
Final Report

The functional diversity - ecosystem functioning relationship in natural phytoplankton communities

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1) Biodiversity – ecosystem functioning relationship in lakes

I have analysed the BEF relationships in two large phytoplankton data sets from Fennoscandia and Hungary. According to the hypothesis, functional diversity components outperformed taxonomic and functional richness in predicting RUE in both data sets. The results have been presented in a general ecological meeting **[1]** but have not been published yet due to the project's suspension in 2019. In co-operative works related to the project, we showed that functional trait composition of benthic algae could summarise ecological status information in a highly efficient way **[2]**; phytoplankton contained both active and non-active elements relevant to better understand phytoplankton diversity **[3]**; high Cyanobacteria dominance over time constrained energy transfer towards higher trophic levels **[4]**.

[1] Abonyi A., Botta-Dukát Z., Borics G., Várbíró G. & Ptacnik R. The functional diversity–ecosystem functioning relationship in natural lake phytoplankton communities. In: 48th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland. (Eds Y. Muraoka & R. Tschirf). Ecology-Meeting the scientific challenges of a complex world. 10–14 September 2018. Gesellschaft für Ökologie e.V. (GfÖ).

Conference summary: Recent studies support a positive biodiversity–ecosystem functioning (BEF) relationship in phytoplankton. Furthermore, functional richness was shown to outperform taxonomic richness in predicting ecosystem functioning in natural phytoplankton communities. However, independent functional diversity (FD) components (evenness, divergence, dispersion) have never been compared with functional richness in BEF. Here, based on the functional trait and functional response groups approaches, we tested whether the three FD components alone, as well as on top of taxonomic richness outperform functional richness in predicting resource-use efficiency in oligotrophic (Fennoscandian lakes) and eutrophic (Hungarian oxbow lakes) phytoplankton communities. FD components alone outperformed functional richness only in oligotrophic phytoplankton communities. However, on top of taxonomic richness, FD components enhanced highly our ability in predicting ecosystem functioning in both the oligotrophic and eutrophic phytoplankton data sets. In all BEF models (FD components alone, taxonomic richness + FD components), the trait-based approach predicted ecosystem function better than the functional response group approach. Our results highlight that functional diversity components add reliable ecological information on top of taxonomic richness, and altogether outperform functional richness in BEF. Furthermore, simple functional traits may potentially enhance our ability in modelling ecosystem functioning in natural lake phytoplankton communities.

Link: https://www.gfoe.org/de/node/1315

[2] Stenger-Kovács C., Körmendi K., Lengyel E., **Abonyi A.**, Hajnal É., Szabó B., Buczkó K. & Padisák J. (2018) Expanding the trait-based concept of benthic diatoms: Development of trait- and species-based indices for conductivity as the master variable of ecological status in continental saline lakes. Ecological Indicators, 95, 63-74.

Abstract: Shallow, saline inland lakes occur over large areas in Central-Europe and they bear exceptionally high biological conservation values. Climate change and anthropogenic activities threaten their natural conditions, or even their existence. These aquatic ecosystems are exposed to multiple stress like naturally high conductivity, pH and nutrient load with very low transparency for light. As they are subjects of criteria set by the EC Water Framework Directive and biological conservation managment, there is an urgent need for developing a suitable quality index for their ecological status assessment. As one major Biological Quality Element, benthic diatoms may provide a reliable basis for their ecological status indication. Here, in a large data set covering the soda lakes of the Carpathian basin, we developed a species- and a trait-based diatom ecological status index. First, based on the weighted average method, we developed a type specific, species-based diatom index (DISP = Diatom Index for Soda Pans) using conductivity as master variable of environmental constrains; and therefore the ecological status in soda lakes. Furthermore, by adapting and improving further the widely-used diatom ecological guild concept, we also developed an alternative trait-based index, which helps avoiding some limitations arising from the obvious complexity of the taxonomy-based approach. Our DISP index covered a significantly larger species pool for index calculation, and responded to conductivity in a more reliable way compared to other available indices. In the trait-based index (TBI) motility, small cell size, and less roundish, more elongated shape as functional and morphological traits indicated pristine ecological conditions (i.e high conductivity) of the soda pans. Planktic life form, high and low ecological guild profiles, as well as the large cell size indicated worse ecological conditions (e.g. lower conductivity). Our study highlights that benthic diatoms provide a reliable basis for ecological status assessment in soda lakes. While both the taxonomic and the functional trait approaches performed well in our analysis, the success of the trait-based approach may enable the use of our TBI index in biomonitoring and conservation management of soda lakes outside of the Carpathian basin, independently of the geographic location.

Link: http://real.mtak.hu/83518/

[3] Görgényi J., Tóthmérész B., Várbíró G., **Abonyi A.**, T-Krasznai E., B-Béres V., Borics G. (2019): Contribution of phytoplankton functional groups to the diversity of a eutrophic oxbow lake, Hydrobiologia, 830, 287–301.

Abstract: The functional group (FG) concept suggests that species having different phylogenetic origins but possessing similar functional characteristics can be considered as functional groups and these co-occur in the phytoplankton. Here, we study how functional redundancy of phytoplankton taxa (within group richness) contribute to the species diversity of assemblages in an oxbow lake in the Carpathian Basin. We found that although the observed functional redundancy was similar among several FGs, the shape of the species accumulation curves of these groups was considerably different, implying that the observed species numbers alone do not represent the real functional redundancy of the groups. We demonstrated that FGs that showed asymptotes in species richness estimates in small spatial

scale, exhibited steady increase in large spatial, and temporal scales. The contribution of FGs to species richness depended strongly on the relative biomass of each FG. Species accumulation curves of those groups of which elements dominated in the phytoplankton, appeared to be approaching asymptotes. Since the shapes of species accumulation curves refer to the strengths of within-group competition among constituent species, our results imply that functional redundancy of phytoplankton is influenced by the role that the elements play within the assemblages.

Link: https://link.springer.com/article/10.1007/s10750-018-3878-3

[4] Selmeczy GB., **Abonyi A.**, Krienitz L., Kasprzak P., Casper P., Telcs A., Somogyvári Z., Padisák J. (2019): Old sins have long shadows: climate change weakens efficiency of trophic coupling of phyto- and zooplankton in a deep oligo-mesotrophic lowland lake (Stechlin, Germany).., Hydrobiologia, 831, 101–117.

Abstract: Analysis of a long-term (1994–2014) data set of phytoplankton and zooplankton in the deep, dimictic, oligo-mesotrophic Lake Stechlin (Germany) revealed trend-like changes: phytoplankton biomass and resource use efficiency increased with proliferation of heterocytic cyanobacteria (Dolichospermum spp. and Aphanizomenon flos-aquae), and those of especially large-sized zooplankton (Eudiaptomus, Eurytemora) decreased. These reverse trends are clear eutrophication symptoms and suggest a long-term trophic decoupling with potential decrease in energy transport towards higher tropic levels. Total phosphorus increased significantly over time; however, there is no known external P load for Lake Stechlin. Causality analysis enabled us to identify the primary reason of the observed changes. According to the results, stronger and longer-lasting stratification (measured as relative water column stability) drove the observed changes and the gradual regime shift was initiated by an extreme weather event—both indicating that climate change has been the crucial driver of the planktic community in this lake. Our study also documents that there might be decadal delays between cause and consequences in aquatic food webs, supporting the essential importance of long-term monitoring efforts.

Link: http://real.mtak.hu/89640/

2) Functional diversity in river ecosystems:

In co-operative works related to the project, we showed that FD of the Danube phytoplankton increased over time **[5]**, while the cell size structure has also been altered **[6]**, both affecting pelagic ecosystem functioning negatively. The combination of benthic and planktic functional approaches helped understand the FD–environment relationship in a large river **[7]**; FD of benthic diatoms were sensitive indicators of drought **[8]**; FD helped understand invasion effects in riverine fishes **[9]**.

[5] Abonyi A., Ács É., Hidas A., Grigorszky I., Várbíró G., Borics G. & Kiss K.T. (2018) Functional diversity of phytoplankton highlights long-term gradual regime shift in the middle section of the Danube River due to global warming, human impacts and oligotrophication. Freshwater Biology, 63, 456-472.

Abstract: 1. Long-term dynamics of phytoplankton have been addressed in marine and lake systems, but rarely in rivers. Large rivers, however, are highly human-impacted, whereas global warming may further affect the functioning of phytoplankton at long-term scale. 2. In

the middle section of the large European Danube River, long-term decrease in phytoplankton biomass (Chl-a) and increase in species diversity have formerly been revealed. The functional community composition that relates to ecosystem functioning directly has not been addressed previously. We analyze a 34-year long phytoplankton dataset from the middle river section at Göd (N-Budapest), Hungary. We focus on gradual changes in the functional composition and functional diversity components based on the functional trait and functional group approaches. 3. We hypothesized that long-term gradual changes in major environmental constraints should be followed by gradual shifts in dominance relationships among functional traits and functional groups of phytoplankton. We further hypothesized that functional shifts were highlighted by gradual changes in functional diversity components: evenness, divergence, and dispersion. 4. Water discharge of the middle Danube shifted towards the more frequent occurrence of lower values. On the other hand, high floods (> 3000 m3s-s) increased significantly with shortening tendency in duration and altered seasonality. The concentration of N- and P- forms, as well as total suspended solids decreased significantly. Water temperature increased significantly, especially in summer. In the phytoplankton, single-celled eutrophic centric diatoms decreased in relative abundance, but flagellated, elongated, and filamentous forms increased. A clear functional shift was the dominance decrease of planktonic taxa and the relative abundance increase of benthic diatoms. 5. All functional diversity components increased significantly in the entire dataset, except functional evenness based on the functional group approach. At seasonal scale, all significant trends showed increases, except the functional evenness components of the functional group approach, which decreased in winter and spring significantly. 6. Long-term increase in functional diversity components could alone indicate enhanced ecosystem functioning of phytoplankton in the middle section of the Danube. However, we argue that the observed increase in functional diversity may be related to a gradual shift from high-biomass communities with the dominance of eutrophic centric diatoms towards the relative increase of several, but low-biomass elements. These include a few planktonic algae well adapted to the altered conditions, diatoms with benthic origin, and dispersed limnophilic taxa.
7. Our results provide the first evidence for a long-term phytoplankton functional regime shift in a European large river. Global warming, human impacts and oligotrophication might potentially increase the functional diversity of large river phytoplankton, but the origin and functional role of taxa should carefully be considered. The observed functional shifts in phytoplankton might also be indicative for alterations in the food web structure of the middle section of the Danube River at long-term scale.

Link: http://real.mtak.hu/79170/

[6] Abonyi A., Kiss K.T., Hidas A., Várbíró G., Borics G. & Ács É., (2020): Cell Size Decrease and Altered Size Structure of Phytoplankton Constrain Ecosystem Functioning in the Middle Danube River Over Multiple Decades. Ecosystems, 23, 1254–1264.

Abstract: Reduced body size is among the universal ecological responses to global warming. Our knowledge on how altered body size affects ecosystem functioning in ectothermic aquatic organisms is still limited. We analysed trends in the cell size structure of phytoplankton in the middle Danube River over a 34-year period at multiple levels: (1) average cell size of assemblages (ACS), (2) within the centric diatom community and (3) in the dominant centric diatom taxon: Stephanodiscus. We asked whether global warming and human impacts affected the average cell size of phytoplankton. Also, whether the altered size structure affected how chlorophyll-a, as an ecosystem functioning measure, relates to the ACS of phytoplankton. The cell size of phytoplankton decreased significantly at all organisation

levels, and the assemblages became more dispersed in cell size over time. Environmental variables related to global warming and human impacts affected the ACS of phytoplankton significantly. The relationship between chlorophyll-a and the ACS of phytoplankton shifted from negative linear to broad and then narrow hump shape over time. Longer water residence time, warming and decline in nutrients and suspended solids decrease the ACS of phytoplankton in the middle Danube and expectedly in other large rivers. Our results suggest that cell size decrease in phytoplankton, especially of centric diatoms, constrains planktic algal biomass production in large rivers, independently of algal density. Such cell size decrease may also affect higher trophic levels and enhance the more frequent occurrence of "clear-water" plankton in large, human-impacted rivers under global change.

Link: https://link.springer.com/article/10.1007/s10021-019-00467-6

[7] Wang C., B-Béres V., Stenger-Kovács C., Li X. & **Abonyi A.** (2018) Enhanced ecological indication based on combined planktic and benthic functional approaches in large river phytoplankton ecology. Hydrobiologia, 818, 163–175.

Abstract: The occurrence of benthic diatoms in large river plankton is considered to be highly stochastic. Accordingly, the widely applied phytoplankton functional group concept sensu Reynolds (FG) classifies all benthic diatom taxa together. Based on data of a high frequency 1-year long phytoplankton survey of the Pearl River (China), we tested whether the combination of the FG system with various trait-based classifications of benthic diatoms enhances our ability in predicting the community composition from the local environment. Using the Self Organizing Map approach, we identified characteristic community compositions based on (i) taxonomic data, (ii) the FG approach, and (iii) the FG system combined with trait-based functional approaches of benthic diatoms: size structure, ecological guilds, and eco-morphological groups. All combined functional approaches enabled better predictions for the community composition than the taxonomic data or the FG system alone. The most reliable approach was the combination of the FG system with ecological guilds of benthic diatoms. Therefore, the occurrence of benthic diatoms in large river phytoplankton can be assessed ecologically in a meaningful way based on combined planktic and benthic functional classifications. The application of such an approach seems to be highly relevant in large river phytoplankton ecology, ecological modelling, or ecological status indication.

Link: http://real.mtak.hu/83104/

[8] B-Béres V., Tóthmérész B., Bácsi I., Borics G., **Abonyi A.**, Tapolczai K., Rimet F., Bouchez Á., Várbíró G., Török P. (2019): Autumn drought drives functional diversity of benthic diatom assemblages of continental intermittent streams, Advances in Water Resources, 126, 129-136.

Abstract: Climate change is predicted to increase drought occurrence and severity in small continental watercourses. Here, we studied the structure and the functional diversity of benthic diatom assemblages in lowland intermittent and permanent watercourses of the Carpathian Basin. We assumed that the community structure of intermittent and permanent watercourses would be markedly different, and the functional diversity in both would be strongly influenced by autumn drought. We found that intermittent streams were primarily characterized by small-sized generalists and aerophilic taxa, while permanent watercourses were inhabited by large-sized planktic or fast moving groups. The functional richness was significantly lower in intermittent than in permanent streams. This decrease in the functional

richness of benthic algal communities may negatively affect the functioning of lotic algal communities. We conclude that diatom assemblages in lowland intermittent watercourses are sensitive indicators of changes in ecosystem properties, and should be considered in appropriate evaluation and management of extreme climatic events on aquatic ecosystems.

Link: http://real.mtak.hu/91791/

[9] Takács P., Abonyi A., Bánó B. & Erős T. (2021) Effect of non-native species on taxonomic and functional diversity of fish communities in different river types. Biodiversity and Conservation, 30, 2511–2528.

Abstract: Recent researches suggest that functional diversity represents the response of communities to environmental alterations better than taxonomic diversity. However, there is scarce information about how the functional diversity of freshwater fishes is affected by habitat type and the dominance of non-native species. To address this question, we analysed a large database containing 15 morpho-functional traits of 61 fish species from the Pannon Biogeographic region (Hungary). Based on a fish faunistic list and relative abundance of taxa, we quantified the taxonomic and functional diversity of riverine communities for > 700 sites of six habitat types. We asked how non-native fishes affected the taxonomic and functional diversity in different river types and at the local scale (i.e. at the site level), and how the diversity measures of native fauna elements changes along the invasion gradient. Our results showed that both functional and taxonomic richness increases with habitat complexity, from small headwater streams to large rivers. Therefore taxonomic diversity served as a good proxy for functional diversity along the environmental gradient of river types. Non-natives showed considerable functional diversity relative to their species number in each habitat type. Diversity values of native fauna elements initially increased, and then showed a major decrease along the invasion gradient. River type-specific evaluations highlighted the importance of considering the proliferation of invasive species based on both taxonomic and functional diversity indices. We argue that type-specific action plans are needed in conservation management to preserve the taxonomic and functional diversity of native fishes in Hungary, but also elsewhere.

Link: https://link.springer.com/article/10.1007/s10531-021-02207-6

3) Review works related to the project:

In co-operative works related to the project, I reviewed the history of Reynolds' FG classification for rivers **[10]**, described the FG approach in a niche-based concept **[11]**, participated in reviewing phytoplankton diversity with the aspect of functional diversity **[12]**, and summarised with colleagues when functional traits were beneficial for biological data **[13]**.

[10] Abonyi A., Descy J.-P., Borics G. & Smeti E. (2021) From historical backgrounds towards the functional classification of river phytoplankton sensu Colin S. Reynolds: what future merits the approach may hold? Hydrobiologia, 848, 131–142.

Abstract: River phytoplankton has been studied to understand its occurrence and composition since the end of the nineteenth century. Later, pioneers addressed mechanisms that affected river phytoplankton by "origin of plankton", "turbulent mixing", "flow heterogeneity", "paradox of potamoplankton maintenance" and "dead zones" as keywords along the twentieth

century. A major shift came with the recognition that characteristic units in phytoplankton compositions could be linked to specific set of environmental conditions, known as the "Phytoplankton Functional Group concept" sensu Reynolds. The FG concept could successfully be applied to river phytoplankton due to its close resemblance to shallow lakes phytoplankton. The FG approach enables one to separate the effects of "natural constraints" and "human impacts" on river phytoplankton and to evaluate the ecological status of rivers. The FG classification has mainly been advocated in the context of how the environment shaped the functional composition of phytoplankton. It may be further developed in the future by a trait-based mechanistic classification of taxa into FGs, and by the exact quantification of FGs on ecosystem functioning. These improvements will help quantify how global warming and human impacts affect river phytoplankton and corresponding alterations in ecosystem functioning.

Link: https://link.springer.com/article/10.1007/s10750-020-04300-3

[11] Nagy-László Zs., Padisák J., Borics g., **Abonyi A.**, B-Béres V. & Várbíró G. (2020) Analysis of niche characteristics of phytoplankton functional groups in fluvial ecosystems. Journal of Plankton Research, 42 (3), 355–367.

Abstract: Assigning species to functional response groups in phytoplankton ecology reduces the number of functional units, which helps understand the processes that shape diversity and functioning of planktonic assemblages. Although the concept has become widespread in recent years, numerical characterization of the groups' positions in the niche space remained a challenging task. Using a large river phytoplankton dataset, we characterized the functional groups (FGs) of phytoplankton by their niche position and niche breadth in the niche space defined by the relevant environmental variables using the Outlying Main Index approach. The niche space has been defined primarily by trophic-related (nutrients) and river size-related variables (water residence time, discharge). Although we hypothesized that FGs with central niche position would have wide, while those with marginal niche position have narrow niche breadth, these have not been corroborated by the results. Rather, FGs occurred both with central niche position and intermediate breadth, as well as with marginal niche position and wide breadth. Niche position of several FGs was different from that suggested by their known habitat templates in lakes. Furthermore, we found no significant relationship between niche position and niche breadth, suggesting that the occurrence of FGs in rivers is simultaneously influenced by both niche characteristics.

Link: https://academic.oup.com/plankt/article/42/3/355/5837349?login=true

[12] Borics G., Abonyi A., Salmaso N. & Ptacnik R. (2021) Freshwater phytoplankton diversity: models, drivers and implications for ecosystem properties. Hydrobiologia, 848, 53-75.

Abstract: Our understanding on phytoplankton diversity has largely been progressing since the publication of Hutchinson on the paradox of the plankton. In this paper, we summarise some major steps in phytoplankton ecology in the context of mechanisms underlying phytoplankton diversity. Here, we provide a framework for phytoplankton community assembly and an overview of measures on taxonomic and functional diversity. We show how ecological theories on species competition together with modelling approaches and laboratory experiments helped understand species coexistence and maintenance of diversity in phytoplankton. The non-equilibrium nature of phytoplankton and the role of disturbances in

shaping diversity are also discussed. Furthermore, we discuss the role of water body size, productivity of habitats and temperature on phytoplankton species richness, and how diversity may affect the functioning of lake ecosystems. At last, we give an insight into molecular tools that have emerged in the last decades and argue how it has broadened our perspective on microbial diversity. Besides historical backgrounds, some critical comments have also been made.

Link: https://link.springer.com/article/10.1007/s10750-020-04332-9

[13] Endrédi A., Jordán F. & Abonyi A. (2018) Trait-based paradise – or only feeding the computer with biology? Community Ecology, 19(3), 319-321.

Abstract: We briefly discuss the relationship between the biological knowledge and the methodological issues related to trait- based ecological analyses. We provide illustrative examples and argue that the biological novelty of trait-based research is generally less than expected - while new information is mostly coming from data management and methodology.

Link: https://link.springer.com/content/pdf/10.1556/168.2018.19.3.13.pdf

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