

## RARE TRAITS OF DIATOMS

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**Abstract:** Rare species is a central topic of conservation biology. Nevertheless, we do not have enough knowledge about their characteristics which can lead to their extinction. For this purpose, this study aimed to establish a diatom trait database (morphological and lifeform traits, a total of 142) and identify rare traits. The developed database contains 13,162 records for diatom species of the Danube catchment area in Hungary and Croatia. Using Rabinowitz's original approach and applying new rarity indices published in the literature, rare diatom traits were determined in different terms. 75% of diatom traits were common features, while 25% of these were small population-sized traits. They were exclusively morphological characteristics of diatoms (four chloroplasts per cell, five different chloroplast shapes and larger size categories) exhibited predominantly by rare species. 7% of the total traits were absolute rare (small population-sized, habitat specialists and geographically restricted at the same time) traits. Namely, nine big size categories and two chloroplast shapes, which were associated with the special conditions provided by the Sava, Drava, and Odra Rivers in Croatia and the Rába in Hungary. Rare species with these unique traits are functionally distinct and vulnerable members of the communities.

**Key words:** diatoms, lifeforms, morphological features, rarity, traits

## INTRODUCTION

To investigate or even to find rare species is a challenge even in the case of organisms visible to the naked eye, not to mention the microscopic ones. For this reason, ecological studies and consequently ecological knowledge about rarity is limited. In aquatic ecosystems, it is especially true for algae. Judit Padisák was

the first ecolimnologist who recognised the ecological importance of rare algal species already in the 1990's. She used an unusual quantity measure to identify rare phytoplankton species, the relative frequency (PADISÁK 1992). In her first study on rarity, she found that around half of the planktic algal species are rare, which is also characteristic in benthic diatoms, revealed by a recent study on regional scale (STENGER-KOVÁCS *et al.* 2025). PADISÁK (1992) also noted that the number of the samplings fundamentally influences the detection of rare species (PADISÁK *et al.* 2010) beside the sampling design (SPECHT *et al.* 2017) and the classification method of a species into the categories of commonness and rarity (NISLOW *et al.* 2011). Moreover, she highlighted that rare species cannot be neglected for understanding ecological processes (PADISÁK *et al.* 2010). Detailed knowledge about these silent species would be crucial, since these species in certain environmental changes can become common or even invasive, therefore, rarity, commonness, and biological invasions must be handled together (PADISÁK *et al.* 2010). However, the significance of rare species among algal ecologists has just been recognised and the journey Padisák began has been continued (GÖRGÉNYI *et al.* 2023, STENGER-KOVÁCS *et al.* 2025). These studies step over the traditional, conservational perspectives focusing on Red List species.

However, what Judit Padisák is internationally known for, is the establishment and development of the functional ecology of phytoplankton. In this approach, the basic theory is that species are grouped into well-defined functional or morpho-functional groups according to their ecological characteristics (REYNOLDS 1980, 1984) and similar morphological features (REYNOLDS *et al.* 2002). This approach was refined and expanded by PADISÁK and REYNOLDS (1998), and the ecological importance of functional and morphological characteristics (traits, e.g. size, shape, colonial, unicellular, flagella) of the phytoplankton species was highlighted by a number of studies published by Padisák and her co-authors (e.g. SALMASO and PADISÁK 2007, VANDERLEY *et al.* 2022, ŽUTINIĆ *et al.* 2014). Following the worldwide spread of trait-based approaches in phytoplankton ecology (e.g. KRUK *et al.* 2002), several decades behind, these analyses have appeared and broadened in benthic diatom ecology (e.g. B-BÉRES *et al.* 2016, 2017, SOININEN *et al.* 2016, STENGER-KOVÁCS *et al.* 2018, 2020, TAPOLCZAI *et al.* 2016, 2017).

Judit Padisák was the person who inspired this study. Thanks to her, our scientific attention has turned to the investigation of rarity, especially diatom rarity from a functional, trait-based perspective. Ecology of outliers can help to understand the effect of biodiversity loss on ecosystem function (VIOLLE *et al.* 2017), therefore identifying functional rarity is crucial.

Accordingly, our main aim in this study was (i) to develop a diatom trait database for the rivers of the Danube catchment area in Hungary and Croatia and (ii)

to identify rare traits of diatoms from different terms following RABINOWITZ's approach (1981) based on rarity indices by MACIEL (2021). Furthermore, (iii) to answer whether common or rare species have rare traits?

## MATERIALS AND METHODS

### Collection and treatment of phytobentos samples

Phytobentos samples were collected from 99 sampling sites in River Danube's network system in Hungary (48 sites) and in Croatia (51 sites) in two seasons (spring and autumn) of 2022 (Table 1). The samples were taken from rock substrates with a toothbrush and preserved in ethanol. These samples were treated by the hot hydrogen-peroxide method (CEN 2003) to clean diatom frustules from organic materials. One drop of the purified valves was embedded in Pleurax© synthetic resin.

**Table 1.** Sampling sites and their GPS coordinates of the Danube catchment area.

| Hungary             |            |            | Croatia     |            |            |
|---------------------|------------|------------|-------------|------------|------------|
| River               | GPS-N      | GPS-E      | River       | GPS-N      | GPS-E      |
| Által-ér            | 47.731578  | 18.32382   | Bednja 1    | 46.2409738 | 16.1690811 |
| Bitva               | 47.2921826 | 17.3730207 | Bednja 2    | 46.291004  | 16.7383304 |
| Cinca               | 47.2909945 | 17.1714543 | Drava 2     | 45.7904535 | 17.980645  |
| Cuhai-Bakony-ér     | 47.70461   | 17.856468  | Drava 3     | 45.7277505 | 18.3197518 |
| Csikvándi-Bakony-ér | 47.4595103 | 17.4466295 | Drava 4     | 45.6673405 | 18.4889481 |
| Csörnök-Herpenyő 1  | 47.2232517 | 16.9464436 | Drava 5     | 45.617589  | 18.583732  |
| Csörnök-Herpenyő 2  | 47.023333  | 16.7016046 | Drava 6     | 45.572097  | 18.6486069 |
| Damásdi-patak       | 47.831161  | 18.853865  | Drava 7     | 45.5530337 | 18.8642468 |
| Dobroda-patak       | 48.207931  | 19.594151  | Drava 8     | 46.1102261 | 17.1525354 |
| Danube HUN1         | 47.816204  | 18.862622  | Drava 9     | 46.128741  | 17.070945  |
| Danube HUN2         | 47.762361  | 18.540508  | Drava 10    | 45.7831074 | 18.2006111 |
| Danube HUN3         | 47.740468  | 18.161742  | Drava 11    | 45.942418  | 17.46927   |
| Danube HUN4         | 47.738873  | 17.825387  | Drava 12    | 46.2413055 | 16.9382756 |
| Danube HUN5         | 47.768855  | 17.695974  | Drava 13    | 46.2971501 | 16.8791159 |
| Fekete-víz          | 48.03547   | 19.21186   | Danube_CRO1 | 45.83849   | 18.852161  |
| Gerence-patak       | 47.4021181 | 17.4716095 | Danube_CRO2 | 45.2306027 | 19.3789696 |
| Hajagos             | 47.3052291 | 17.2925608 | Karašica 1  | 45.7086722 | 18.294293  |
| Hosszú-víz          | 47.2287199 | 16.8408572 | Karašica 2  | 45.7283359 | 17.966283  |
| Ipoly 1             | 48.097534  | 19.482762  | Krapina 1   | 45.8347708 | 15.8228039 |
| Ipoly 2             | 48.23556   | 19.605588  | Krapina 2   | 46.104752  | 16.2011741 |
| Ipoly 3             | 48.065698  | 19.107886  | Kupa 1      | 45.4836406 | 16.3688803 |
| Ipoly 4             | 48.031432  | 18.82434   | Kupa 2      | 45.645271  | 15.3564433 |
| Ipoly 5             | 47.846207  | 18.827692  | Kupa 3      | 45.614169  | 15.479493  |

**Table 1.** Sampling sites and their GPS coordinates of the Danube catchment area.

| Hungary           |             |            | Croatia    |            |            |
|-------------------|-------------|------------|------------|------------|------------|
| River             | GPS-N       | GPS-E      | River      | GPS-N      | GPS-E      |
| Kodó              | 47.2106331  | 17.159439  | Mura 1     | 46.419121  | 16.6912483 |
| Kozár-borzó       | 47.2070853  | 16.7520865 | Mura 2     | 46.5145696 | 16.4405221 |
| Lókos stream      | 48.04637    | 19.202505  | Mura 3     | 46.325253  | 16.8711927 |
| Marcal 1          | 47.4488467  | 17.383294  | Odra       | 45.30072   | 16.205618  |
| Marcal 2          | 47.3187165  | 17.2749847 | Orljava 1  | 45.2862258 | 17.805124  |
| Marcal 3          | 47.1800447  | 17.203338  | Orljava 2  | 45.145141  | 17.704758  |
| Marcal 4          | 47.019367   | 17.1780178 | Plitvica 1 | 46.2682566 | 16.3809813 |
| Marcal 5          | 47.609778   | 17.514591  | Plitvica 2 | 46.2948749 | 16.7145553 |
| Ménés-patak       | 48.110939   | 19.515189  | Sava 1     | 45.040493  | 18.6959194 |
| Mosoni-Danube     | 47.733882   | 17.755304  | Sava 2     | 45.0601558 | 18.5047005 |
| Pándzsa           | 47.645157   | 17.663524  | Sava 3     | 45.139754  | 18.073944  |
| Pápai-Bakony ér   | 47.3407368  | 17.4011407 | Sava 4     | 45.0990681 | 17.7378568 |
| Perint            | 47.2852455  | 16.591909  | Sava 5     | 45.2688108 | 16.9154738 |
| Rába 1            | 46.9804976  | 16.5266711 | Sava 6     | 45.4014717 | 16.53887   |
| Rába 2            | 47.1268512  | 16.8504796 | Sava 7     | 45.479194  | 16.384163  |
| Rába 3            | 47.2450628  | 16.9525601 | Sava 8     | 45.788939  | 15.8593526 |
| Rába 4            | 47.621064   | 17.488968  | Sava 9     | 45.8624521 | 15.688058  |
| Rába 5            | 47.4230911  | 17.1328756 | Sava 10    | 45.44469   | 16.1347    |
| Rátka-patak       | 47.2410121  | 16.7989645 | Sava 10    | 45.74637   | 16.229709  |
| Sokorói-Bakony-ér | 47.561259   | 17.574898  | Sava 11    | 45.1340401 | 17.6729085 |
| Sorok stream      | 47.125671   | 16.7602657 | Sava 12    | 45.6477778 | 16.3396059 |
| Szávai channel    | 47.746114   | 17.683105  | Sava 13    | 45.3622414 | 16.7577718 |
| Torna stream      | 47.10381177 | 17.2611613 | Sava 14    | 45.16701   | 17.25817   |
| Únyi stream       | 47.67255    | 18.675955  | Sava 15    | 45.8343174 | 15.7710688 |
| Vörös stream      | 46.9700392  | 16.4077611 | Sava 16    | 44.8513247 | 18.9595429 |
|                   |             |            | Una 1      | 45.2615941 | 16.9128728 |
|                   |             |            | Una 2      | 45.2220957 | 16.549762  |
|                   |             |            | Una 3      | 45.0497854 | 16.3725921 |

### Microscopic analyses of diatoms

Altogether 183 diatom slides were adequate for microscopic analyses. Diatom taxa were identified to species and variates level using the taxonomic guides of LANGE-BERTALOT *et al.* (2017), BEY and ECTOR (2013), PEETERS and ECTOR (2018, 2019), and Ács *et al.* (2023). Around 400 diatom valves per slide were counted in a light microscope (Zeiss Axio Imager A1, Plan-apochromat DIC lens) for the calculation of the relative abundance of the species.

### Development of a diatom trait database

Based on RIMET and BOUCHEZ (2012), eight morphological traits and 19 lifeforms as diatom traits (Table 2) were determined for 409 diatom species. The missing traits of the species were collected from open databases and publications. Diatom data were looked for in ALVERSON *et al.* (2021), BAHLS (2016), BAĞ *et al.* (2014), BEAUGER *et al.* (2015), BEDOSHVILI *et al.* (2009), BERTOLLI *et al.* (2020), BEY and ECTOR (2013), BISHOP (2017), BISHOP and STANCHEVA (2017), BUDZYŃSKA and WOJTAL (2011), BURGLE and EDLUND (2015), COX (1997), COX and WILLIAMS (2006), DE STEFANO and ROMERO (2005), ENVIRONMENTAL AGENCY (2020), FROHN (2016), FUREY (2010), GRUNOW (1860), HATCHER (2018), HILLEBRANDT (1999), HUSTEDT (1930), JOVANOVSKA *et al.* (2019), JOVANOVSKA and WINTER (2021), JÜTTNER (2025a, b, c), JÜTTNER and COX (2025), JÜTTNER and MANN (2025), JÜTTNER and VAN DE VIJVER (2025), JÜTTNER *et al.* (2025a, b, c), KELLY (2025), KEZLYA *et al.* (2022), KISS *et al.* (2013), KOCIOLEK (2011), KOCIOLEK *et al.* (2015), KRAMMER (1997, 2002), KULIKOVSKIY *et al.* (2011, 2019, 2023), LANGE-BERTALOT and FUHRMANN (2016), LANGE-BERTALOT *et al.* (2011, 2017, 2020), LEVKOV *et al.* (2013), LIU *et al.* (2012), MANN (2025a, b, c, d, e, f), MANN and JÜTTNER (2025a, b, c), MANN *et al.* (2025), MENDOZA (2015), MORALES *et al.* (2010), PATRICK and REIMER (1975), PEETERS and ECTOR (2018, 2019), PHYTOPLANKTON GUIDE (2012 a, b), POLASKEY and BISHOP (2015), POTAPOVA (2009, 2020), POTAPOVA *et al.* (2008), RIMET (2011), RIMET *et al.* (2024), ROUND *et al.* (1990), SPAULDING and EDLUND (2008a, b, c, d), STANCHEVA *et al.* (2020), STEPANEK (2011), TAPOLCZAI *et al.* (2019), TUJI and WILLIAMS (2006), VAN DE VIJVER *et al.* (2022), WETZEL *et al.* (2019), WILLIAMS (2025), and the OMNIDIA software 6.1 (LECOINTE *et al.* 1993).

**Table 2.** The studied morphological and lifeform traits.

| Morphological traits | Lifeform traits         |                        |
|----------------------|-------------------------|------------------------|
| chloroplast number   | motile / non motile     | colonial/ non colonial |
| chloroplast shape    | pioneer / non pioneer   | mucous tube colony     |
| valve length         | attached / not attached | chain colony           |
| valve width          | adnate                  | zig-zag colony         |
| valve height         | pedunculate             | rosette colony         |
| length/width ratio   | pad                     | ribbon colony          |
| cell biovolume       | stalk                   | stellate colony        |
| valve shape          |                         | arbuscular colony      |

First, the shape of the diatom valves was determined relying primarily on the work of HILLEBRAND *et al.* (1999), and then biovolumes were calculated using the length, width, and height data. If we could not find any information about them (mainly in the case of the valve height), we estimated it from our photo documentation or from the generalized generic data.

For each trait, the extent of the trait was determined, the distribution of the data, furthermore, where and how much jumps were found in the data. Based on this, the continuous variables were converted into categorical variables resulting in 142 different trait categories (Appendix 1). Including four morphological trait categories related to the number of chloroplasts, 15 to the shape of the chloroplasts, 37 to lengths, ten to widths, and 19 to heights. These latter morphological parameters were also used as the basis for the 27 volume and 11 length /width trait categories (Appendix 1, electronic supplement).

Rarity indices

For the 142 trait categories rarity indices were calculated like geographic range (gr), habitat specificity (hs), and population size (ps) indices based on studies by MACIEL (2021) and STENGER-KOVÁCS *et al.* (2025) guided by Rabinowitz's approach (RABINOWITZ 1981). The formulae of the calculated indices are as follows:

- (1)  $psi = 1 / p_{max}$ ;  $p_{max}$  = maximal population size
- (2)  $hsi = 1 / h_{max}$ ;  $h_{max}$  = maximal number of occurrence
- (3)  $gri = 1 / \{[(latitude\ range) * (longitude\ range)] + 1\}$

Finally, the absolute rarity index (rr) was calculated as the median of the previous three indices (psi, hsi, gri). The range of these indices varied between 0 and 1. Values close to 0 indicate more common features, and values closer to 1 indicate rarer traits. In our analysis, the trait was considered as a rare character if its index value was one. Finally, traits were classified into rarity categories based on Rabinowitz's approach (RABINOWITZ 1981) (Table 3).

Table 3. Number of diatom traits in the categories of the Rabinowitz system.

| Local population size  | Geographic range | Habitat demand | Number of diatom traits | commonness/rarity    |
|------------------------|------------------|----------------|-------------------------|----------------------|
| at least somewhere big | wide             | generalist     | 106                     | frequent, common     |
|                        |                  | specialist     | 0                       |                      |
|                        | narrow           | generalist     | 0                       | rare in certain term |
|                        |                  | specialist     | 0                       |                      |
| always small           | wide             | generalist     | 25                      |                      |
|                        |                  | specialist     | 0                       |                      |
|                        | narrow           | generalist     | 0                       |                      |
|                        |                  | specialist     | 11                      | absolute rare        |

## RESULTS

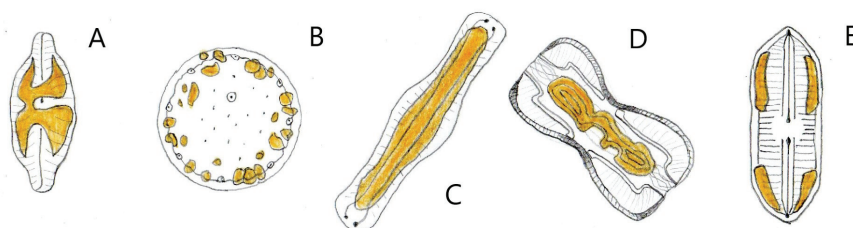
## Diatom trait database of the Danube catchment area

Our database contains 183 samples, a total of 409 diatom species with a combination of 142 categories of 27 traits (eight morphological and 19 life-form traits) (Appendix 1). This database is freely available at the following link: <https://zenodo.org/records/17062977>

## Rarities

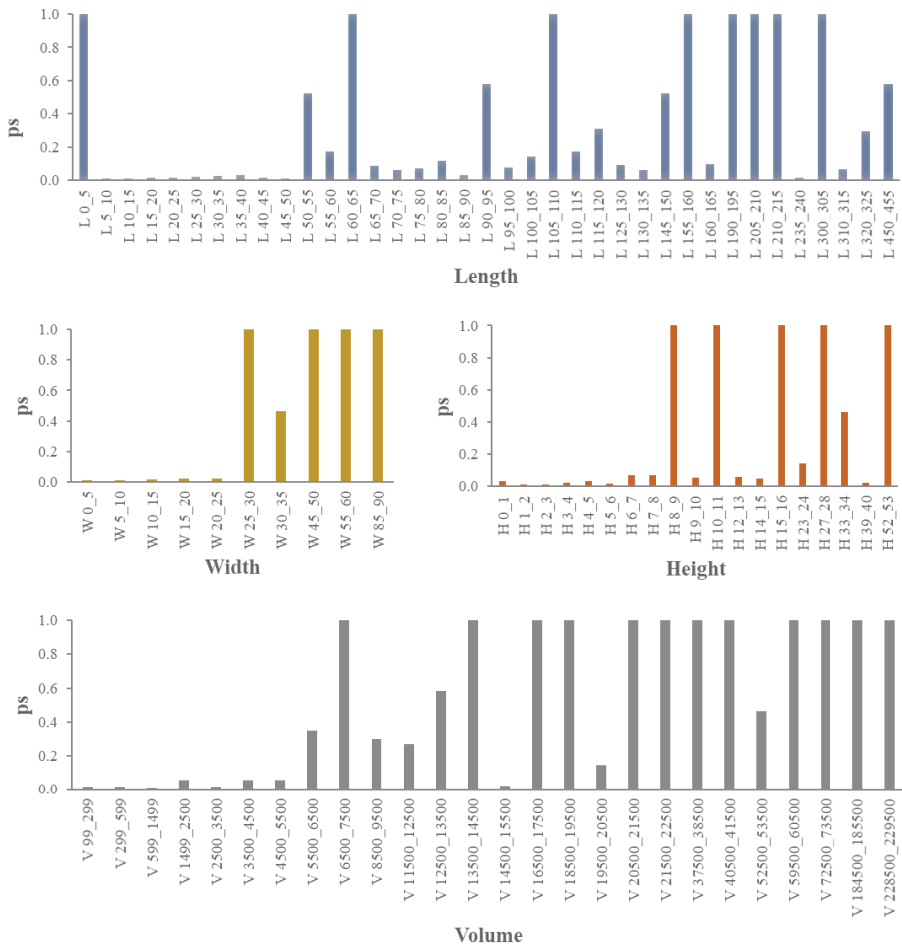
*Small population traits*

In total, 36 traits could be considered as rare in terms of population size (psi index was equal to one). One trait was concerned to chloroplast number (Chloroplast number is 4) and five traits to the chloroplast shape (X shaped, shapeless at rim, large plate, lamellar, appressed) (Fig. 1A–E). Four rare traits



**Fig. 1.** Drawings of rare chloroplast shapes based on population size (illustrations not scaled, drawn by Orsolya Halmai). A = X-shaped chloroplast (*Placoneis undulata*); B = shapeless chloroplasts at rim (*Praestephanos* cf. *triporus*); C = large plate chloroplast (*Epithemia gibba*); D = lamellar chloroplast (*Entomoneis paludosa*); E = appressed chloroplasts (*Neidium cuneatiforme*).

connected to the width of the valve (width between 25–30  $\mu\text{m}$ , 45–50  $\mu\text{m}$ , 55–60  $\mu\text{m}$  and 85–90  $\mu\text{m}$ ), eight for the length (e.g. 0–5  $\mu\text{m}$ , 205–210  $\mu\text{m}$ , 210–215  $\mu\text{m}$ , 300–305  $\mu\text{m}$ ), five are for the height of the valve (8–9  $\mu\text{m}$ , 10–11  $\mu\text{m}$ , 15–16  $\mu\text{m}$ , 27–28  $\mu\text{m}$ , 52–53  $\mu\text{m}$ ). Twelve traits belong to the biovolume category (e.g. 6,500–7,500  $\mu\text{m}^3$ ; 228,500–229,500  $\mu\text{m}^3$ ), and one to the length/width category (40–50) (Fig. 2). These 36 traits were carried by 37 different diatom species. Of these, 36 are rare species in terms of population size (e.g. *Cymatopleura apiculata*, *Surirella ovalis*), among these species 16 were absolutely rare since they were also habitat specialists and even rare in terms of geographic distribution (e.g. *Amphora lange-bertalotii* var. *tenuis*, *Tryblionella gracilis*, *Ulnaria danica*, *Neidium cuneati-*



**Fig. 2.** The ps index values of morphological traits, such as length, width, height, and volume (size unit in  $\mu\text{m}$ ).

forme). Only one common species (*Nitzschia gracilis*) had one rare trait (length 60–65  $\mu\text{m}$ ). Seventeen rare diatom species were identified that have more than one rare, small population-sized trait (Table 4), e.g. *Cymbella neolanceolata* with four rare traits. These traits created a very unique morphological feature of this species with the length of 155–160  $\mu\text{m}$ , width of 25–30  $\mu\text{m}$ , height 27–28  $\mu\text{m}$ , and consequently, the volume of 20,500–21,500  $\mu\text{m}^3$ .

**Table 4.** Rare diatom species and their rare traits. (A = rare in terms of small population size; B = rare in terms of geographical distribution; C = rare in terms of habitat specificity; Chp = chloroplast; D = absolute rare; H = height; L = length; V = volume; W = width)

| Species                                                                                        | A | B | C | D | Trait                              | A | B | C | D |
|------------------------------------------------------------------------------------------------|---|---|---|---|------------------------------------|---|---|---|---|
| <i>Amphipleura pellucida</i> Kützing (Kützing)                                                 | × | × | × | × | L: 105–110 $\mu\text{m}$           | × |   |   |   |
| <i>Amphora lange-bertalotii</i> var. <i>tenuis</i> Levkov et Metzeltin                         | × | × | × | × | H: 8–9 $\mu\text{m}$               | × |   |   |   |
| <i>Amphora lange-bertalotii</i> Levkov et Metzeltin                                            | × |   |   |   | L: 60–65 $\mu\text{m}$             | × |   |   |   |
| <i>Aulacoseira pfaffiana</i> (Reinsch) Krammer                                                 | × | × | × | × | L: 0–5 $\mu\text{m}$               | × |   |   |   |
| <i>Cymatopleura apiculata</i> W. Smith (Ralfs)                                                 | × |   |   |   | V: 21,500–22,500 $\mu\text{m}^3$   | × |   |   |   |
| <i>Cymbella neocistula</i> Krammer                                                             | × |   |   |   | V: 6,500–7,500 $\mu\text{m}^3$     | × |   |   |   |
|                                                                                                | × |   |   |   | L: 155–160 $\mu\text{m}$           | × |   |   |   |
| <i>Cymbella neolanceolata</i> W. Silva                                                         |   |   |   |   | V: 20,500–21,500 $\mu\text{m}^3$   | × |   |   |   |
|                                                                                                |   |   |   |   | W: 25–30 $\mu\text{m}$             | × |   |   |   |
|                                                                                                |   |   |   |   | H: 27–28 $\mu\text{m}$             | × |   |   |   |
| <i>Didymosphenia geminata</i> (Lyngbye) M. Schmidt                                             | × |   |   |   | V: 21,500–22,500 $\mu\text{m}^3$   | × |   |   |   |
| <i>Diploneis elliptica</i> (Kützing) Cleve                                                     |   | × | × | × | H: 15–16 $\mu\text{m}$             | × | × | × | × |
|                                                                                                |   |   |   |   | V: 40,500–41,500 $\mu\text{m}^3$   | × | × | × | × |
| <i>Ellerbeckia arenaria</i> (Moore ex Ralfs) Crawford                                          | × | × | × | × | V: 72,500–73,500 $\mu\text{m}^3$   | × | × | × | × |
|                                                                                                |   |   |   |   | W: 85–90 $\mu\text{m}$             | × | × | × | × |
| <i>Encyonema leibleinii</i> (C. Agardh) W. J. Silva, R. Jahn, T. A. Veiga Ludwig et M. Menezes | × |   |   |   | V: 13,500–14,500 $\mu\text{m}^3$   | × |   |   |   |
|                                                                                                |   |   |   |   | H: 10–11 $\mu\text{m}$             | × |   |   |   |
| <i>Entomoneis paludosa</i> (W. Smith) Reimer                                                   | × |   |   |   | Chp: shape lamellar                | × |   |   |   |
|                                                                                                |   |   |   |   | V: 6,500–7,500 $\mu\text{m}^3$     | × |   |   |   |
| <i>Epithemia gibba</i> Kützing                                                                 | × |   |   |   | Chp: shape large-plate             | × |   |   |   |
|                                                                                                |   |   |   |   | V: 184,500–185,500 $\mu\text{m}^3$ | × |   |   |   |
| <i>Fistulifera saprophila</i> (Lange-Bertalot et Bonik) Lange-Bertalot                         | × |   |   |   | Chp: number 4                      | × |   |   |   |
| <i>Fragilaria perdelicatissima</i> Lange-Bertalot et Van de Vijver                             | × |   |   |   | L: 60–65 $\mu\text{m}$             | × |   |   |   |
| <i>Gyrosigma attenuatum</i> (Kützing) Rabenhorst                                               | × |   |   |   | L: 190–195 $\mu\text{m}$           | × |   |   |   |
| <i>Iconella tenera</i> (W. Gregory) Ruck et Nakov                                              | × |   |   |   | V: 37,500–38,500 $\mu\text{m}^3$   | × |   |   |   |
|                                                                                                |   |   |   |   | W: 25–30 $\mu\text{m}$             | × |   |   |   |
| <i>Lindavia balatonis</i> (Pantocsek) Nakov, Guillory, Julius, Theriot et Alverson             | × |   |   |   | H: 8–9 $\mu\text{m}$               | × |   |   |   |

Table 4. (continued)

| Species                                                                               | A | B | C | D | Trait                              | A | B | C | D |
|---------------------------------------------------------------------------------------|---|---|---|---|------------------------------------|---|---|---|---|
| <i>Neidiomorpha binodeformis</i> (Krammer)<br>Cantonati, Lange-Bertalot et Angeli     | × | × | × | × | Chp: shape appressed               | × |   |   |   |
| <i>Neidiomorpha binodis</i> (Ehrenberg) Can-<br>tonati, Lange-Bertalot et Angeli      | × | × | × | × | Chp: shape appressed               | × |   |   |   |
| <i>Neidium ampliatus</i> (Ehrenberg) Kram-<br>mer                                     | × | × | × | × | Chp: number 4                      | × |   |   |   |
|                                                                                       |   |   |   |   | Chp: shape appressed               | × |   |   |   |
| <i>Neidium cuneatiforme</i> Levkov                                                    | × | × | × | × | Chp: number 4                      | × |   |   |   |
|                                                                                       |   |   |   |   | Chp: shape appressed               | × |   |   |   |
| <i>Neidium dubium</i> (Ehrenberg) Cleve                                               | × |   |   |   | Chp: number 4                      | × |   |   |   |
|                                                                                       |   |   |   |   | Chp: shape appressed               | × |   |   |   |
| <i>Nitzschia graciliformis</i> Lange-Bertalot et<br>Simonsen                          | × |   |   |   | L/W: 40–50 $\mu\text{m}$           | × |   |   |   |
| <i>Nitzschia gracilis</i> Hantzsch                                                    |   |   |   |   | L: 60–65 $\mu\text{m}$             | × |   |   |   |
| <i>Pinnularia viridis</i> (Nitzsch) Ehrenberg                                         | × |   |   |   | V: 16,500–17,500 $\mu\text{m}^3$   | × |   |   |   |
|                                                                                       |   |   |   |   | L: 105–110 $\mu\text{m}$           | × |   |   |   |
| <i>Placoneis undulata</i> (Østrup) Lange-Ber-<br>talot                                | × | × | × | × | Chp: shape x                       | × | × | × | × |
| <i>Praestephanos</i> cf. <i>triporus</i> (Genkal et G.<br>V. Kuzmin) Tuji et J.-S. Ki | × | × | × | × | Chp: shapeless at rim              | × | × | × | × |
|                                                                                       |   |   |   |   | L: 0–5 $\mu\text{m}$               | × |   |   |   |
| <i>Stauroneis phoenicenteron</i> (Nitzsch)<br>Ehrenberg                               | × | × | × | × | L: 210–215 $\mu\text{m}$           | × | × | × | × |
|                                                                                       |   |   |   |   | V: 21,500–22,500 $\mu\text{m}^3$   | × |   |   |   |
| <i>Surirella librile</i> (Ehrenberg) Ehrenberg                                        | × |   |   |   | H: 27–28 $\mu\text{m}$             | × |   |   |   |
|                                                                                       |   |   |   |   | V: 59,500–60,500 $\mu\text{m}^3$   | × |   |   |   |
| <i>Surirella ovalis</i> Brébisson                                                     | × |   |   |   | W: 25–30 $\mu\text{m}$             | × |   |   |   |
|                                                                                       | × |   |   |   | H: 52–53 $\mu\text{m}$             | × |   |   |   |
| <i>Surirella undulata</i> (Ehrenberg) Ehren-<br>berg                                  |   |   |   |   | V: 22,8500–22,9500 $\mu\text{m}^3$ | × |   |   |   |
|                                                                                       |   |   |   |   | W: 55–60 $\mu\text{m}$             | × |   |   |   |
| <i>Thalassiosira lacustris</i> (Grunow) Hasle in<br>Hasle et Fryxell                  | × | × | × | × | V: 18,500–19,500 $\mu\text{m}^3$   | × | × | × | × |
|                                                                                       |   |   |   |   | W: 45–50 $\mu\text{m}$             | × | × | × | × |
|                                                                                       |   |   |   |   | H: 10–11 $\mu\text{m}$             | × |   |   |   |
| <i>Tryblionella angustata</i> W. Smith                                                | × |   |   |   | L: 60–65 $\mu\text{m}$             | × |   |   |   |
| <i>Tryblionella gracilis</i> W. Smith                                                 | × | × | × | × | V: 6,500–7,500 $\mu\text{m}^3$     | × |   |   |   |
| <i>Ulnaria capitata</i> (Ehrenberg) Compère                                           | × | × | × | × | L: 300–305 $\mu\text{m}$           | × | × | × | × |
| <i>Ulnaria danica</i> (Kützing) Compère et<br>Bukhtiyarova                            | × | × | × | × | L: 205–210 $\mu\text{m}$           | × | × | × | × |
|                                                                                       |   |   |   |   | L/W: 40–50 $\mu\text{m}$           | × |   |   |   |

*Habitat specialist, geographically restricted, and absolute rare traits*

Of the 36 small population-sized traits, 11 were also considered to be rare in terms of both habitat specificity and geographic distribution. These are therefore absolute rare traits: two chloroplast forms (X-shaped, shapeless at rim) (Fig. 1A–B), two width (45–50  $\mu\text{m}$ , 85–90  $\mu\text{m}$ ), three length (205–210  $\mu\text{m}$ , 210–215  $\mu\text{m}$ , 300–305  $\mu\text{m}$ ), one height (15–16  $\mu\text{m}$ ), and three biovolume (18,500–19,500  $\mu\text{m}^3$ , 40,500–41,500  $\mu\text{m}^3$ , 72,500–73,500  $\mu\text{m}^3$ ) (Fig. 3). These rare features are carried by 8 absolute rare species like *Diploneis elliptica*, *Ellerbeckia arenaria*, *Placoneis undulata*, *Praestephanos cf. triporus*, *Stauroneis phoenicenteron*, *Thalassiosira lacustris*,

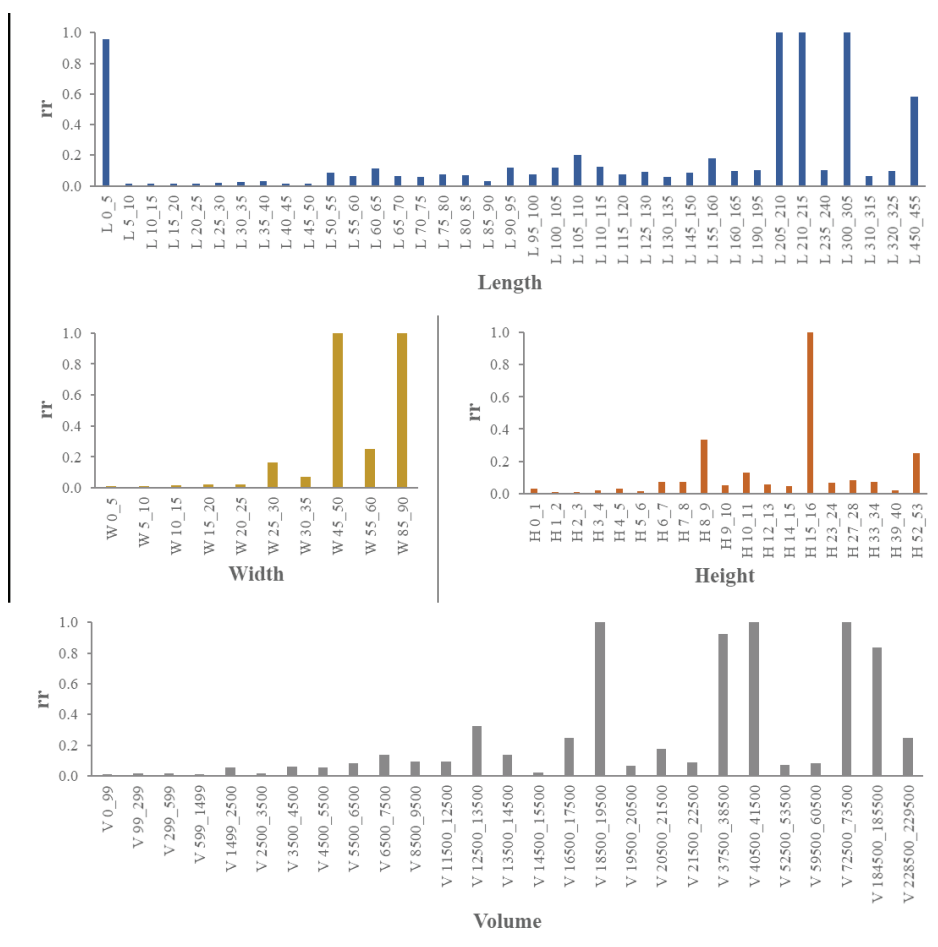


Fig. 3. The rr index values of morphological traits, such as length, width, height, and volume (size unit in  $\mu\text{m}$ ).

*Ulnaria capitata*, and *Ulnaria danica*. Three of them (*Diploneis elliptica*, *Ellerbeckia arenaria*, and *Thalassiosira lacustris*) carried more than one absolutely rare trait (Fig. 4). *Diploneis elliptica* can be characterised by the height of 15–16  $\mu\text{m}$  and the volume of 40,500–41,500. *Ellerbeckia arenaria* has also two absolutely rare traits like the width 85–90  $\mu\text{m}$  and the volume 72,500–73,500  $\mu\text{m}^3$ . *Thalassiosira lacustris* has two absolute rare traits (width 45–50  $\mu\text{m}$ , volume 18,500–19,500  $\mu\text{m}^3$ ) and one rare trait (height 10–11  $\mu\text{m}$ ) in terms of population size.

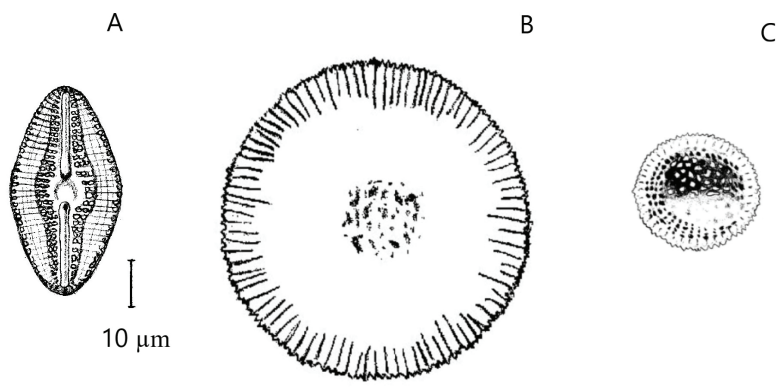


Fig. 4. Three absolute rare diatom species with more absolute rare traits (drawn by Orsolya Halmai). A = *Diploneis elliptica*, B = *Ellerbeckia arenaria*, C = *Thalassiosira lacustris*.

Nine of the 11 traits were identified in diatom species, mainly present in samples from the Sava, Drava, and Odra rivers in Croatia, and the remaining two traits being observed in the Rába River in Hungary (Table 5). In two different

| Table 5. Absolute rare diatom traits with example species found in special habitats and regions. |       |            |                                   |
|--------------------------------------------------------------------------------------------------|-------|------------|-----------------------------------|
| Trait                                                                                            | River | Settlement | Species example                   |
| Length 300–305 $\mu\text{m}$                                                                     | Drava | Legrad     | <i>Ulnaria capitata</i>           |
| X-shaped chloroplast                                                                             | Drava | Petrijevci | <i>Placoneis undulata</i>         |
| Length 205–210 $\mu\text{m}$                                                                     | Odra  | Sisak      | <i>Ulnaria danica</i>             |
| Length 210–215 $\mu\text{m}$                                                                     | Odra  | Sisak      | <i>Stauroneis phoenicenteron</i>  |
| Width 85–90 $\mu\text{m}$                                                                        | Rába  | Sárvár     | <i>Ellerbeckia arenaria</i>       |
| Biovolume 72,500–73,500 $\mu\text{m}^3$                                                          |       |            |                                   |
| Shapeless chloroplast at rim                                                                     | Sava  | Topolje    | <i>Praestephanos cf. triporus</i> |
| Height 15–16 $\mu\text{m}$                                                                       | Sava  | Lukavec    | <i>Diploneis elliptica</i>        |
| Biovolume 40,500–41,500 $\mu\text{m}^3$                                                          |       |            |                                   |
| Width 45–50 $\mu\text{m}$                                                                        | Sava  | Županje    | <i>Thalassiosira lacustris</i>    |
| Biovolume 18,500–19,500 $\mu\text{m}^3$                                                          |       |            |                                   |

sampling sites of the Drava River, one–one trait was absolutely rare (Length 300–305  $\mu\text{m}$  and X-shaped chloroplast). In the Odra River, two rare traits (Length 205–210  $\mu\text{m}$  and 210–215  $\mu\text{m}$ ) occurred in samples taken at Sisak. In the Sava River at Topolje the shapeless chloroplast at rim, at Lukavec the height 15–16  $\mu\text{m}$  and volume 40,500–41,500  $\mu\text{m}^3$  traits were found as rare. In the Sava River at Županje, the rare traits were the width 45–50  $\mu\text{m}$  and volume 18,500–19,500  $\mu\text{m}^3$  were also found. Finally, in the sample of the Rába River at Sárvár, the rare traits were the width of 85–90  $\mu\text{m}$  and volume of 72,500–73,500  $\mu\text{m}^3$ .

#### *System of rare traits following Rabinowitz's approach*

Among 142 traits 106 were common features of the diatom species (mostly lifeform traits like attachment types, colony forms, and motility), which are generalist with high population size and wide distribution. 25 traits (chloroplast shapes: plate, large plate, and compressed; number of chloroplasts 4; length 0–5  $\mu\text{m}$ , 60–65  $\mu\text{m}$ , 105–110  $\mu\text{m}$ , 155–160  $\mu\text{m}$ , and 190–195  $\mu\text{m}$ ; length/width 40–50  $\mu\text{m}$ ; height 8–9  $\mu\text{m}$ , 10–11  $\mu\text{m}$ , 27–28  $\mu\text{m}$ , and 52–53  $\mu\text{m}$ ; width 25–30  $\mu\text{m}$  and 55–60  $\mu\text{m}$ ; biovolume 6,500–7,500  $\mu\text{m}^3$ , 13,500–14,500  $\mu\text{m}^3$ , 16,500–17,500  $\mu\text{m}^3$ , 20,500–21,500  $\mu\text{m}^3$ , 21,500–22,500  $\mu\text{m}^3$ , 37,500–38,500  $\mu\text{m}^3$ , 59,500–60,500  $\mu\text{m}^3$ , 184,500–185,500  $\mu\text{m}^3$ , and 228,500–229,500  $\mu\text{m}^3$ ) had small population size, but they were generalist with wide geographic distribution (Table 3). Only 11 traits (chloroplast shapes: shapeless at rim, X-shape; length 205–210  $\mu\text{m}$ , 210–215  $\mu\text{m}$ , and 300–305  $\mu\text{m}$ ; height 15–16  $\mu\text{m}$ , width 45–50  $\mu\text{m}$ , 85–90  $\mu\text{m}$ ; biovolume 18,500–19,500  $\mu\text{m}^3$ , 40,500–41,500  $\mu\text{m}^3$ , and 72,500–73,500  $\mu\text{m}^3$ ) were considered as absolute rare (Table 3). These traits were habitat specialists with small population size and geographically restricted distribution. We found any diatom trait in other categories of the Rabinowitz system (Table 3).

## DISCUSSION

### Database

In ecology, trait-based approaches are rapidly spreading and starting to come into general use taking advantage of this method. Among other organisms, benthic diatoms are especially suitable for trait-based studies because these organisms have well-defined, measurable, and investigable traits similar to soft algal species (LARAIB *et al.* 2023). However, a coherent, trans-regional diatom trait database is missing in contrast to phytoplankton (LARAIB *et al.* 2023) or plants (SONKOLY *et al.* 2023). Therefore, using the only existing and available French database of RIMET and BOUCHEZ (2012) and completing it with data

from different sources we established an integrated (taxonomic and traits information) diatom database with 13,162 records for the Danube catchment area in Hungary and Croatia. This database provides further possibilities for functional analyses in the future and can be integrated into an extended dataset of a large biogeographic area.

### Ecological significance of rare diatom traits

In the benthic diatom communities that were studied, despite the high number of lifeform traits that were considered (19 in total), exclusively morphological characteristics were among the rare diatom traits. Consequently, all lifeform traits – including those such as colony formation with specific shapes, which are generally assumed to be rare – were classified as common.

It was found that approximately 25% of the trait categories were associated with low population sizes. These include: four chloroplasts per cell, five distinct chloroplast shapes, and variation in cell wall dimensions, including width, length, height, and biovolume.

Although the membrane structures of diatom species are very similar, their chloroplast shape, number, and location in the cell are more diverse than in other groups of the Heterokontophyta division (MANN 1996). The chloroplast morphology and number can have ecological and functional significance since these traits can considerably influence the light trapping and the photosynthesis activity (HÄDER *et al.* 2022), but these are rarely investigated in the case of algae (VAN DEN DRIESCHE 1966). In this study, chloroplast morphology and its number were among the small population size traits and also the absolute rare traits. These traits are strongly connected to different diatom evolutionary lineages with fixed number and shape (JULIUS and THERIOT 2010) and therefore can be used for identification of diatom taxa in live samples (COX 1996). However, environmental stress can modify the number of chloroplasts (JULIUS 2007). The more and smaller chloroplasts in an algal cell (e.g. in centric diatoms) have a bigger total surface, furthermore, they can move more freely within the cell to access an adequate light environment (SOLYMOSI 2012). Consequently, their efficiency of light interception is higher. On the other hand, one big chloroplast – which is very common in algae (SOLYMOSI 2012) and characteristic for pennate diatoms – can be also optimal in a certain (e.g. less scattered light) environment (GŁOWACKA *et al.*, 2023). Four chloroplasts as a rare trait is located between these two common chloroplast types, which may not be a “perfect” light trap and may lead to its rarity.

Certain chloroplast shapes (e.g. stellate, spiral) of algae can also enhance the inner surface of the chloroplast and as a dynamic system can adapt to differ-

ent light conditions (SOLYMOSI 2012). However, these features are completely missing in diatom species. But the X-shaped chloroplasts found rare here can also have various benefits (CAO *et al.* 2011) like high inner surface area, better light absorbance from different directions, more efficient pigment distribution, and quick transportation of photosynthetic products. Not to mention better space filling, which can provide mechanical stability for the cell. However, despite these advantages, this trait remained rare and in the absence of studies, we could only guess its reason.

This study revealed that larger size categories are rarer in the studied diatom communities, whether in terms of width, length, height or biovolume. However, it should be noted that these four morphological traits are not independent. Our analyses showed (not published data), that the biovolume of a diatom cell is primarily influenced by the height and length of the valve, while the effect of the width on the biovolume is less expressed. Larger cell volume  $> 6,500 \mu\text{m}^3$  can be considered as a rare trait in terms of small population, while  $> 18,500 \mu\text{m}^3$  the biovolume was absolutely rare. RIMET and BOUCHEZ (2012) in their study distinguished 5 different biovolume categories, where the biggest one was the size class 5 ( $1,500 \mu\text{m}^3$  and above). Since this study showed that biovolume can reach even  $229,500 \mu\text{m}^3$  it would be worth, to classify further size classes to understand the ecological role of the larger, rarer sizes. Namely, biovolume is an important morphological trait, which is closely related to important physiological processes, such as nutrient uptake and growth rate. Larger cells have slower nutrient uptake. Very large or very small cells grow 30 times more slowly than the others. Cells around  $100 \mu\text{m}^3$  are the fastest growing (HILLEBRAND *et al.* 2022). Moreover, larger cell size is associated with cells being more resistant to grazing (PANČIĆ and KIØRBOE 2018). In terms of their ecological strategy, large, slow-growing cells are K-strategists, compared to small, fast-growing r-strategists (WENTZKY *et al.* 2020).

The small population sized traits were carried by 37 different diatom species. Most of them (36) were rare species (e.g. *Cymatopleura apiculata*, *Amphipleura pellucida*) and only one was a common species (*Nitzschia gracilis* with a length of 60–65  $\mu\text{m}$ ) (STENGER-KOVÁCS *et al.* 2025). Furthermore, 17 rare species displayed more than one rare trait, in terms of small population sizes, creating very unique morphological features. This finding indicates that rare traits are predominantly exhibited by rare diatom species, which also confirms that the large size, as a rare trait clearly contributes to the rarity of the species that possess them.

Approximately 7% of the total traits (i.e. exactly 11) were both habitat specialists and geographically restricted, while 93% of them can be considered to be generalist and widespread. Since these rare traits were among the small popu-

lation sized traits, therefore, they can be considered as absolute traits. Nine of them were connected to the big sizes of the species through their length, width, height or biovolume and only two chloroplast shapes (X-shaped, Shapeless chloroplast at rim) were absolutely rare. These 11 absolute rare traits are possessed by eight absolutely rare species (e.g., *Thalassiosira lacustris*, *Ellerbeckia arenaria*, and *Diploneis elliptica*, STENGER-KOVÁCS *et al.* 2025). Each of these three example species exhibited two absolute rare traits and, in addition, shared a common preference for oligotrophic environments (LANGE-BERTALOT *et al.* 2017). Furthermore, these absolute rare features were primarily associated with Croatian rivers (Sava, Drava, and Odra), with the exception of the Hungarian Rába river. These regions and river sites (Drava at Légrád and Petrijevci, Odra at Sisak, Rába at Sárvár, and Sava at Topolje, Lukavec, and Županje) may ensure special conditions to host rare species with rare traits. This suggests that the Sava, Drava, Odra, and Rába rivers may be particularly important for maintaining regional biodiversity due to their environmental characteristics. Based on our water chemistry measurements these sampling sites had lower conductivity (mean is  $477 \mu\text{S cm}^{-1}$ ), COD/chemical oxygen demand (mean =  $7 \text{ mg L}^{-1}$ ), and nutrient concentrations (mean TP/total phosphorous  $78 \mu\text{g L}^{-1}$ , SRP/soluble reactive phosphorous  $11 \mu\text{g L}^{-1}$ , nitrite  $9 \text{ mg L}^{-1}$ ) than of the other 183 sites (mean conductivity =  $579 \mu\text{S cm}^{-1}$ , COD =  $15 \text{ mg L}^{-1}$ , TP =  $150 \mu\text{g L}^{-1}$ , SRP =  $59 \mu\text{g L}^{-1}$ , nitrite =  $17 \text{ mg L}^{-1}$ ) in the studied area. The presence of diatoms with large biovolumes in surface waters that have lower nutrient concentrations seems somewhat controversial. However, this pattern can be explained by the fact that diatoms in oligotrophic environments often adopt a K-selected strategy (FINKEL *et al.* 2010). Larger cell volume can support more storage vacuoles for nutrients and ensure a great surface area for uptake (FINKEL *et al.* 2010). In such environments, large diatoms can survive longer in low-nutrient conditions by storing resources (LITCHMAN *et al.* 2007) and growing at a slower rate. Furthermore, these waters often have higher transparency, allowing light to penetrate deeper (LEACH *et al.* 2018). In nutrient-poor systems, competition can be lower because there are fewer fast-growing species (LITCHMAN *et al.* 2007). Some studies also highlight that large diatoms not just occur occasionally but can thrive in environments that are nutrient-poor or have fluctuating nutrient content under specific conditions, such as deep mixing, high light availability, and low grazing pressure (FINKEL *et al.* 2010, KEMP and VILLAREAL 2018, LITCHMAN *et al.* 2009).

In summary, the bigger sizes and special chloroplasts are unique characteristics of diatoms. Rare species carrying these rare traits become a functionally distinct and potentially vulnerable member of the local or regional community. However, these species can serve as core species (STENGER-KOVÁCS *et al.* 2025)

and ecological memory of the communities (PADISÁK 1992). Quoting Judit Padisák they “will influence the present and future responses of the communities”, and consequently, determine ecosystem functioning.

\* \* \*

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*Dedication* – We offer this study on the occasion of the 70th birthday of our Professor Judit Padisák, who is one of the most famous and renowned limnoecologists. She is that person, who we all could have learned the hard work and scientific humility from and who we get never ending scientific, personal and familiar support from. Thank you Judit and we wish you health and happiness not only on your birthday but also other times of your life.

**Összefoglaló:** A ritka faj a természetvédelem központi témája. Ennek ellenére nem rendelkezünk elegendő ismerettel azokról a tulajdonságokról, amelyek a kihalásukhoz vezethetnek. Éppen ezért ebben a tanulmányban egy kovaalga jelleg adatbázis (morfológiai és életforma jellegek, összesen 142 féle) létrehozását és a ritka jellemzők azonosítását tűztük ki célul. A kifejlesztett adatbázis 13 162 rekordot tartalmaz a Duna vízgyűjtőterületén Magyarországon és Horvátországban előforduló kovaalga fajokról. Rabinowitz eredeti megközelítését és a szakirodalomban közzétett új ritkassági indexeket alkalmazva a kovaalgák jellegeinek ritkaságát különböző szempontok alapján határoztuk meg. A kovaalgák jellegeinek 75%-a gyakori jelleg, míg 25%-uk kis populációjú (ritka) jelleg volt. Ezek kizárólag a kovaalgák morfológiai jellemzői voltak (sejtenkénti négy kloroplasztisz, öt különböző kloroplasztiszforma és a nagyobb méretkategóriák), amelyek elsősorban a ritka fajok jellemző tulajdonságai voltak. Az összes vizsgált jelleg 7%-a abszolút ritka (kis populációméretű, élőhely-specialista és földrajzilag korlátozott elterjedésű) tulajdonság volt. Ezek nevezetesen kilenc nagy méretkategória és két kloroplasztiszalak volt, amelyek a különleges állapotú horvátországi Száva, Dráva és Odra folyók, valamint a magyarországi Rába folyókhoz kötődtek. Ezekkel az egyedi tulajdonságokkal rendelkező ritka fajok funkcionálisan elkülönülő és sebezhető tagjai a kovaalga közösségeknek.

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