

## DISTANCE-DECAY RELATIONSHIPS IN LOTIC ENVIRONMENTS: A CASE STUDY FROM THE LAKE BALATON REGION, HUNGARY

Géza B. SELMECZY<sup>1,2,3\*</sup>, Edit KIRÁLY<sup>1,2,3</sup>, Edina LENGYEL<sup>1,2,3</sup>,  
Rita ZSUGA-BIRÓ<sup>1,2,3</sup>, Csilla STENGER-KOVÁCS<sup>1,2,3</sup> and Azal ABBAS<sup>1,4,5</sup>

<sup>1</sup>Center for Natural Science, Research Group of Limnology, University of Pannonia,  
H–8200 Veszprém, Egyetem u. 10 Hungary; \*selmeczy.geza@mk.uni-pannon.hu

<sup>2</sup>HUN-REN-PE, Limnoecology Research Group, H–8200 Veszprém, Egyetem u.10, Hungary

<sup>3</sup>National Laboratory for Water Science and Water Security, Center for Natural Science,  
University of Pannonia, H–8200 Veszprém, Egyetem u. 10, Hungary

<sup>4</sup>Doctoral School of Biology, Institute of Biology, Eötvös Loránd University,  
H–1117 Budapest, Pázmány Péter sétány 1/C, Hungary

<sup>5</sup>Department of Diwanayah Education, Ministry of Education, Diwanayah City 58001, Iraq

Selmeczy, G. B., Király, E., Lengyel, E., Zsuga-Biró, R., Stenger-Kovács, Cs. & Abbas, A. (2025): Distance-decay relationships in lotic environments: a case study from the Lake Balaton region, Hungary. – *Studia bot. hung.* **56**(1): 15–24.

**Abstract:** A high number of processes and parameters are responsible for shaping phytoplankton communities, among which nutrient availability and light intensity most often receive particular attention; however, the distance between communities (distance-decay relationships – DDRs) has been little studied in this context. Thus, to extend our knowledge, DDRs were studied in lotic waterbodies in the region of Lake Balaton (Hungary). Our analysis shows that the distance-decay relationship does not affect the structure of the phytoplankton community across different streams. However, when examining different locations in the same streams, we found a small but significant effect. We conclude that deterministic processes like environmental filtering and species interaction are more important mechanisms shaping the structure of communities than stochastic processes like dispersal mechanisms and random effects.

**Key words:** algal communities, diversity, Reynolds's functional group, tychoplankton

### INTRODUCTION

Studying the various aspects of diversity plays a central role in ecological research. The Convention on Biological Diversity (CBD; article 2) defines biodiversity as the variability among living organisms from all sources, including terrestrial, marine, and other aquatic ecosystems, as well as the ecological complexes of which they are a part; this encompasses diversity within species, between species, and among ecosystems (GASTON and SPICER 2013). Thus, measuring biodiversity is quite complex and involves the analysis of genetic diversity, species types, assemblages, biotic communities, traits, functional groups, and their abundance, biomass, or other measures (DELONG 1996).

Understanding the structure and changes of phytoplankton assemblages through species alone is a major challenge. Although taxonomic information at species level can provide the most complete level of information, the defined species niches are missing in many cases. The classification of species into different traits and functional groups has greatly aided this understanding, and a few of them have become widespread: Reynolds's functional groups (RFG) (PADISÁK *et al.* 2009, REYNOLDS 1980, REYNOLDS *et al.* 2002), morpho-functional groups (MFG) (SALMASO and PADISÁK 2007), and the morphologically based functional groups (Kruk *et al.* 2010). It was a long journey to arrive at these classifications, during which algologists tried to classify the species along different ecological concepts, such as *r* and *K* selection (MARGALEF 1978) and CSR strategy (e.g. REYNOLDS 1988). Nowadays, in addition to the traditional microscopy-based identification, DNA-based methods are gaining an increasingly important role in phytoplankton research (e.g., TAPOLCZAI *et al.* 2025). Judit Padisák played a decisive role in developing the categorization of phytoplankton species and developing the concepts. This study is a tribute to her work, as it is exciting and challenging to gain a more precise understanding of the functioning of phytoplankton assemblages, which is largely based on her work. Although the explanations are becoming more precise, there is still a lot of information missing to accurately understand the changes occurring in phytoplankton assemblages. This is obvious when a typical phytoplankton biomonitoring data set (phytoplankton and classical environmental variables data matrix) is analysed with variation partitioning: a significant part of the variance cannot be explained. In this regard, we investigate a variable that is rarely considered, namely the effect of the geographical distance between communities on their composition.

The distance–decay relationship (DDR) indicates the similarity between ecological communities decreases as geographical distance increases. Consequently, it is anticipated that communities that are geographically distant will exhibit greater dissimilarity in their structure and composition than those that are closer (NEKOLA and WHITE 1999, SOININEN *et al.* 2007).

According to BAAS BECKING (1934) “Everything is everywhere, but the environment selects.”, which means that the taxa in a microbial community are determined primarily by environmental factors and not the limitation of migration. This idea is actually the forerunner of the niche theory (HUTCHINSON 1957). But is it truly the case that “Everything is everywhere”? To test the theory, we examined whether the composition of phytoplankton communities could be related to the distance between sampling points (both within and between streams).

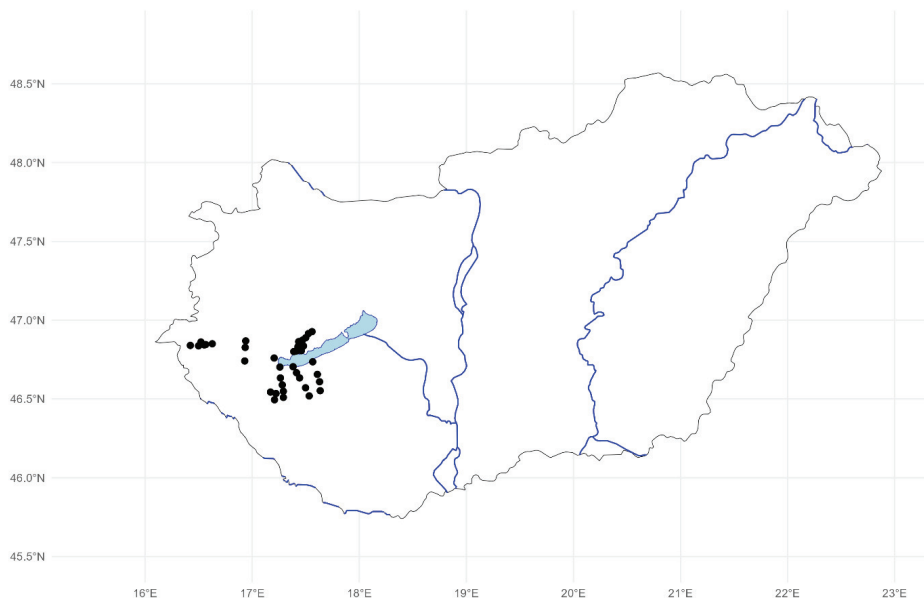
Thus, in this study, we aimed to explore the diversity and the distance-decay relationships of the phytoplankton community of the main inflows of Lake Balaton. We hypothesise that there is no DDR among the sampled locations, because the effects of the local environment are the most important driving mecha-

nism of the community structure. However, in case of the same watercourses, distance should be an important variable, because of the high number of drifting cells.

## MATERIALS AND METHODS

### *Study site and the measured variables*

A total of 38 locations of 18 watercourses were included in this study (Fig. 1) All the sampled streams and rivers are located in West Hungary and flows into Lake Balaton. Eight out of 18 watercourses were sampled at one location, all the other watercourses were sampled at least at two different locations. Thus, it was possible to analyse DDR within and between watercourses. Sampling was carried out in September 2022. Physical and chemical variables ( $T$  = temperature ( $^{\circ}\text{C}$ ),  $\text{DO}$  = oxygen concentration ( $\text{mg/L}$ ) and  $\text{DO\%}$  = saturation (%),  $\text{pH}$ ,  $\text{Cond}$  = conductivity ( $\mu\text{Scm}^{-1}$ ), and  $\text{Turb}$  = turbidity ( $\text{FNU}$ )) were measured with a Hach Lange HQ40d multimeter and a Hach Lange TSS portable turbidimeter at the sampling sites. Additionally,  $\sim 1.5$  litres water sample was collected and carried to the laboratory to measure the following variables: total phosphorus, soluble reactive phosphorus, total nitrogen, nitrite, nitrate, ammonium, soluble reactive silica, sulphate, chloride, bicarbonate, alkalinity, and chemical oxygen demand according to APHA (2012)



**Fig. 1.** Location of the sampling sites (black dots) in the Balaton region. Lake Balaton and the largest rivers (Duna and Tisza) are indicated in light blue and blue.

methods. Phytoplankton samples were collected in glass containers and Lugol's solution was added immediately. At least 400 settling units (cells, filaments, and colonies) were counted in each sample using a Zeiss Axiovert 100 (Oberkochen, Germany) inverted microscope according to the standard methods developed by LUND *et al.* (1958) and UTERMÖHL (1958). Phytoplankton biomass was calculated based on the most similar geometric forms according to HILLEBRAND *et al.* (1999) using the Opticount cell counting software (HEPPERLE 2008) and supposing  $1 \text{ g cm}^{-3}$  density. Phytoplankton taxa were sorted into Reynolds' functional groups according to the classification of REYNOLDS *et al.* (2002) updated by PADISÁK *et al.* (2009).

### *Statistical analysis*

Data analysis was carried out in R 4.5.1. environment (R Core Team 2025). Principal component analysis (PCA) was used to explore the main patterns among environmental variables and the phytoplankton community. Intercorrelations of the environmental variables were checked, thus oxygen saturation and alkalinity were not used to keep  $r < 0.8$ . Then environmental variables were scaled and the phytoplankton dataset was Hellinger transformed. "Envfit" function in the "vegan" package (OKSANEN *et al.* 2022) was used to fit the environmental variables onto the PCA ordination.

DDR analysis "Geodist" function from the geodist package (PADGHAM and SUMNER 2025) was used to calculate the spatial distances among the sampling locations and "vegdist" function in the "vegan" package (OKSANEN *et al.* 2022) was adopted to get the Bray-Curtis dissimilarity matrix of the phytoplankton communities. Linear regression was used to analyse the relationship between the spatial distances and the dissimilarity values. Analyses of the samples occurred separately within and between the watercourses in the linear regression, thus the hierarchical structure is handled properly.

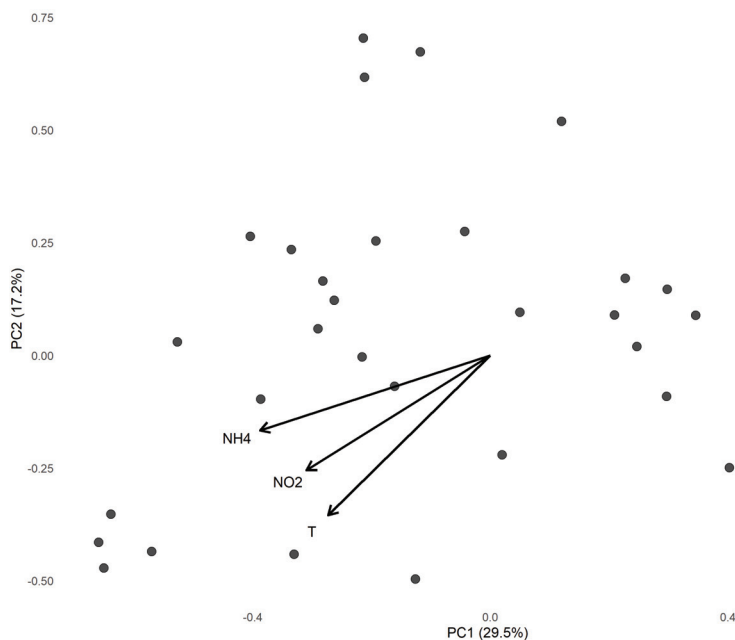
Variation partitioning was used to quantify the pure and the shared effects of the spatial and environmental variables on the RFG-based community composition. First, the most important environmental and spatial variables were selected with forward selection in an RDA model using the "ordistep" function. The VIFs of the explanatory variables were limited to ten in the RDA model following BORCARD *et al.* (2018). Secondly, variation partitioning was implemented with the "varpart" function and, third, the significance of the different fractions (the variation explained by a given set of variables) was tested by ANOVA with 1000 permutations. Spatial variables used in the variation partitioning were calculated as follows: First, a distance matrix was acquired based on the GPS coordinates, then spatial predictors were calculated using the PCNM (Principal Coordinates of Neighbour Matrices) method with the "pcnm" function. All functions used in the variation partitioning are available in the "vegan" package (OKSANEN *et al.* 2022).

## RESULTS

*Description of the phytoplankton assemblages and environmental variables*

Altogether, 253 taxa were found in the 38 locations (Fig. 1) belonging to 30 RFG's and 8 main taxonomic groups. Chlorophyta and Bacillariophyceae were the richest taxonomic groups with 89 and 56 taxa, respectively. The Bacillariophyceae group was dominated by tychoplanktonic elements, which is characteristic of small lotic waterbodies. Coda **X2** and **T<sub>b</sub>** were the most frequently occurring groups, which were found in 36 and 35 sampling spots. *Rhodomonas* spp. were typical taxa in the **X2** group; additionally, *Navicula* and *Nitzschia* spp. represented mostly the **T<sub>b</sub>** coda. In the case of biomass, **W1** and **Y** groups were the most dominant, represented primarily by *Euglena* spp. and *Cryptomonas* spp.

The first two axes of the principal component analysis explained 36.7% of the total variance of the phytoplankton community (Fig. 2). Significant relationships were visualised on the PCA ordination among the phytoplankton functional groups and environmental variables. Three variables  $\text{NO}_2^-$  ( $R^2 = 0.161$ ,  $P = 0.045$ ),  $\text{NH}_4^+$  ( $R^2 = 0.178$ ,  $P = 0.029$ ) and  $T$  ( $R^2 = 0.2$ ,  $P = 0.019$ ) were correlated significantly with the community structure.



**Fig. 2.** PCA ordination based on the phytoplankton community and environmental variables (only significant ones are indicated).

### *Distance decay relationship*

The distance among sampling locations varied between 1 and 100 km. Bray–Curtis dissimilarity of the phytoplankton community was not changed significantly with increasing spatial distance in the case of different streams (Fig. 3). However, if we compared the dissimilarity of the phytoplankton community in the case of given streams but at different locations, we found a small ( $R^2 = 0.1053$ ) but significant ( $p = 0.047$ ) effect (Table 1).

Variation partitioning revealed that the phytoplankton assemblages categorised according to RFG's were determined by the analysed environmental variables in 6.4%, additionally variance explained by spatial structure was 9.7%. The shared effect was 3.5% and quite a significant part (80.4%) remained unexplained (Fig. 4).

## DISCUSSION

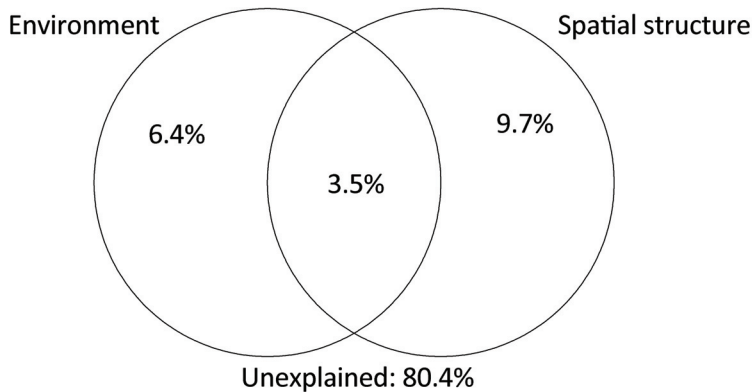
Our results suggest that the distance-decay relationship does not affect the structure of the phytoplankton communities across different streams. However, when examining different locations within the same stream, we found a small but significant effect. Additionally, variation partitioning has shown that both environ-



**Fig. 3.** Distance decay relationship based on Bray–Curtis dissimilarities of the phytoplankton assemblages. Red dots are indicated values from different streams and blue dots are indicated values comparing locations from the same waterbodies.

**Table 1.** Results of the linear models.

| Type            | Predictor   | Estimate  | Std. error | t value | M. R <sup>2</sup>     | p                      | Significance |
|-----------------|-------------|-----------|------------|---------|-----------------------|------------------------|--------------|
| Within stream   | (Intercept) | 0.6077    | 0.0591     | 10.286  | 0.1053                | $2.91 \times 10^{-12}$ | ***          |
|                 | distance    | 0.0075    | 0.00364    | 2.058   | 0.1053                | 0.0469                 | *            |
| Between streams | (Intercept) | 0.8771    | 0.0105     | 83.406  | $4.43 \times 10^{-5}$ | $< 2 \times 10^{-16}$  | ***          |
|                 | distance    | -0.000040 | 0.000234   | -0.171  | $4.43 \times 10^{-5}$ | 0.864                  |              |



**Fig. 4.** Results of the variation partitioning analysis conducted on phytoplankton functional groups. Percentages indicate the proportion of variation explained by environmental and spatial variables, and the shared and unexplained components.

mental variables and spatial structure are responsible for explaining some part of the variance; moreover, spatial structure accounts for 9.7%. These results indicate that distance plays a negligible role in shaping phytoplankton communities across streams, suggesting that deterministic processes are far more important than stochastic ones. The most important deterministic processes (niche theory – HUTCHINSON (1957)) are environmental filtering and interaction among species, while neutral theory (HUBBEL 2001) assumes that stochastic processes are shaping the communities like dispersion, stochastic fluctuations in birth and death rates, and other random events/effects. Thus, in our case, dispersal processes appear unimportant for shaping a given community. Migration of species between waterbodies in the case of phytoplankton is a relatively poorly studied topic (GREEN *et al.* 2023), with a few exceptions: TESSON *et al.* (2018) studied the survival of resting cysts of dinoflagellates by migratory waterbirds, whereas MANNING *et al.* (2021) showed the survival of diatoms transported externally on waterbirds. Although CELLAMARE *et al.* (2010) suggested quite long time ago that waterbirds could be an important vector for the dispersal of phytoplankton species from Africa to Europe. However, experimental studies in this topic appeared only quite recently, during which it was discovered that

*Raphidiopsis raciborskii* (SHA *et al.* 2025) and many other species (GÖRGÉNYI *et al.* 2023) can survive passing through a waterfowl's digestive system, as they remain viable in the faeces. This phenomenon probably contributed to the spread of some successful species, such as *Raphidiopsis raciborskii*, across continents (PADISÁK 1997).

In the case of within-stream analysis we found a small but significant DDR. It would be really interesting to know what the reader thinks about this result. Phytoplankton samples taken in a small stream only show a small degree of similarity as a function of distance. As stated in the hypothesis, we expected greater similarity due to the masses of cells drifting down in the watercourse. DDR can be explained by various factors, both intrinsic and extrinsic ones (NEKOLA and WHITE 1999). Although different factors are important for different organisms, the dispersal ability is a determining variable in the characteristics of DDR. DDR of the phytoplankton communities was analysed in the tributaries of the Amazon River (WETZEL *et al.* 2012). Although these waterbodies are much larger than those we studied, and the distances are much longer as well, the authors found higher similarities among the locations compared to our results. The results of the authors confirmed that higher dispersal abilities cause lower distance decay rate. Unfortunately, we cannot compare how well the spatial structure explains the variance of the data. In our case, it is quite low (10%). It suggests that despite the drifting cells, other variables are so important that they largely shape the communities. Most of the studies found that environmental variables are critically important (e.g. WOJCIECHOWSKI *et al.* 2017). However, only ~7% of the variance of the phytoplankton community data is explained by the measured environmental variables. The unexplained variance could be due to species interaction, microhabitat effects, or other factors that are difficult to measure and study.

Taken together, these findings highlight the complexity of phytoplankton community assembly and emphasize that our understanding of the principles governing the functioning and structure of phytoplankton communities is still far from complete.

\* \* \*

*Acknowledgements* – We are thankful to the contribution of colleagues and students of the Limnology Research Group, University of Pannonia. This study was supported by the RRF-2.3.1-21-2022-00008 project and GBS was supported by the Hungarian National Research, Development and Innovation Office (NKFIH) FK 137979.

**Összefoglaló:** Számos tényező és különböző folyamatok felelősek a fitoplankton közösségek alakításáért, amelyek közül a tápanyagok hozzáférhetősége és a fényintenzitás kap leggyakrabban kiemelt figyelmet. A közösségek közötti távolság hatását (distance-decay relationship (DDR)) kevésbé vizsgálták ebben az összefüggésben, ezért munkánk során a DDR hatást vizsgáltuk a Balatonba befolyó víztestekben. Eredményeink alapján, a DDR nem befolyásolja a fitoplankton közösség szerkezetét a különböző vízfolyások között. Azonban, amikor ugyanazon vízfolyások különböző

helyszíneit vizsgáltuk, kicsi, de szignifikáns hatást találtunk. A kutatás eredményei arra engednek következtetni, hogy a determinisztikus folyamatok, mint például a környezeti szűrés és a fajok kölcsönhatása fontosabb mechanizmusok a közösségek szerkezetének alakításában, mint a sztochasztikus folyamatok, úgymint a diszperziós mechanizmusok és a véletlenszerű hatások.

## REFERENCES

- APHA (2012): *Standard methods for the examination of water and wastewater*, 22nd ed. – APHA American Public Health Association, Washington.
- BAAS-BECKING, L. G. M. (1934): *Geobiologie; of inleiding tot de milieukunde*. – WP Van Stockum & Zoon NV.
- BORCARD, D., GILLET, F. and LEGENDRE, P. (2018): *Numerical ecology with R*. – Springer International Publishing, Cham., pp. 35–57.
- CELLAMARE, M., LEITÃO, M., COSTE, M., DUTARTRE, A. and HAURY, J. (2010): Tropical phytoplankton taxa in Aquitaine lakes (France). – *Hydrobiologia* **639**: 129–145.  
<https://doi.org/10.1007/s10750-009-0029-x>
- DELONG, J. R., D. C. (1996): Defining biodiversity. JSTOR. – *Wildlife Soc. Bull.*: 738–749.
- GASTON, K. J., and SPICER, J. I. (2013): *Biodiversity: an introduction*. – John Wiley & Sons.
- GÖRGÉNYI, J., KÓKAI, Z., BORICS, G., SEBASTIÁN-GONZÁLEZ, E., TÓTH, P. and LOVAS-KISS, Á. (2023): The role of the migratory waterbirds in algae dispersion. – *Acta Biol. Plant. Agr.* **11**: 12. <https://doi.org/10.21406/abpa.2023.11.2.12>
- GREEN, A. J., LOVAS-KISS, Á., REYNOLDS, C., SEBASTIÁN-GONZÁLEZ, E., SILVA, G. G., VAN LEEUWEN, C. H. A. and WILKINSON, D. M. (2023): Dispersal of aquatic and terrestrial organisms by waterbirds: A review of current knowledge and future priorities. – *Freshw. Biol.* **68**: 173–190. <https://doi.org/10.1111/fwb.14038>
- HEPPERLE, D. (2008): *OPTICOUNT – Software for the enumeration of plankton*. – [available on internet at [http://science.do-mix.de/software\\_opticount.php](http://science.do-mix.de/software_opticount.php)]
- HILLEBRAND, H., DÜRSELEN, C., KIRSCHTEL, D., POLLINGER, U. and ZOHARY, T. (1999): Biovolume calculation for pelagic and benthic microalgae. – *J. Phycol.* **35**: 403–424.  
<https://doi.org/10.1046/j.1529-8817.1999.3520403.x>
- HUBBELL, S. P. (2001): *The unified neutral theory of biodiversity and biogeography (MPB-32)*. – Princeton University Press.
- HUTCHINSON, G. E. (1957): Concluding remarks. – *Cold Spring Harbor Symposia on Quantitative Biology* **22**: 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>
- KRUK, C., HUSZAR, V. L. M., PEETERS, E. T. H. M., BONILLA, S., COSTA, L., LÜRLING, M., REYNOLDS, C. S. and SCHEFFER, M. (2010): A morphological classification capturing functional variation in phytoplankton. – *Freshw. Biol.* **55**: 614–627.  
<https://doi.org/10.1111/j.1365-2427.2009.02298.x>
- LUND, J. W. G., KIPLING, C. and LE CREN, E. D. (1958): The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. – *Hydrobiologia* **11**: 143–170. <https://doi.org/10.1007/BF00007865>
- MANNING, F. S., CURTIS, P. J., WALKER, I. R. and PITHER, J. (2021): Potential long-distance dispersal of freshwater diatoms adhering to waterfowl plumage. – *Freshw. Biol.* **66**: 1136–1148. <https://doi.org/10.1111/fwb.13706>
- MARGALEF, R. (1978): Life-forms of phytoplankton as survival alternatives in an unstable environment. Gauthier-Villars. – *Oceanol. Acta* **1**: 493–509.
- NEKOLA, J. C. and WHITE, P. S. (1999): The distance decay of similarity in biogeography and ecology. Wiley. – *J. Biogeogr.* **26**: 867–878. <https://doi.org/10.1046/j.1365-2699.1999.00305.x>

- OKSANEN, J., SIMPSON, G. L., BLANCHET, F. G., KINDT, R., LEGENDRE, P., MINCHIN, P. R., O'HARA, R. B., SOLYMOS, P., STEVENS, M. H. H., SZOECS, E., WAGNER, H., BARBOUR, M., BEDWARD, M., BOLKER, B., BORCARD, D., CARVALHO, G., CHIRICO, M., CACERES, M. D., DURAND, S., EVANGELISTA, R., FITZJOHN, H. B. A., FRIENDLY, M., FURNEAUX, B., HANNIGAN, G., HILL, M. O., LAHTI, L., MCGLINN, D., OUELLETTE, M.-H., CUNHA, E. R., SMITH, T., STIER, A., BRAAK, C. J. F. T. and WEEDON, J. (2022): *Vegan: community ecology package*. – [available on internet at <https://CRAN.R-project.org/package=vegan>].
- PADGHAM, M., SUMNER, M. D. and C. F. F. K. (Original author of included code for geodesic distances) (2025): *geodist: fast, dependency-free geodesic distance calculations*.
- PADISÁK, J., CROSSETTI, L. O. and NASELLI-FLORES, L. (2009): Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. – *Hydrobiologia* **621**: 1–19. <https://doi.org/10.1007/s10750-008-9645-0>
- REYNOLDS, C. S. (1980): Phytoplankton assemblages and their periodicity in stratifying lake systems. – *Ecography* **3**: 141–159. <https://doi.org/10.1111/j.1600-0587.1980.tb00721.x>
- REYNOLDS, C. S. (1988): *Functional morphology and the adaptive strategies of freshwater phytoplankton*. – In: Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, pp. 388–433.
- REYNOLDS, C. S., HUSZAR, V., KRUK, C., NASELLI-FLORES, L. and MELO, S. (2002): Towards a functional classification of the freshwater phytoplankton. – *J. Plankton Res.* **24**: 417–428. <https://doi.org/10.1093/plankt/24.5.417>
- SALMASO, N. and PADISÁK, J. (2007): Morpho-functional groups and phytoplankton development in two deep lakes (Lake Garda, Italy and Lake Stechlin, Germany). – *Hydrobiologia* **578**: 97–112. <https://doi.org/10.1007/s10750-006-0437-0>
- SOININEN, J., MCDONALD, R. and HILLEBRAND, H. (2007): The distance decay of similarity in ecological communities. Wiley. – *Ecography* **30**: 3–12. <https://doi.org/10.1111/j.0906-7590.2007.04817.x>
- SHA, Z., CHEN, H., JIN, L., ZHENG, Q., LU, Y., SIDO, M. Y., WILLIS, A., LIU, C. and YANG, J. (2025): Evidence of global dispersal of the harmful cyanobacterium, *Raphidiopsis raciborskii*, in lentic freshwaters through migratory waterbirds. – *Harmful Algae* **142**: 102786. <https://doi.org/10.1016/j.hal.2024.102786>
- TAPOLCZAI, K., RIMET, F., ČIRIĆ, M., BALLOT, A., LAPLACE-TREYTURE, C. and ALRIC, B. (2025): A novel framework for phytoplankton biomonitoring: Trait assignment of 23S rRNA sequences. Elsevier. – *Ecol. Indicators* **173**: 113361. <https://doi.org/10.1016/j.ecolind.2025.113361>
- TESSON, S. V. M., WEISSBACH, A., KREMP, A., LINDSTRÖM, Å. and RENGEFORS, K. (2018): The potential for dispersal of microalgal resting cysts by migratory birds. – *J. Phycol.* **54**: 518–528. <https://doi.org/10.1111/jpy.12756>
- TEAM, R. C. (2016): *R: a language and environment for statistical computing*. – R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- UTERMOHL, H. (1958): Zur Vervollkommung der quantitativen phytoplankton-Methodik. – *Mitt. Intern. Verein. theoret. angew. Limnol.* **9**: 1–38.
- WETZEL, C. E., BICUDO, D. D. C., ECTOR, L., LOBO, E. A., SOININEN, J., LANDEIRO, V. L. and BINI, L. M. (2012): Distance decay of similarity in neotropical diatom communities. – *PLoS ONE* **7**: e45071. <https://doi.org/10.1371/journal.pone.0045071>
- WOJCIECHOWSKI, J., HEINO, J., BINI, L. M. and PADIAL, A. A. (2017): Temporal variation in phytoplankton beta diversity patterns and metacommunity structures across subtropical reservoirs. – *Freshw. Biol.* **62**: 751–766. <https://doi.org/10.1111/fwb.12899>

(submitted: 04.08.2025; accepted: 11.09.2025)