, temperature, conductivity, N and P forms) compared to common species (large spatial scale, temperature, conductivity, silica). The results of the present research highlight the need to define and investigate rarity in different ways, to consider spatial and environmental processes together, and to develop new statistical approaches.

1. Introduction

Biodiversity has been a central focus of numerous ecological studies and theories for a long time (e.g. MacArthur, 1965). Nowadays, understanding the drivers of the community structure is even more crucial due to the rapid biodiversity loss caused, for instance, by habitat degradation and fragmentation (e.g. Fischer and Lindenmayer, 2007; Krauss et al., 2010; Brauer and Beheregaray, 2020).

Natural communities typically consist of only a few common and many rare species. Despite the early evidence that rare species make up the majority of species richness (e.g. Williams, 1964), they are often routinely removed from datasets before ecological analyses are conducted (Jousset et al., 2017). This is justified on the grounds that rare species are often considered to have little contribution to community analyses, they are merely source of statistical noise, cause bias in multivariate analyses and lead to low levels of explained variation (e.g. Cao et al., 1998; Clarke and Green, 1988; Székely and Langenheder, 2014). This approach has been criticized by many researchers since it can result in the loss of valuable information (Blackburn et al., 1990; Fore et al., 1996). Consequently, our current understanding is focused primarily on the dominant species, with limited knowledge about the rare species, particularly regarding their ecological preferences. Rare species play significant ecological roles e.g. in ecosystem functions, stability, resilience and resistance (e.g. Walker et al., 1999; Lyons and Schwartz, 2001; Lyons et al., 2005; Shade et al., 2014; Leitão et al., 2016; Jousset et al., 2017). Thus, identifying the drivers shaping their distribution facilitates and their conservation is of prime importance. Rare species are expected to have a particularly high risk of extinction (Purvis et al., 2000), making this research area even more urgent.

Traditionally, biodiversity has been studied using two fundamental approaches: the niche- (Hutchinson, 1957) and island biogeography theories (MacArthur and Wilson, 1967), which refer to environmental/niche-related and dispersal/spatial/neutral processes, respectively. However, in ecological studies, the niche-related processes were considered to be determinant allocating a major role to environmental conditions in species distribution. In contrast, the neutral processes - expecting a substantial role of dispersal dependence - were overlooked until the 1990s (Tokeshi, 1990; Legendre, 1993). The emergence of metacommunity theory was essential for synthesising and combining these two processes of species distribution (Leibold et al., 2004; Logue et al., 2011).

Common and rare species tend to differ in various aspects including environmental preferences (e.g. Magurran and Henderson, 2003; Lennon et al., 2011; Sgarbi and Melo, 2018) and consequently the mechanisms shaping their distribution (e.g. László et al., 2014; Bispo et al., 2017; Tsang and Bonebrake, 2017). Despite highlighting the importance of integrating the niche (environmental filters) and neutral (e.g. dispersion) theories in order to describe these potential differences (Cottenie, 2005; Bispo et al., 2017; Hu et al., 2018), comparing the response of rare and common species to niche and neutral factors has been seldom investigated. No general consensus has been found about their community assembly mechanisms. The question is whether the distributions of rare and common species have similar patterns (e.g. Siqueira et al., 2012; Alahuhta et al., 2014) or remarkably different (e.g. Bispo et al., 2017; Iop et al., 2024). The answer appears to differ depending on the studied taxa (Heegaard et al., 2013, van Proosdij et al., 2016).

Previous ecological studies focusing on rarity investigated aquatic bacteria (Zhao et al., 2023; Malazarte et al., 2024), macrophytes (Alahuhta et al., 2014), macroinvertebrates (Heino and Soininen, 2010; Siqueira et al., 2012; Rádková et al., 2014), terrestrial invertebrates (Pandit et al., 2009), anurans (Iop et al., 2024), butterflies (Tsang and Bonebrake, 2017) and trees (Bispo et al., 2017; Hu et al., 2018), whilst numerous taxa have remained unexplored. Moreover, rarity can be defined in many ways (e.g. in terms of the population size or geographic distribution) determining the main ecological processes affecting them, the extent of their contribution to community structure (e.g. Stenger-Kovács et al., 2025) and the degree of extinction risk (Harnik et al., 2012). In general, rare species are more vulnerable than common species, but this depends on rarity types: species with small populations are threatened by demographic, environmental, and genetic stochasticity (Simberloff, 1986); habitat specialists (species with narrow tolerance for habitat conditions) are vulnerable to environmental discrepancies; and geographically restricted species are threatened by a wide range of factors, such as dispersal (e.g. insufficient dispersal ability, habitat alteration and loss), competition, disturbances, and environmental preferences (having particular conditions/special ecotype to survive and reproduce; e.g. Harnik et al., 2012; Leitão et al., 2016). Overall, the degree of extinction risk is influenced as follows: geographic range plays a primary role, habitat breadth a secondary role, and local abundance only a tertiary one (Nogueira et al., 2010; Harnik et al., 2012). Nevertheless, the detailed and comprehensive investigation of the "rare biosphere", even if defined in different ways, has been missing.

Benthic diatoms carry important ecological roles since they significantly contribute to numerous ecosystem services (B-Béres et al., 2023). Our current knowledge about these important organisms has been very limited regarding the research on rare species within a metacommunity framework. Traditionally, diatom communities are considered to be driven primarily by abiotic environmental variables (Soininen et al., 2004). However, recent studies revealed the importance of spatial processes shaping their distribution (e.g. Pajunen et al., 2016; Soininen and Teittinen, 2019; Szabó et al., 2019; Blanco et al., 2020), but differentiation between rare and common species is very scarce and based on only a single definition of rarity (Heino and Soininen, 2010; Ovaskainen and Soininen, 2011; Soininen et al., 2019; Fuß et al., 2025). Since the differentiation in rarity types is very important (e.g. their different ecological roles and extinction risk), the present study defined rare species in different ways, thus using different rarity types (geographic distribution, population size, habitat specialization) following Rabinowitz's approach (Rabinowitz, 1981). Then, the assembly rules in

common and variously defined rare benthic diatoms were investigated by integrating the niche- and neutral-based ecological theories. The present research addressed the following specific questions and hypotheses:

(1) What are the differences in the environmental and/or spatial factors that determine common and rare species? According to our hypothesis, neutral processes are expected to dominate over niche processes for common species, because of their generally broad environmental tolerances. For rare species, niche and neutral processes are hypothesized to have similar importance because of their dispersal limitation and their narrow ecological tolerance.

(2) Do different rarity types have different ecological drivers? Based on our hypothesis, the relative importance of niche and neutral processes is not expected to differ among the rarity types. However, significant differences are anticipated in the key environmental and spatial factors driving the distribution of these species, as they are defined according to different criteria.

2. Material and methods

2.1. Study area, sampling and preparation of samples

The study was conducted in lotic environments of the River Danube catchment (Central Europe). Samples were taken from 50 sites in Hungary and 50 sites in Croatia (Fig. 1). The Hungarian study sites are influenced by the oceanic, continental and Mediterranean climate, whilst there are three main climate zones in Croatia, namely continental, mountain and coastal climate. These differences in climates lead to highly variable weather conditions in the studied area with a mean temperature of 8–13 °C, and a mean annual precipitation of 500–2255 mm.

The sampling was performed twice in 2022 (spring and autumn) collecting altogether 200 samples. Finally, 183 samples had

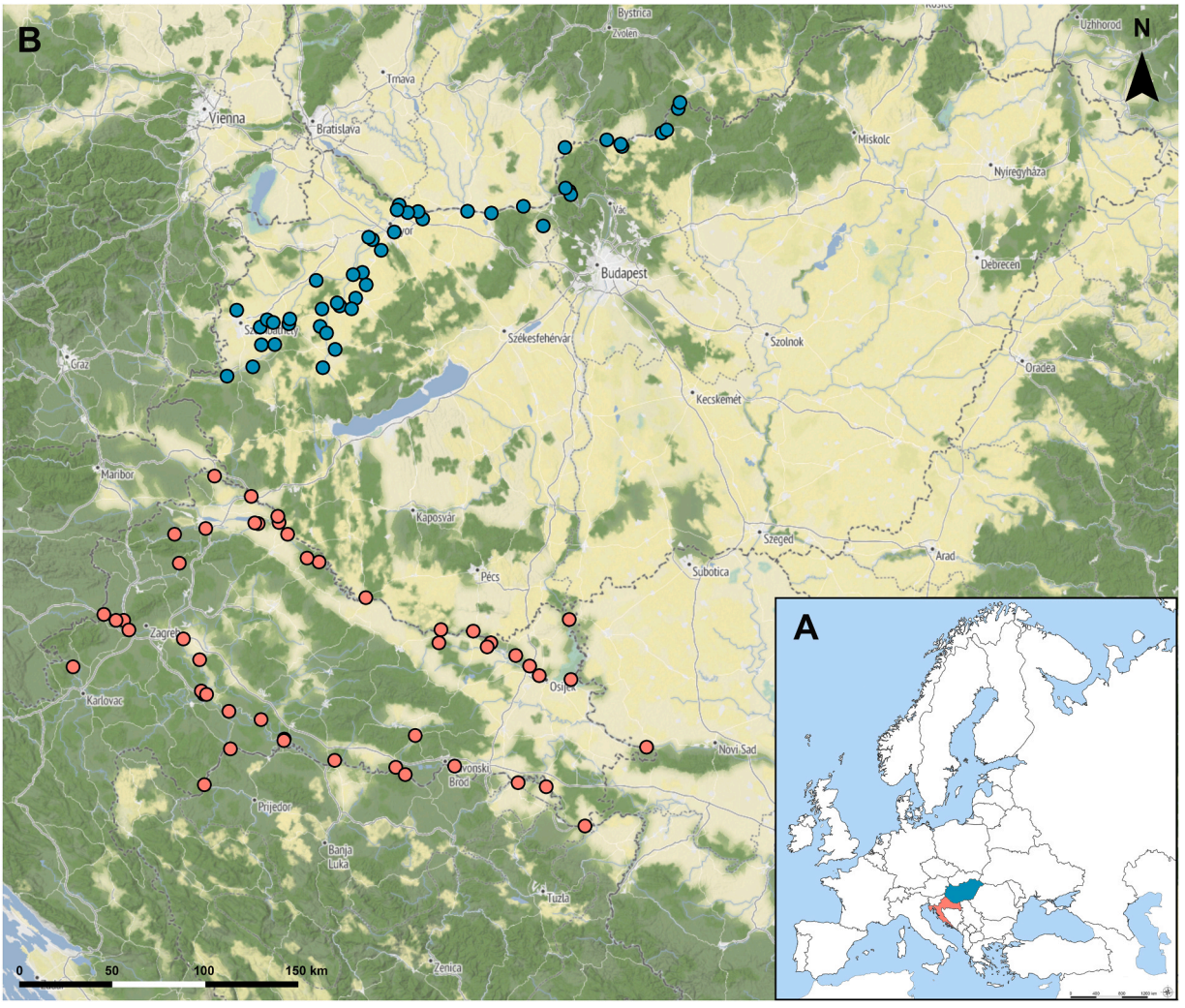

Fig. 1. – Sampling sites of the River Danube network system in Hungary (blue dots) and Croatia (red dots).

adequate quality for subsequent laboratory processing and analyses. These samples were treated as independent in the analyses.

During each sampling campaign, water temperature (°C), pH, conductivity (μS cm^{-1}), oxygen saturation (%) and dissolved oxygen (mg L^{-1}) were measured *in situ* using a portable multimeter (Hach Lange, HQ40d). In the laboratory, the contrations of inorganic nitrogen, (in forms of nitrite-N [μg L^{-1}], and ammonium-N [mg L^{-1}]), soluble reactive phosphorus (SRP, μg L^{-1}), total phosphorus (TP, μg L^{-1}), sulphate (mg L^{-1}) and soluble reactive silica (SRSi, mg L^{-1}) were determined using spectrophotometric methods, following (APHA, 2005). Chloride content (mg L^{-1}), chemical oxygen demand (COD, mg O_2 L^{-1}) as well as alkalinity were measured using titrimetric methods (APHA, 2005). Concentration of nitrate-nitrogen (mg L^{-1}) was determined with an HQ40d multimeter equipped with an ion-specific probe (Hach Lange, Model ISENO3181) and was added to total inorganic N concentrations determined (see above) by titrimetry.

Benthic diatom communities were collected from the most characteristic substrates and were preserved in ethanol until their preparation. Diatom valves were cleaned using a hot hydrogen-peroxide method (CEN, 2003), and embedded in Naphrax resin. A total of 400–415 diatom valves were carefully identified at species level under a light microscope (Zeiss Axiovert 1, 1000x magnification, plan-apochromat lens with DIC) using up-to-date taxonomic books (e.g. Lange-Bertalot, 2020; Bey and Ector, 2013).

2.2. Statistical analyses

Diatom species were classified as rare or common based on their population size, habitat specificity and geographic range following Rabinowitz's approaches (Rabinowitz, 1981). For their separation, rarity indices (PSI: population size index, HSI: habitat specificity index, GRI: geographical range index; Maciel, 2021) were calculated. Additionally, absolute rare species were defined using the median values of these three indices. Equations applied for the indices' calculation were summarized in Table 1. The values of indices range from 0 (meaning common) to 1 (meaning rare), where a threshold of 1.00 (0.995 due to rounding) was applied to classify rare species. Finally, five species groups were identified and used for statistical analyses: small population species (SP), habitat specialists (HS), geographically restricted species (GR), absolute rare species (AR) and common species, which served as a complement to the four rare species group.

Distance-based Moran's Eigenvector Maps (dbMEMs, Dray et al., 2012; Legendre and Legendre, 2012) were created to analyse the spatial structure of the dataset. Only the MEMs with positive spatial autocorrelations were included in subsequent multivariate analyses. After visually examining their semi-variograms (by comparing the range and the values of the sill and the corresponding log distance) and spatial distribution (Fig. 2), the spectral decomposition they presented was categorized into three main groups: broad-scale (MEM 1–8), medium scale (MEM 9–20), and fine-scale (MEM 21–30). Prior to analysing the environmental factors, data transformations were applied to improve normality. A $\log_{10}(x)$ transformation was used for nitrate, nitrite, soluble reactive phosphorus and sulphate, whilst a sqrt(x) transformation was applied to total phosphorus and ammonium.

Variation partitioning was employed to distinguish the pure and shared effects of the groups of explanatory variables (environmental and spatial factors) on each type of diatom species group composition. Ecological niches of each species were determined by outlying mean index (OMI) analyses (Dolédec et al., 2000) with a Monte-Carlo test (1000 random permutations). Two niche parameters were calculated: niche position (NP) representing the habitat conditions utilized by a species, and niche breadth (NB) indicating the species' tolerance to environmental conditions. After the exclusion of zero values, pairwise Welch's tests were conducted to compare the niche breadth and niche position across the species groups. Distance-based Redundancy Analysis (dbRDA; McArdle and Anderson, 2001) was used to investigate the relationship between diatom species and the spatial and environmental variables. The dbRDA analyses were conducted using presence/absence data and Jaccard dissimilarity indices. These methods were recently applied in ecological studies focusing on rarity (e.g. Juračka et al., 2019, Liu et al., 2021; Pearman et al., 2022), and they introduce a low-to-medium degree of bias when weighting community data compared to usage of abundance data and Bray-Curtis dissimilarity indices (Cao et al., 1997). To assess the significance of each constraint involved in the dbRDA, anova.cca function in the 'vegan' R package with the setting of 'by = term' was performed using 999 permutations.

All statistical analyses were performed in R statistical software (4.4.0 version, R Core Team, 2024) using the 'vegan' (Oksanen et al., 2024), 'ade4' (Dray et al., 2023), 'adespatial' (Dray et al., 2024), 'adegraphics' (Siberchicot et al., 2017), 'subniche' (Karasiewicz et al., 2017), circlize (Gu et al., 2014) packages.

3. Results

The measured environmental variables are summarised in Table 2. Across sampling periods, the water temperature varied between

Table 1
– The equations used for the calculation of the rarity indices (Maciel, 2021).

Index	code	Equation	Explanations
population size	PSI	$1/p_{max}$	p_{max}: maximum population of a species
habitat specificity	HSI	$1/h_{max}$	h_{max}: maximum habitat number
geographical range	GRI	$1/\{[(lat_{range})*(long_{range})]+c\}$	lat_{range}: range of the two extreme latitude points of a species; $long_{range}$: range of the two extreme longitude points of a species. c: constant, c= 1
absolute rare	AR	med(PSI,HIS,GRI)	

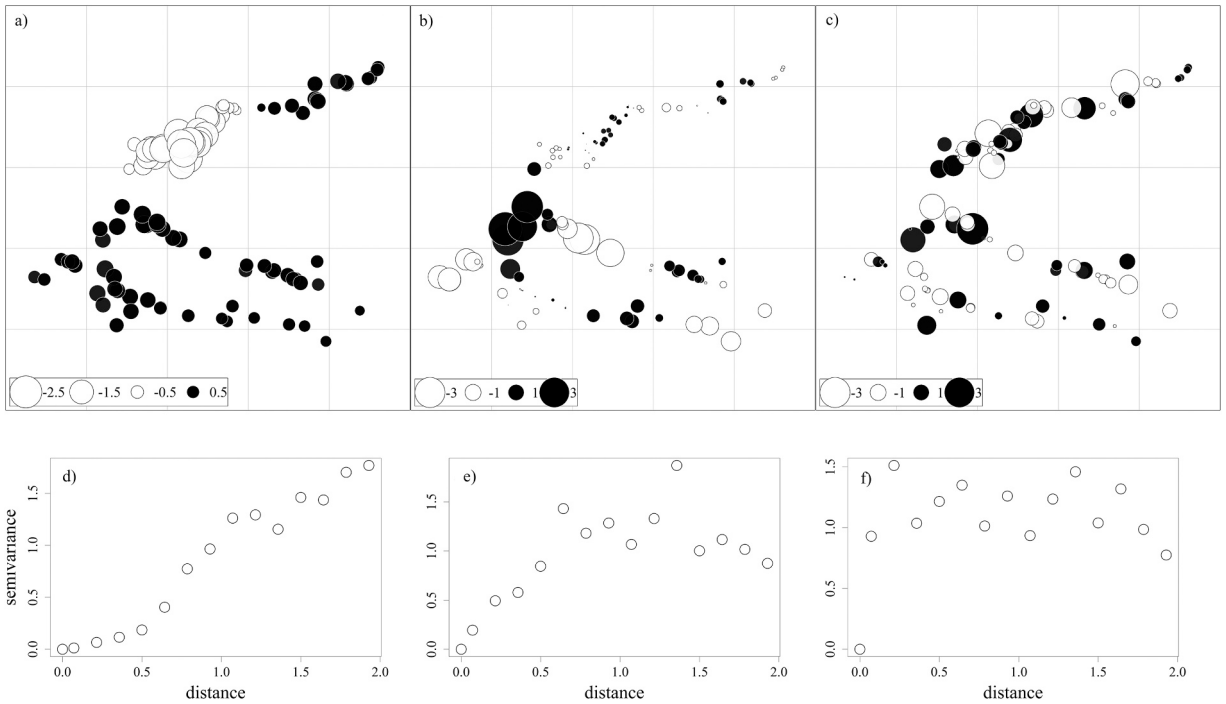

Fig. 2. – Distance-based Moran's eigenvectors maps (a-c; the colour and size of symbols represent site scores, as indicated in the legend below graphs) and their semi-variograms (d-f; where the lower the variances, the more similar the samples are to each other) describes the three main spatial scales (a,d: large presented by the example of MEM1; b,e: medium presented by the example of MEM11; c, f: fine presented by the example of MEM30).

6 and 22 °C with a mean of 14.2. Dissolved oxygen content varied over a wide range (0.5–18.8 mg L^{-1}), similar to the oxygen saturation (4.9–194.8 %). The mean pH was 8.3 ± 0.3. The lowest conductivity was 200 μS cm^{-1}, and the highest was 1628 μS cm^{-1}. The sampling sites were characterised by a dominance of hydrogen-carbonate (228.3 ± 85.6 mg L^{-1}), whilst carbonate was zero at all sites. On average, the concentration of sulphate ions (44 mg L^{-1}) was almost twice as high as that of chloride ions (27.8 mg L^{-1}). The two forms of P varied over a wide range (TP: 0–1840 μg L^{-1}, SRP: 1–818 μg L^{-1}). Nitrate was predominant among the nitrogen forms (mean value: 3.1 mg L^{-1}). The concentration of SRSi was relatively high (mean: 4.8 mg L^{-1}), it varied from 0 to 15.4 mg L^{-1} during the study period.

Altogether 409 diatom species belonging to 84 genera were identified during the study. On the basis of the rarity indices, 205 species were common (e.g. *Achnanthidium minutissimum*, *Nitzschia dissipata*) and 204 can be regarded as rare. With regard to Rabinowitz's rarity categories, altogether 193 species had small population size (SP), 91 were habitat specialists (HS), and 96 were geographically-restricted (GR). A total of 94 species could be regarded as absolute rare (AR). Table 3 shows the overlaps between these

Table 2
– Physical and chemical parameters measured in the studied lotic ecosystems (SD: standard deviation, CV: coefficient of variation, d.l.: detection limit, DO: dissolved oxygen, COD: chemical oxygen demand, TP: total phosphorus, SRP: soluble reactive phosphorus, SRSi: soluble reactive silica).

Variables	Unit	Sample size	Minimum	Maximum	Mean	SD	CV
Temperature	°C	183	6.2	21.8	14.2	2.8	19.5
Conductivity	μS cm^{-1}	182	200	1628	578	273	47.3
DO	mg L^{-1}	183	0.5	18.8	9.7	2.1	22.1
Oxygen saturation	%	181	4.9	194.8	94.3	22.6	24.0
pH		183	7.1	9.1	8.3	0.3	4.2
COD	mg L^{-1} O_2	183	0.1	13.1	3.0	2.4	80.1
HCO_3^-	mg L^{-1}	183	128.1	600.9	228.3	85.6	37.5
Cl^-	mg L^{-1}	180	2.0	127.2	27.8	25.1	90.3
SO_4^{2-}	mg L^{-1}	183	1.0	344.7	44.0	55.7	126.7
TP	μg L^{-1}	178	< d.l.	1839.4	149.8	251.6	167.9
SRP	μg L^{-1}	183	1.5	817.7	59.2	116.1	196.1
NH_4^+-N	mg L^{-1}	180	< d.l.	4.1	0.1	0.4	379.7
NO_3^--N	mg L^{-1}	183	0.5	19.0	3.1	3.0	97.2
NO_2^--N	μg L^{-1}	183	0.8	234.0	17.3	22.0	127.0
SRSi	mg L^{-1}	183	< d.l.	15.4	4.8	3.1	65.1

species groups using standard operations of mathematical sets. The whole species list and their rarity categories are involved as a supplementary material in Stenger-Kovács et al. (2025).

The result of the variation partitioning (Fig. 3) indicated that the pure effects of the groups of explanatory variables (environmental and spatial), along with their shared effects, were equally important in explaining the variation in common species. For rare species with small population size, their distribution was primarily influenced by the shared effects of the two groups of the explanatory variables, followed by the pure effects of the spatial and then environmental variables. The occupancy of the habitat specialists, geographically restricted and absolute rare species were explained exclusively by the pure effects of spatial and environmental factors. Nevertheless, a significant proportion of variation in species composition (81–98 %) remained unexplained by the variables examined in this study.

The OMI analysis showed that rare and common species significantly differ in their niche characteristics based on the Welch tests (Fig. 4a, b). Regardless of the rarity type, rare diatoms had high NP and low NB values (with the exception of HS, because all species classified to this group are singletons and the calculation of their niche breadth is ecologically not meaningful), hence, occupying marginal niche positions and narrow niches. In contrast, the common species occupied a non-marginal position (low NP) and broad niches (high NB).

As a result of the dbRDA analysis (Table 4), the cumulative importance of Axis 1 and Axis 2 significantly differed among the species groups. The common and small population-sized species (SP) were similar to each other, as Axis 1 and Axis 2 together explained 29.8 % and 26.9 % of the variance in their occupancy, respectively. Both species groups were primarily determined by conductivity, temperature, concentration of dissolved oxygen, SRSi, sulphate and chloride ion, as well as by MEMs 1–8 describing large spatial patterns. Additionally, small population-sized species were also affected by nitrate concentration and showed spatial patterns at medium large scale (MEM 14, 19). The habitat specialists, geographically restricted and absolute rare diatom species exhibited greater similarity to each other: their occupancies were explained to a lower extent by the two axes of the dbRDAs (4.6 %, 9.6 % and 9.6 %, respectively). Regarding the habitat specialist diatom species, the most important variables were the concentration of dissolved oxygen, ammonium, sulphate, phosphorus forms (TP, and SRP) and spatial factors (MEMs >13) representing medium-fine spatial patterns. The occupancy of geographically restricted and absolute rare diatom species were mainly explained by temperature, conductivity, concentration of nitrite, ammonium, sulphate, chloride and SRP. Furthermore, these species groups showed spatial patterns at all the three spatial scales (from fine to large scales, MEM 1–28).

4. Discussion

To combine effects of spatial and environmental factors was recommended for studying the differences between the assembly patterns of rare and common species (e.g. Bispo et al., 2017; Hu et al., 2018) as the extent of their contribution is expected to differ. The results of these studies tend to be highly dependent on the studied group of organisms (Heegaard et al., 2013; van Proosdij et al., 2016) and the attention has been rarely paid to benthic diatoms. Identifying the ecological processes that determine the distribution of diatom species is of prime importance, especially due to their significant contribution to ecosystem functions (B-Béres et al., 2023). Therefore, the present study is addressed to provide valuable and missing information about the rare and common benthic diatom species and the processes determining their distribution in lotic ecosystems.

In contrast to our hypothesis but consistent with other studies focusing on entire lotic diatom communities (e.g., Soininen and Weckstrom, 2009; Virtanen and Soininen, 2012), the importance of niche-related processes (environmental parameters) and neutral processes (spatial scales) was found to be equivalent in shaping the composition of common diatom species. However, this pattern contradicts most studies on rarity. In macroinvertebrate communities, environmental factors explained most of the variation in community composition regardless of species commonness (Siqueira et al., 2012; Rádková et al., 2014; Sgarbi and Melo, 2018), and spatial processes explained only a small or non-significant proportion of community variation (Iop et al., 2024). Spatial processes became more important than niche-related processes only in cases of common tree species (Hu et al., 2018), aquatic invertebrates (Pandit et al., 2009), and bacterial communities (Zhao et al., 2023; Malazarte et al., 2024).

Regarding the niche-related processes, common diatom species are associated with non-marginal niche and broad tolerance with regard to the environmental conditions. Therefore, common species tend to be relatively unresponsive to environmental variation (Lennon et al., 2011), and probably have high resistance to disturbances (reviewed by Cao et al., 2001). These attributes could be particularly expressed and competitive in streams and rivers, which are highly dynamic ecosystems and are naturally subjected to severe disturbances and/or stress (e.g. Stanley et al., 2010). But, due to their wide-range tolerance of environmental conditions,

Table 3
– The number of diatom species found in the different categories of rarity with some examples (SP: small population, HS: habitat specialist, GR: geographically restricted, AR: absolute rare) according to standard operations of sets.

Overlaps	Species number	Examples
SP	108	*Nitzschia communis, Simonsenia delognei*
HS	0	-
GR	2	*Amphora minutissima, Fragilaria austriaca*
SP ∩ HS	0	-
SP ∩ GR	0	-
GR ∩ HS	0	-
SP ∩ HS ∩ GR (=AR)	94	*Mayameae agrestris, Placoneis gastrum*

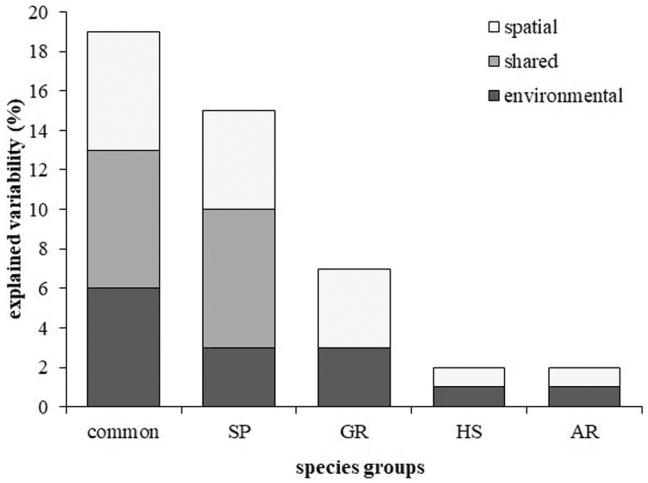

Fig. 3. – Partitioning of variation in the composition of diatom species belonging to different rarity categories (SP: small population, HS: habitat specialist, GR: geographically restricted, AR: absolute rare, and common) between the two groups of explanatory variables (spatial and environmental). Individual and shared fractions are shown as percentages of total variation on the basis of adjusted R^2 values.

common species can be assembled also by dispersal-related mechanisms (Pandit et al., 2009; Rádková et al., 2014). Thus, in view of metacommunity theory, common species may colonize a number of patches via mass effects as they have more propagules (Muscarella and Fleming, 2007; Leboucher et al., 2020). Mass effects can become more important at smaller spatial scales (e.g. Ng et al., 2009), a theory supported by our results, since common diatoms showed spatial patterns only at large scales, which may require more time to occupy.

Similarly to the common species, the rare diatom species were also governed by a mix of niche- and neutral-based processes in accordance with our hypothesis. Both ecological processes were also found to be important for common and rare aquatic macroinvertebrates (Heino and Soininen, 2010; Siqueira et al., 2012), macrophytes (Alahuhta et al., 2014), zooplankton and phytoplankton (Heino and Soininen, 2010) and microbes (Lynch and Neufeld, 2015). However, in some cases, niche processes (e.g. Liao et al., 2017) or neutral processes (e.g. Iop et al., 2024) prevailed.

Rare species are considered to differ from common ones in their environmental requirements and tolerances (e.g. Walker et al., 1999; Lennon et al., 2011). On the basis of our results, rare diatom species unequivocally occupied marginal and narrow ecological niches similar to rare bacteria (Malazarte et al., 2024) or grassland species (Lennon et al., 2011). Rare species could be considered as habitat specialists favouring habitats with special physical and chemical characteristics, which makes it difficult for them to find and colonise environmentally suitable patches (Horsák et al., 2012). Thus, the presence of marginal habitats is a strong determinant of the rarity in agreement with Sgarbi and Melo's (2018) conclusion. Rare species can occupy key niches providing them an outstanding ecological role (Stenger-Kovács et al., 2025), for instance, they can slow down establishment of invasive species (van Elsas et al., 2012; Vivant et al., 2013). Due to strong environmental selection, rare species are generally highly vulnerable to shifts in environmental conditions and face a high risk of extinction (Harnik et al., 2012; Lennon et al., 2011). Despite diatom communities are traditionally considered to be primarily driven by local environmental parameters (Soininen, 2007), recent studies indicated their dependence on climate-related variables (Pajunen et al., 2016; Soininen and Teittinen, 2019), thus their combined study at different spatial scales is recommended. Taxa with active dispersal ability have been frequently observed to be less spatially structured than taxa with passive dispersal mechanisms (e.g. Rádková et al., 2014; Curry and Baird, 2015), such as diatoms. In accordance with our results, stream diatoms were often shaped by dispersal-related processes at regional scales (e.g. Bottin et al., 2014; de Oliveira et al., 2020). Additionally, neutral processes can become determinant due to drift caused by demographic stochasticity (Magurran and Henderson, 2003).

The importance of both ecological processes is supported in shaping rare and common diatom species, but the important explanatory variables differed between them, confirming that common and rare diatom species represent ecologically distinct groups within a metacommunity. The distributions of common species were affected by environmental gradients (such as conductivity, temperature, concentration of sulphate and chloride), which are closely related to human-induced global change (e.g. Dokulil, 2014; Stenger-Kovács et al., 2023). This environmental differentiation is reflected in the spatial patterns too, since common species were affected by large spatial scales. Additionally, SRSi was also a key determinant, which is essential for the development and maintenance of the large populations (Giri et al., 2022). Rare species are assumed to respond to different gradients than common species; probably to more local factors or less determinant parameters of the community composition (Cao et al., 2001). For instance, less abundant herbs and shrubs were found to be related to less determinant factors (e.g., swampy vs. non-swampy habitats) rather than to major environmental gradients (e.g. seasonal moisture, soil types; Webb et al., 1967). Based on our results, small population-sized (SP) diatoms form a transition between the common and the other rarity categories of diatom species. These species are influenced by the same parameters as common species, but there are also other determinant factors that are specific to other rare species (e.g. nitrate, medium spatial scale). Habitat specialist diatoms were affected by fine spatial scale and many environmental factors (e.g. phosphorus

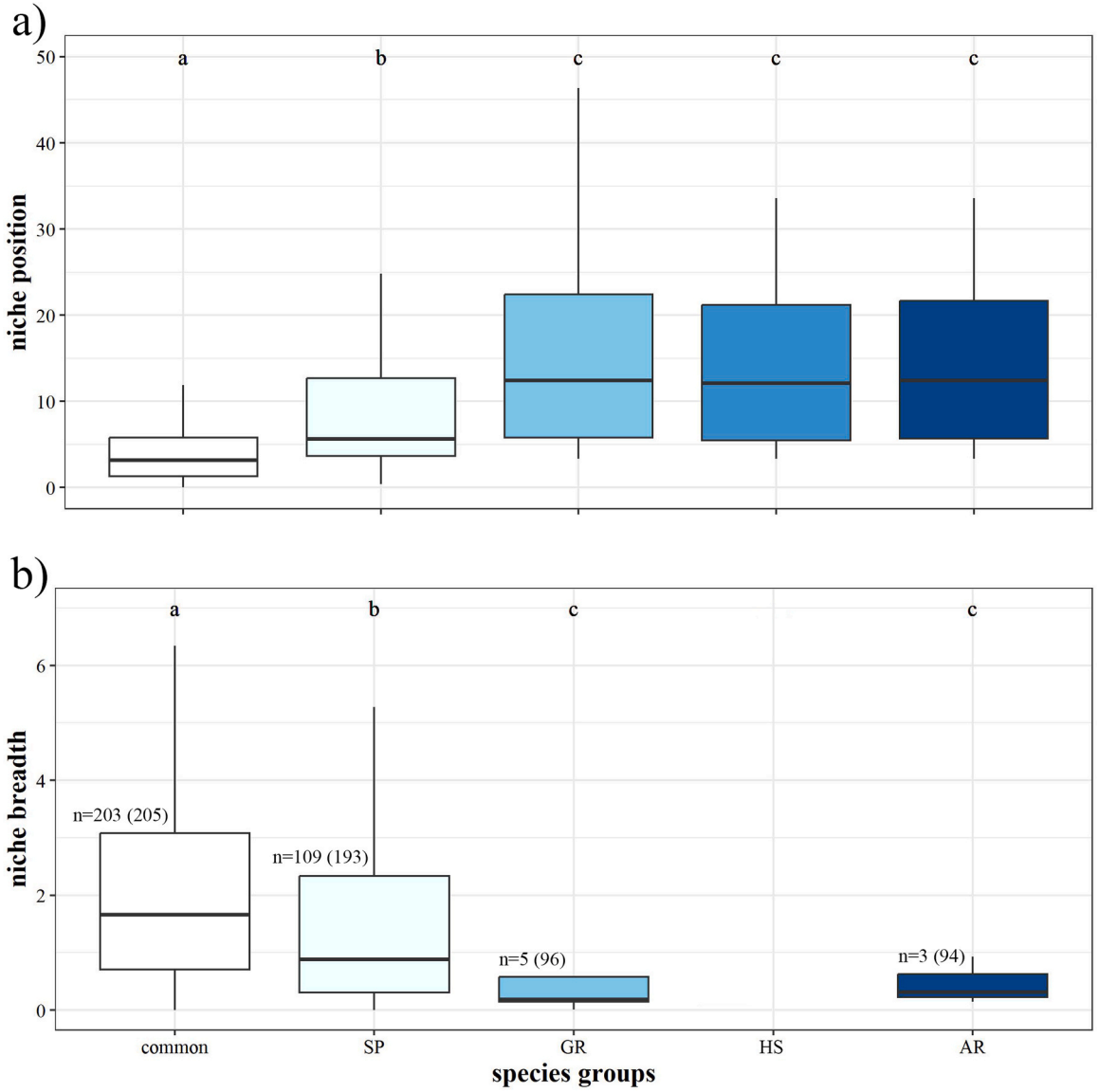

Fig. 4. – Boxplots represent the differences in the niche position (a) and niche breadth (b) among each diatom species group (SP: small population, HS: habitat specialist, GR: geographically restricted, AR: absolute rare, and common). Letters above the boxplots mark significant differences obtained by Welch's tests (same letters mean statistical indifference, whereas different letters mean significant differences). The niche breadth of HS was excluded, since all species classified to this group are singletons whose niche breadth is ecologically meaningless to calculate. The species number included in the calculation of the niche breadth were also marked above the boxplots, where numbers in the bracelets mean the total species number per each group.

forms, ammonium content). The geographically restricted and absolute rare diatom species showed spatial patterns from fine to large scales. In summary, we recommend a detailed study of different rarity categories, since their distribution can be driven by different ecological variables. These species can also differ in their response to extinction risks (Harnik et al., 2012). Therefore, detailed knowledge of these species is crucial for nature conservation.

A large part of the observed variation in rare diatoms remained unexplained (80 %>), similar to many other metacommunity studies (e.g. Beisner et al., 2006; Bispo et al., 2017, Iop et al., 2024). Possible reasons for this low-level explanation could be that rare species are affected by complex and difficult-to-measure variables (e.g. biotic interactions, topography, habitat heterogeneity), or they are stochastically assembled (e.g. Lennon et al., 2011; Székely and Langenheder, 2014; Markham, 2014; Bispo et al., 2017). Both the demographic stochasticity and the patch stochasticity can lead to spatial and temporal drift in the community (Leibold and Chase, 2018). In addition, species interactions (e.g. competition) can explain even 50 % of the entire variance (Leibold and Chase, 2018). Our study is based on only two sampling campaigns, thus the limitation of lower sample size can also contribute to the low explained variance. Furthermore, different methods (PCNM, MEM, AEM) can be used to study spatial distribution, of which MEM is still the most

Table 4
– Results of the dbRDAs analysis present the relationship between the occupancy of the common, small population (SP), habitat specialist (HS), geographically restricted (GR), absolute rare (AR) diatom species and the measured environmental (DO: dissolved oxygen, TP: total phosphorus, SRP: soluble reactive phosphorus, SRSi: soluble reactive silica) and spatial explanatory variables (Moran's eigenvectors, MEM 1–30).

		Common			**SP**			**HS**			**GR**			**AR**		
p values for dbRDAs			0.001			0.001			0.048			0.01			0.046	
explained variation (%)		dbRDA1 16.2	dbRDA2 10.7	p	dbRDA1 21.7	dbRDA2 8.1	p	dbRDA1 2.3	dbRDA2 2.3	p	dbRDA1 5.7	dbRDA2 3.5	p	dbRDA1 5.7	dbRDA2 3.5	p
Environmental parameters	Temperature	0.56		***	0.46		***	-0.19		*	-0.31		**	-0.31	0.19	**
	DO		-0.43	***		-0.39	**	-0.21		*						
	Conductivity	-0.61	0.55	***	-0.60	0.29	***					0.42	**		-0.41	**
	NH_4^+-N							0.25		*	-0.26		*	-0.27		*
	NO_3-N				-0.59		***				0.19		*	0.19		*
	SO_4^{2-} -N	-0.80		***	-0.68		***	-0.18		*		0.43	**		-0.39	**
	Cl^-		0.37	**								0.28	*		-0.32	**
	SRP							0.26		*					-0.29	*
	TP							0.29		*						
	SRSi	-0.63		**	-0.55		**									
Large spatial scale	MEM1	0.43	-0.45	***	0.25	-0.23	*					-0.57	*		0.56	**
	MEM2	0.15		*		0.32	**				-0.63		***	-0.63		**
	MEM3		0.33	***												
	MEM4	-0.63	-0.21	**		-0.32	*									
	MEM5		-0.34	***												
	MEM7	0.20		*	0.36		**									
	MEM8				0.25	0.30	*									
Medium spatial scale	MEM9										-0.41		*	-0.41		**
	MEM14				0.27		*		0.13	*	0.30	-0.23	*	0.31	0.22	*
	MEM16										0.31	-0.16	*	0.31		*
	MEM18								0.26	*						
	MEM19					0.27	*	-0.25		*						
	MEM20								-0.62	***						
Fine spatial scale	MEM21								-0.32	**	0.23		*	0.23		*
	MEM22							0.37	0.14	*						
	MEM25											-0.18	*		0.16	*
	MEM26							-0.29		*						
	MEM28							0.36	-0.36	**		0.31	*		-0.33	**
	MEM29								-0.19	*						

frequently used analyses for rivers and streams. This method was applied here due to comparability despite its potential limitation; it can oversee spatial patterns of community structure which are produced by directional spatial processes such as passive unidirectional dispersal downstream the river network (Blanchet et al., 2008; Liu et al., 2013). Additionally, the spatial and environmental variables included in the applied statistical analyses strongly affect the contribution of niche- and neutral-based processes to community assembly (Chang et al., 2013). For instance, involving insufficient environmental variables in variation partitioning can overestimate the importance of spatial processes (Smith and Lundholm, 2010). The results of the present research highlight the need to consider spatial and environmental processes together. However, the investigation of rarity cannot be fully successful using traditional and currently most commonly used methods, and new approaches are needed.

CRediT authorship contribution statement

Ruqayah Ali Grmasha: Writing – review & editing, Investigation. **Katalin Hubai:** Writing – review & editing, Investigation. **Viktória B-Béres:** Writing – review & editing, Investigation. **Marija Gligora Udovič:** Writing – review & editing, Investigation. **Judit Padisák:** Writing – review & editing. **Géza B. Selmeczy:** Writing – review & editing, Investigation. **Dunja Jurina:** Writing – review & editing, Investigation. **Edit Király:** Investigation. **Rita Zsuga-Biró:** Resources, Project administration, Investigation, Data curation. **Edina Lengyel:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Csilla Stenger-Kovács:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Bassam Abubaker:** Investigation. **Kálmán Tapolczai:** Writing – review & editing, Investigation.

Ethics Statement

X Not applicable: This manuscript does not include human or animal research.
☐If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

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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.

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Data availability

The authors do not have permission to share data.

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