The role of spatial constraints in the organization and biodiversity conservation of aquatic communities

The main aim of our project was to increase our knowledge about the importance of spatial structuring in the organization of communities, especially in the field of freshwater ecology and from a metacommunity context. Specifically, we tested how patterns and associated ecological mechanisms change depending on topological and environmental features of the sampling sites in a variety of aquatic groups (benthic algae, macrophytes, macroinvertebrates and fish). We examined the recolonization dynamics of fishes following a massive fish kill along a whole river system (i.e. red sludge disaster in the Marcal system) with emphasis on the role of the spatial position of the sampling site in successional dynamics. We also intended to improve former community evaluation tools, including diversity analysis and the application of multivariate or network based methods.

In general, I believe, the project was successful. We could finish the project and could deal with all of our study aims, although clearly we were more successful in developing some subprojects than in others. In general we could produce a lot's of scientific articles which further our knowledge about the organization of freshwater communities, and especially about the role of spatial factors in their organization. In brief, we showed the outmost importance of environmental variables in the organization of aquatic metacommunities, and the less important role of spatial factors. We developed new evaluation methods in the study of community structure and organization and/or tested the applicability of novel evaluation tools. In fact, we explored the drawback of some current evaluation tools in some of our papers, which may highlight that common evaluation tools had to be used with caution in future community analyses. Most of our study design was devoted to dendritic stream networks, and here we explored the role of network position, the effect of natural environmental variables and human modifications on community organization. Below I summarize most (but not all) subprojects in detail to show the specific main results of this project. Note, that some of our materials are still in manuscript form, especially those ones which deal with macroinvertebrate organisms and applied network analysis, but I think the value of our work can already be evaluated based on the already published scientific papers.

The role of spatial constraints (i.e. here the factors which influence dispersal) is not static, but may show temporal variations. In one of our former study (Erős et al., Freshwater Biology, 2012, 57: 1914–1928) we showed that the role of environmental and spatial drivers changes seasonally for fish metacommunities. In the project we further evaluated our data and applied elements of metacommunity structure analysis to examine variations in the spatial distributions of stream fishes over time and to explore possible structuring mechanisms (Erős et al., 2014). We showed that although the major environmental gradients influencing species distributions remained largely the same in time, the best-fit pattern of metacommunity structure varied according to sampling occasion and whether or not we included non-native species in the analyses. Quasi-Clementsian and Clementsian structures were the predominant best-fit structures, indicating the importance of species turnover among sites and the existence of more or less discrete community boundaries. The environmental gradient most correlated with metacommunity structure was defined by altitude, area of artificial ponds in the catchment, and dissolved oxygen content. Our results suggested that the best-fit metacommunity structure of the native species can change in time due to seasonal changes in distribution patterns. However, the distribution of non-native species throughout the landscape homogenizes the temporal variability in metacommunity structure of native species. We emphasized that further studies are necessary from other regions to examine best-fit-metacommunity structures of stream fishes within relatively short environmental gradients. During this study, we have realized some of the drawback of the elements of metacommunity structure method, and these thoughts were developed in a critical evaluation article (see Schmera et al., 2018b below)

In another study we explored the temporal variability of fish assemblages in a closely natural (reference) stream and showed that local scale factors were more important than regional ones (i.e. dispersal dynamics, spatial position in the network) in the taxonomic and functional variability of the assemblage (Czeglédi and Erős, 2013). We found the occurrence of the most abundant species was persistent, while their relative abundance was variable. Rare, satellite species formed less than 3% of the assemblage and contributed little to variations in relative abundance. Assemblage level trophic function proved to be relatively stable across years, but showed clear seasonality. The pattern of long-term taxonomic composition indicated that seasonal differences in trophic function were primarily due to a switch to alternate food resources by some species between seasons and not due to periodic immigration/emigration of fish. Overall, our study showed significant directional changes in taxonomic variability in time, but relative stability in trophic function, and suggested that local processes (i.e. population dynamics of resident species and seasonality of food resources) influenced assemblage dynamics, while the relative role of regional scale processes (periodic immigration/emmigration) was low.

We also examined the role of spatial, temporal and ontogenetic factors on the assemblage structure and diet variability of lake fish assemblages using direct ordination analyses and variance partitioning and revealed the role of spatial factors (Specziár and Erős, 2013, 2014). The role of spatial vs environmental factors in aquatic assemblage organization was also the topic of another paper (Árva et al., 2015) in which we showed that spatial factors (i.e. dispersal limitation) can have significant importance in the assemblage organization of macroinvertabrates even at relatively small spatial extent (i.e. within a lake).

We reviewed the role of large scale spatial and environmental factors on the trait based diversity and composition of stream communities by providing a synthesis of trait patterns of stream communities from a macroecological perspective (Heino et al., 2013). We argued that although both natural and anthropogenic filters shape community traits, examination of poorly understood natural filters, including those acting at large-scales, should receive increasing attention. Such knowledge is vital for reliably inferring anthropogenic impacts on stream communities and ecosystems. We synthesised knowledge of two large-scale spatial patterns of stream communities: among drainage basins (i.e. geographic variation) and within drainage basins (i.e. longitudinal variation). Our review highlighted clear evidence for large-scale influences on the trait composition in stream systems. We concluded that the question of how the trait composition of stream communities varies along geographical and environmental gradients is far from settled. A challenge for large-scale stream ecology is to provide a more specific view of trait variation in multiple taxonomic groups (e.g. do traits vary similarly in different organisms groups?), along major environmental gradients (e.g. is trait variation similar along the same environmental gradients in different regions?) and among different regional entities (e.g. do the traits vary, on average, among different regions?).

Of the community evaluation tools, we developed a new approach to the measurement of functional diversity based on two state nominal traits from the florula diversity concept of P. Juhász-Nagy (Podani et al., 2013). We also suggested a procedure which quantifies the role of different levels of sampling hierarchy (relative beta diversity) and the share of landscape elements in the corresponding relative beta diversity (contribution value). Our novel method uses pairwise dissimilarities and is based on partitioning a dissimilarity matrix of sampling units. It is suitable to testing various null hypotheses via permutation techniques. The method is a valuable tool in ecology because it complements existing approaches while providing a unique way to understand community diversity in space (Schmera and Podani, 2013). We also tested whether within-catchment natural variation in community traits allows or hinders the separation of catchments based on macroinvertebrates (Schmera et al., 2013). The main implication of this study is that the sensitivity of trait-based analyses to natural spatial environmental variation should be carefully incorporated in the assessment tools used in the applied projects of stream ecosystems. For clarifying terms, we raised weighting and scaling issues in data analyses and using example data sets, we illustrated how to perform trait-based data analysis in community ecology in a meaningful way (Schmera et al. 2014). We also clarified terms related to trait based categorization in stream ecology (Schmera et al. 2015). In papers led by senior researchers of the team a unified framework for quantifying taxon, phylogenetic and functional beta diversity via pairwise comparisons of communities was proposed, which allows these types of beta diversity to be partitioned into ecologically meaningful additive components (Cardoso et al., 2014). A new methodological scheme for exploring and quantifying structure in bipartite ecological networks was also developed (Podani et al. 2014).

Effective conservation of freshwater biodiversity requires accounting for spatial connectivity and the propagation of threats along river networks. We used systematic conservation planning to identify priority conservation areas for freshwater fish conservation in Hungary using our large scale data set from this and our previous OTKA projects (Dolezsai et al 2015). We paid special attention on accounting the spatial proximities of segments in the network while also evaluating the importance of transboundary rivers to achieve conservation goals by systematically deleting some rivers from the prioritization procedure in MARXAN and assessing the trade-offs between complexity of conservation recommendations (e.g., conservation areas located exclusively within Hungary vs. transboundary) and cost (area required). We found that including the segments of the largest transboundary rivers (i.e. Danube, Tisza) in the area selection procedure yielded smaller total area compared with the scenarios which considered only smaller national and transboundary rivers. However, analyses which did not consider these large river segments still showed that fish diversity in Hungary can be effectively protected within the country’s borders in a relatively small total area (less than 20% of the country’s size). Since the protection of large river segments is an unfeasible task, we suggested that transboundary cooperation should focus on the protection of highland riverine habitats and their valuable fish fauna, in addition to the protection of smaller national rivers and streams. Our approach highlights the usefulness of network based approaches and also the necessity of examining different options for selecting priority areas for conservation in countries where transboundary river systems form the major part of water resources.

Based on my works on spatial graphs in dendritic networks I was invited to participate in the writing of a review/opinion paper which is about studying connectivity relationships and about the importance of connectivity in aquatic systems (Crook et al., 2015). In this paper, we reviewed anthropogenic impacts on connectivity, ranging from well recognised examples like the damming of rivers to other forms of river regulation, habitat loss and alteration, human-assisted connectivity and climate change. We highlighted that improved understanding of aquatic connectivity is needed to predict, assess and when possible mitigate or manage anthropogenic impacts on connectivity. Using case studies we showed that the evidence needed to understand the nature and implications of connectivity, and to underpin conservation and management strategies, has only been achieved when many methods of analysis are combined. The combined application of existing and novel methods to understand species’ basic autecology, population structure, movements, environmental tolerance and phenotypic plasticity is likely to improve our capacity to understand connectivity and to better conserve and manage aquatic ecosystems in the face of growing anthropogenic pressure.

We emphasized the better incorporation of landscape ecological methods in studying fragmentation effects in stream networks (Erős and Grant, 2015). We showed that while there is an increasing emphasis on determining the relative influence of habitat surrounding patches (the landscape 'matrix') relative to focal habitat patch characteristics in terrestrial landscapes, this line of thinking has not been systematically applied in running-water ecosystems. We outlined the conceptual foundations of matrix ecology for stream and river ecosystems ('riverscapes'). We discussed how a hierarchical patch-based perspective is necessary for the delineation of habitat and matrix patches, and through which we may identify two classes of habitat edges in riverscapes. Under this conceptual framework, we revealed the potential role of the matrix in influencing resource quality and quantity, and suggest types of empirical and modelling approaches which may advance our understanding of fragmentation effects in these systems advocating the use of network (graph) based analyses as a primary modelling tool. Fragmentation of habitats is a critical issue in the conservation and management of stream networks at multiple spatial scales. Although the effects of individual barriers (e.g. reservoir dams) are well documented, we argued that a more comprehensive patch-matrix landscape model would improve our understanding of fragmentation effects, and improve management in riverscapes.

We followed the recolonization dynamics of fishes in the Marcal River (Erős et al., 2015). Our study about one of the largest scale and most serious documented fish kill showed that both taxonomic and trait based structure of fish assemblages can regenerate remarkable fast even at the whole river scale (here 70.7 km long section). We found that largely the original assemblage recovered during the successional process. The proliferation of non-native invasive species could not be justified. The study highlighted the importance of the permeability of the stream network in the recovery process, and showed that large infrequent disturbances by unfortunate chemical spills provide insights into the assembly of stream fish assemblages. Another, recently published study conducted in the Marcal waterbasin showed the role tributary confluences play in the dispersal of organisms, and consequently, in shaping regional scale diversity in stream networks (Czeglédi et al., 2016a). We found that not only the junctions presented a strong filter on the species pool, but some species were filtered out if they passed this critical habitat bottleneck. In addition, spatial position of the tributaries along the river also contributed to assemblage variability in the confluences. Our results suggested high variability in fish assemblages across multiple scales at tributary confluences (see also Czeglédi et al. 2016b). We emphasized that environmental management should take a more critical care on the filtering role of tributary confluences in species dispersal, for better understanding patterns and processes in the branches of dendritic stream networks.

Variation partitioning is one of the most frequently used method to infer the importance of environmental (niche based) and spatial (dispersal) processes in metacommunity structuring. However, the reliability of the method in predicting the role of the major structuring forces is less known. We studied the effect of field sampling design on the result of variation partitioning of fish assemblages in a stream network (see Sály and Erős, 2016). Along with four different sample sizes, a simple random sampling from a total of 115 stream segments (sampling objects) was applied in 400 iterations, and community variation of each random sample was partitioned into four fractions: pure environmentally (landscape variables) explained, pure spatially (MEM eigenvectors) explained, jointly explained by environment and space, and unexplained variance. Results were highly sensitive to sample size. Even at a given sample size, estimated variance fractions had remarkable random fluctuation, which can lead to inconsistent results on the relative importance of environmental and spatial variables on the structuring of metacommunities. Interestingly, all the four variance fractions correlated better with the number of the selected spatial variables than with any design properties. Sampling interval proved to be a fundamentally influential sampling design property because it affected the number of the selected spatial variables. Our findings suggest that the effect of sampling design on variation partitioning is related to the ability of the eigenvectors to model complex spatial patterns. Hence, properties of the sampling design should be more intensively considered in metacommunity studies.

We tested the network position hypothesis (NPH) of metacomunity organization in stream networks, which is one of the most influential concept in stream community ecology. The NPH postulates that the degree of isolation of local habitats in the landscape may substantially influence the relative role of environmental filtering and spatial mechanisms in metacommunities. Dendritic stream networks are unique habitats in the landscape, where more isolated upstream sites have been predicted to be primarily structured by environmental, while more central mainstream rivers by both environmental and spatial variables (hereafter the network position hypothesis, NPH). However, the NPH has almost exclusively been tested for stream macroinvertebrates, and therefore its predictions warrant confirmation from multiple taxa. We examined the validity of the NPH for benthic algae (diatoms), macrophytes, macroinvertebrates and fish in the Pannon Ecoregion, Hungary (Schmera et al., 2018a). Following the NPH we predicted the clear dominance of environmental variables over spatial ones in headwaters, and the larger effect of spatial variables in rivers compared to headwaters. We tested these predictions using variance partitioning analyses separately for the different taxa in headwater and in riverine habitats. We found large differences in the explained community variance when the impact of environmental (physical and chemical) and spatial variables (overland and watercourse distance) for various taxa was studied. In general, total explained variance was lower for the more passively distributing plant taxa than for animal taxa with more active dispersal in both streams and rivers. However, similarly to other studies, the total explained variance was low for both headwater streams and rivers. Community structure of diatoms could be best explained by both environmental and spatial variables in streams, whereas their community structure could not be explained by either variable group in rivers. The significance of environmental and spatial variables depended on the distance measure (overland vs watercourse) in case of macrophytes. Community structure of macroinvertebrates could be explained by environmental variables in streams and by both environmental and spatial variables in rivers. Finally, community structure of fishes could be explained by both environmental and spatial variables in streams and only by environmental variables in rivers. In conclusion, we found no clear evidence of the NPH in multitaxa comparisons. While patterns in macroinvertebrate communities seem to support, those in fish communities run counter with the predictions of the NPH. This study thus shows that different taxa may behave differently to isolation effects in stream networks. We discuss alternatives in the interpretation of dispersal limitation effects which may partly explain differences in the observed patterns from the NPH, and emphasize the need for further studies in unravelling the importance of isolation in stream metacommunity structuring.

As part of our project which examined the role of network position and environmental factors, we examined the role of environmental selection (niche based species sorting), dispersal and drift (i.e. stochastic changes in species abundance) mechanisms on the structuring of fish metacommunities in riverscapes (Erős et al, 2017). We used a hierarchical design and examined metacommunity structuring 1) in individual running water habitat types, namely highland streams, lowland streams, highland rivers, and lowland rivers, 2) in landscape types, where patterns in highland and in lowland types were examined separately, and 3) at the level of the whole riverscape, where samples from all running water types were pooled. Elements of metacommunity structure (EMS) analysis, community-environmental relationships in redundancy analysis, and decay of community similarity with distance (distance decay) complemented with partial Mantel tests were used to reveal the mechanisms behind the observed patterns. Both the EMS framework and community-environment relationships revealed the prevalent role of selection (niche based species sorting mechanisms) on fish metacommunity structuring, although stochastic variability also influenced the results.

Metacommunity structures reflecting niche based mechanisms (Clementsian or Quasi-Clementsian) were observed at higher hierarchical levels (i.e. at the riverscape and the landscape type levels), while Quasi-Clementsian or random patterns were found within single running water types. Distance decay relationships indicated that dispersal limitation did not clearly affect metacommunity structuring in any combination of running water types. Partial Mantel tests showed that some part of the variation in distance decay could be explained by the correlation between environmental variables and fish assemblage structure in some habitat types, which further suggests the importance of niche based mechanisms in metacommunity structuring. Our study shows that different metacommunity structures can arise in a hierarchy of habitat types in riverscapes, and niche based species sorting mechanisms are more influential in their structuring than dispersal ones. Landscape classifications are useful for a better understanding of the structuring of metacommunities in both the freshwater and the terrestrial realm.

Dispersal is one of the key mechanisms affecting the distribution of individuals, populations and communities in nature. Despite advances in the study of single species, it has been notoriously difficult to account for dispersal in multispecies metacommunities, where it potentially has strong effects on community structure beyond those of local environmental conditions. Dispersal should thus be directly integrated in both basic and applied research by using proxies. We reviewed the use of proxies in the current metacommunity research, suggested new proxies and discussed how proxies could be used in community modelling, particularly in freshwater systems (Heino et al., 2017). We suggested that while traditional proxies may still be useful, proxies formerly utilized in transport geography may provide useful novel insights into the structuring of biological communities in freshwater systems. We also suggested that understanding the utility of such proxies for dispersal in metacommunities is highly important for many applied fields, such as freshwater bioassessment, conservation planning and recolonization research in the context of restoration ecology. These research fields have often ignored spatial dynamics, and focused mostly on local environmental conditions and changes therein. Yet, the conclusions of these applied studies may change considerably if dispersal is taken into account.

We have just finished mss on the occupancy, niche position and the role of spatial and environmental factors on the organization of stream macroinvertebrates based on the collated data set. The material has already been presented on conferences (Szivák et al., 2017, Csercsa et al., 201). Specifically we examined the following research questions as follows. The role of environmental control and spatial structuring may vary depending on dispersal mode within a metacommunity. However few studies examined in detail the role of dispersal mode in the metacommunity structuring of stream macroinvertebrates in different habitats and seasons. Here, we used variance partitioning analyses separately for three dispersal mode groups (aquatic passive, terrestrial passive, terrestrial active) in different running water types (river vs stream) and seasons (summer vs spring) in the Pannon Ecoregion, Hungary (Csercsa et al., submitted ms). We found strong environmental control without spatial structuring of active dispersers in both seasons while passive dispersers (terrestrial and aquatic) were influenced predominantly by environmental factors with various additional impact of the spatial component. The role of these factors, however, varied between seasons and did not depend on the running water types. Our findings suggest that metacommunities with moderate or low dispersal capacity are under both spatial and environmental control, but when species have good flying ability environmental control become prevalent. These results further emphasize the use of dispersal traits in metacommunity research for a better understanding of the relative role of environmental and spatial processes.

The positive relationship between local abundance and regional distribution of species is one of the few general patterns in ecology. Several models were developed to find the underlying processes behind this relationship and to predict the occupancy-frequency distribution (OFD) pattern of species and assemblages. For instance, the core-satellite species hypothesis predicts bimodal OFD pattern which indicates the main role of dispersal processes in structuring assemblage compositions. While, the niche-based model predicts unimodal right-skewed OFD pattern which indicates that assemblages are driven by niche processes. The extreme environmental heterogeneity and the hierarchically branching spatial structure make lotic systems (i.e. streams and rivers) ideal candidates for studying OFDs and their determining processes. It was suggested that the relative role of niche and dispersal processes can vary depending on the position of habitats along the upstream-downstream gradient, which may cause differences in the OFD patterns of stream and riverine organisms. We studied the OFD patterns of freshwater insect assemblages in temperate streams and rivers in the Pannon Ecoregion, Hungary. We also examined the possible effects of several ecological variables on the shape of OFD to reveal processes behind patterns. For this, we deconstructed the entire insect assemblage by the niche characteristics of species (niche breadth, niche position) and compared the form and modality of the OFDs of specialist and generalist species groups for the entire region and separately for streams and rivers in two seasons. We found that the OFDs of stream and riverine insect communities did not differ. The right-skewed pattern indicated the importance of environmental heterogeneity (i.e. niche based processes) in both systems. However, contrasting differences were found in the form of OFDs based on the niche characteristics of species. Specialist species showed strongly right-skewed OFD patterns, while generalist species with wide habitat availability (non-marginal niche position) showed much variation in occupancy. Niche position was a more influential determinant of species distribution than niche breadth in both streams and rivers indicating that rare species could have high environmental tolerance (broad niche breadth) and species with wide habitat availability can be the most common abundant in both streams and rivers. The results also showed that environmental and biological variability of temperate streams and rivers are high and comparable at regional scales, which may determine the right-skewed distribution pattern and the lack of differences in the OFDs of their ecological assemblages. An interesting future research avenue is to explore why bimodal distribution pattern in OFD is more abundant in case of terrestrial organisms compared with streams and rivers, where, as our study also proves, the unimodal distribution seems to be predominant.

The Elements of Metacommunity Structure (EMS) framework originally suggested by Leibold and Mikkelson (2002) in Oikos is a popular approach to identify idealized metacommunity patterns (i.e. checkerboard, nested, evenly spaced, Clementsian, Gleasonian), and hereby to infer the existence of structuring processes in metacommunities. Essentially, the EMS framework consists of the rearrangement of the species-by-site incidence matrix followed by a series of tests for coherence, turnover and boundary clumping in species distributions. In a though provoking, critical study we gave a critical evaluation of the EMS framework in separating idealized metacommunity patterns based on theoretical considerations and simulations (Schmera et al., 2018b). We found that user defined site ordering may influence the coherence test (number of embedded absences) depending also on the ordering of species, and therefore we argue that the application of user-defined matrix rearrangement has strong limitations. The recommended ordering by correspondence analysis is sensitive to matrix structure and may even include arbitrary decisions in examining special incidence matrices. Further, we revealed different meanings of the checkerboard pattern and showed that negative coherence is not necessarily associated with checkerboard pattern as assumed in the EMS framework. We found also that the turnover test cannot always detect nested pattern, because turnover and nestedness are not necessarily the opposite endpoints of a continuum. We argue that the boundary clumping test can only be used for separating Clementsian, Gleasonian and evenly spaced patterns if sites are ordered according to a real environmental gradient rather than along a latent one identified by correspondence analysis. We found that the series of tests in the EMS framework are burdened by anomalies and that the detection of some metacommunity patterns is sensitive to type II error. In sum, our findings suggest that the analytical methodology of the EMS framework, as well as the conclusions drawn from its application to metacommunity studies require careful reconsideration.