Effects of anthropogenic disturbances on freshwater biodiversity
final report

In response to the growing threat of biodiversity loss in nearly every ecological system, many ecologists seek better understanding of, and improve the ability to predict the consequences of anthropogenic disturbances. Freshwater ecosystems are among the most endangered ecosystems in the world since they suffer from water pollution, habitat degradation, flow modification, overexploitation and invasion by alien species, all of which affecting their diversity and integrity. For maintaining and protecting biodiversity in freshwater ecosystems, it is essential to understand how anthropogenic disturbances influence the variability of biodiversity. Our project aimed to contribute to freshwater biodiversity research by studying the effect of urbanization on freshwater biodiversity, by examining subfossil chironomid assemblages, and by developing new methodology.

In general, I believe, the project was successful. We produced 17 scientific articles in high-quality journals and there are some further manuscripts under preparation. We were successful in studying the effect of urbanization on freshwater biodiversity and in developing novel methodologies. The project shows the weakest performance with subfossil chironomid assemblages. The explanation is that Mónika Tóth left the Centre of Ecological Research and the research career (already noted in report 2020). As subfossil chironomid-related subproject was based mostly on her special and irreplaceable knowledge, we had to make moderate changes on this subproject by connecting the analysis of subfossil chironomid assemblages to methodological developments.

We define taxonomic, phylogenetic and functional beta diversity of species assemblages based on the generalized Jaccard dissimilarity index (Podani et al. 2018). This coefficient does not give equal weight to species, because traditional site dissimilarities are lowered by taking into account the taxonomic, phylogenetic or functional similarity of differential species in one site to the species in the other. These, together with the traditional, taxon- (species-) based beta diversity are decomposed into two additive fractions, one due to taxonomic, phylogenetic or functional excess and the other to replacement. The approach was illustrated by examples coming from vegetation surveys representing different ecological conditions.

We wrote a systematic review on how urbanization influences freshwater biodiversity focusing on macroinvertebrates (Gál et al. 2019). We observed significant heterogeneity among individual case studies, reporting negative, neutral and positive effects (Fig. 1).

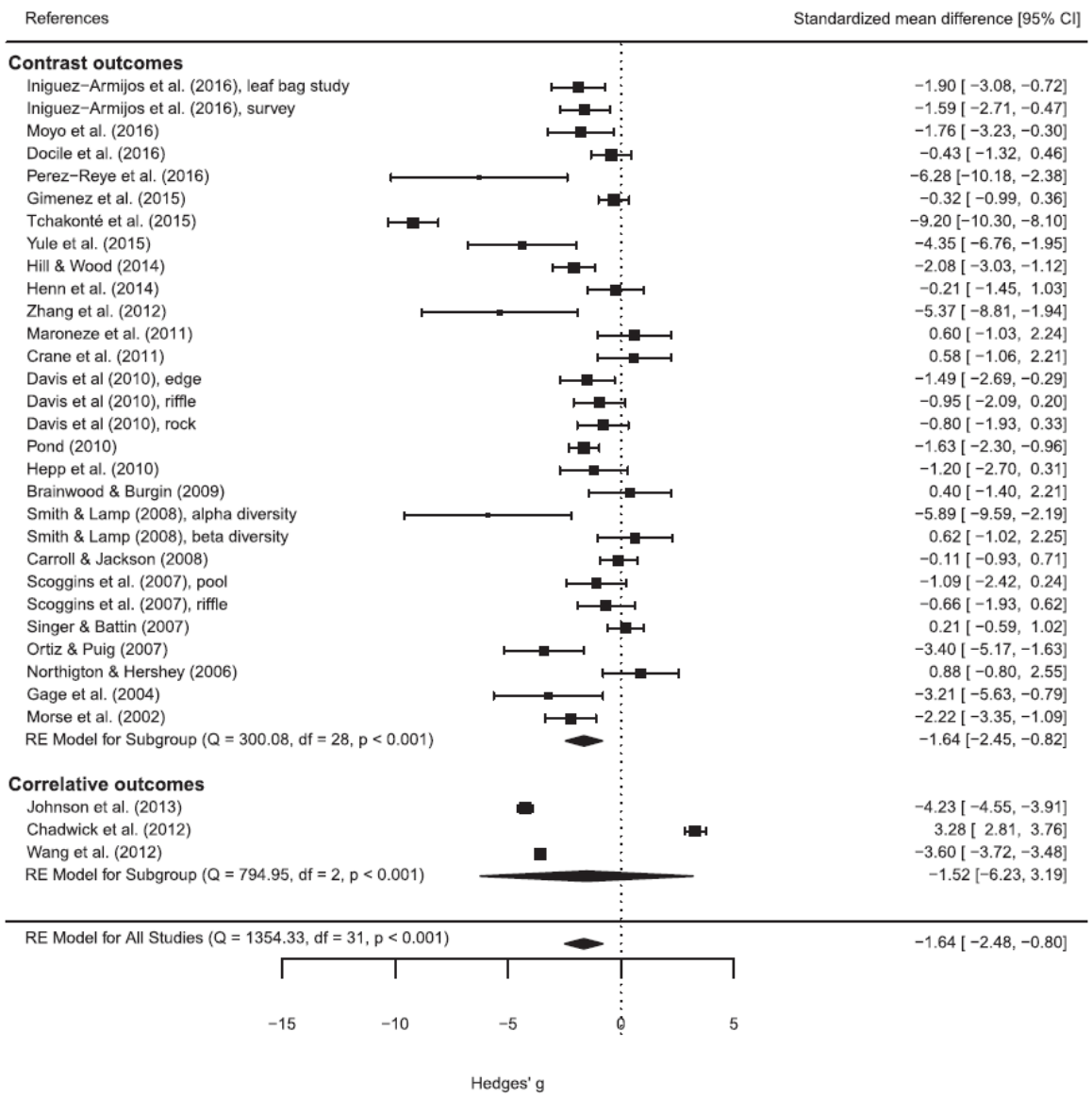

Fig. 1: Forest plot of effect sizes (Hedges' g) measuring the effect of urbanization on macroinvertebrate diversity

As expected, urbanization had an overall negative effect on the diversity of freshwater macroinvertebrates. These results are based mainly on the study of lotic (stream and river) ecosystems because there are insufficient data available for lentic (pond and lake) ecosystems. Compared to individual case studies, our review reports an evidence-based synthesis for the first time. We identified knowledge gaps regarding case studies reporting the effects of urbanization on pond and lake ecosystems, case studies examining the phylogenetic and functional facets of biodiversity, as well case studies investigating the effect of urbanization on the beta diversity component of macroinvertebrate communities. The identification of these knowledge gaps allowed us to make recommendations for future research: (1) report results on specific taxonomic groups and not only the entire macroinvertebrate community, (2) study the impacts of urbanization on macroinvertebrate diversity in different habitat types and understudied continents, (3) focus on the functional and phylogenetic facets of diversity and (4) examine community differentiation (e.g. beta diversity) in urban freshwater ecosystems. Our results also suggested that the analysis of diversity- environment relationships is crucial for developing macroinvertebrate indicators especially in the increasingly urbanized world.

We examined the response of beta diversity of aquatic and terrestrial beetles to ecological variables, including climate, land cover and land use, across Norther Europe (Heino et al. 2019). The magnitude of total beta diversity was relatively similar between ground beetles and diving beetles, but the richness difference component contributed more than the replacement component to total beta diversity in ground beetles, whereas the opposite was true for diving beetles. Our findings suggest that the study of the determinants of biodiversity patterns benefits from the partitioning of beta diversity into different components.

We examined how biodiversity is distributed within and among protected, agricultural and urban land use types in streams (Tóth et al. 2019). We studied environmental characteristics of streams and patterns of species richness and other community attributes of stream fish communities in these three characteristic land use types in the catchment of the Danube River, Hungary. Land use separated streams to some degree based on their environmental characteristics. However, both between stream environmental and fish community variability were high in most types, and comparable to land use type level differences in case of many streams. A variety of environmental gradients influenced fish community structure rather independently of land use type, which was also influenced by spatial drivers. Non-native fishes modified the structure of native fish communities, especially in agricultural streams, although their modification effect varied more among individual streams than among land use types. In conclusion, land use type proved to be a poor predictor of fish communities in this human modified landscape. We found that even intensively managed areas (i.e. agricultural and urban) can contribute to the maintenance of fish diversity in this biogeographic region, or at least their potential can be comparable to those streams which flow in protected areas. Thus, conservation management should focus on maintaining streams in more natural condition in protected areas and/or use the potential of non-protected agricultural and urban streams in maintaining fish diversity in human modified landscapes.

We studied the importance of the degree of urbanization, the local stream environment and the regional species pool on the assembly of stream fishes in the Pannon Biogeographic Region, Hungary (Czeglédi et al. 2020). Correlation analyses between urbanization variables (human population size and a recently developed urbanization index) and local stream and riparian environmental variables did not show significant relationships, indicating that the examined 29 streams reacted to the degree of urbanization in a strongly individual manner. Variance partitioning in both linear regression and redundancy analyses showed that the downstream species pool was the most important determinant of fish species richness, community composition and abundance at urban stream sites. The effect of the local stream environment proved to be moderate, while purely urbanization variables explained only a very small proportion of variance in the data. The relative importance of shared fractions depended on the examined fish assemblage variable, but, in general, was also low or moderate. Additional principal component analyses indicated that community similarity between urban and associated non-urban "reference sites" varied widely, and that the sites did not separate to urban and reference fish community types. Overall, the results highlight that the degree of urbanization is not a strong determinant of local stream habitat and fish community characteristics in this region. Rather, historical species pool and stream characteristics shape fish communities with urbanization playing a rather individual role in some streams. Thus, rehabilitation of urban streams should not only focus on local habitat improvements, but rather consider how dispersal mechanisms from non- urban segments influence community organization at the urban sites.

We examined the effects of urbanization on alpha, beta and zeta diversities of native fish communities in wadeable streams and non-wadeable rivers in the Danube basin, Hungary (Erős et al. 2020). Urbanization was characterized by land use, local scale environmental (in-stream habitat degradation) and biotic stressors (invasive species). Relationships among land use and local scale environmental and biotic stressors were weak both in streams and rivers, suggesting that these stressors act relatively independently. Alpha diversity decreased strongly with increasing local scale environmental stressor intensity in rivers. On the contrary, its response to stressors was more obscure in streams, where the best-fit statistical model indicated the importance of the interaction between land use, local scale environmental and biotic stressors, while the secondly ranked model highlighted the negative impact of local scale environmental stressors. Analysis of variance using distance matrices provided evidence that stressors alone and in interactions explained compositional differences of pairs of study sites (beta diversity). Considering the degree of overall degradation, both local (alpha) and among-site (beta and zeta) diversity indices responded to increasing stressor intensity, generally negatively. Riverine fish communities showed higher degrees of similarity (lower beta and higher zeta) than stream fish communities. They also showed increasing similarity (i.e. homogenization) with increasing overall stressor intensity, unlike stream fish communities, which showed no relationship with overall stressor intensity. Our results suggest that the relationships between land use and local scale environmental and biotic stressors can be complex and so do their effects on biodiversity. While stressor specific indices can provide information on the role of specific stressors in some cases, the examination of overall stressor effects is needed to assess realistically the effects of anthropogenic disturbances on native fish diversity. Diversity indices that quantify among-site changes in species composition, such as measures of beta and zeta diversity, can be fruitful for better understanding the role of multiple stressors in structuring ecological communities.

We collected stream macro-invertebrates from road crossings (bridges and culverts) and compared their diversity with upstream and downstream sections (Gál et al. 2019). We found that road crossings had negative effects on the richness (Fig. 2) and abundance of native macro-invertebrates, as well as on the number of protected taxa. Our results showed also that alien individuals were more abundant at road crossings. These findings support the assumption that road crossings contribute to the spread of alien species. The assessment of environmental variables indicated that road crossings caused habitat modifications, and based on these it can be assumed that habitat modifications and associated phenomena (e.g. pollutants and storm events) were the major drivers of the observed patterns in biodiversity. Our results fill a knowledge gap and contribute to the deeper understanding of the effect of road crossings on freshwater biodiversity.

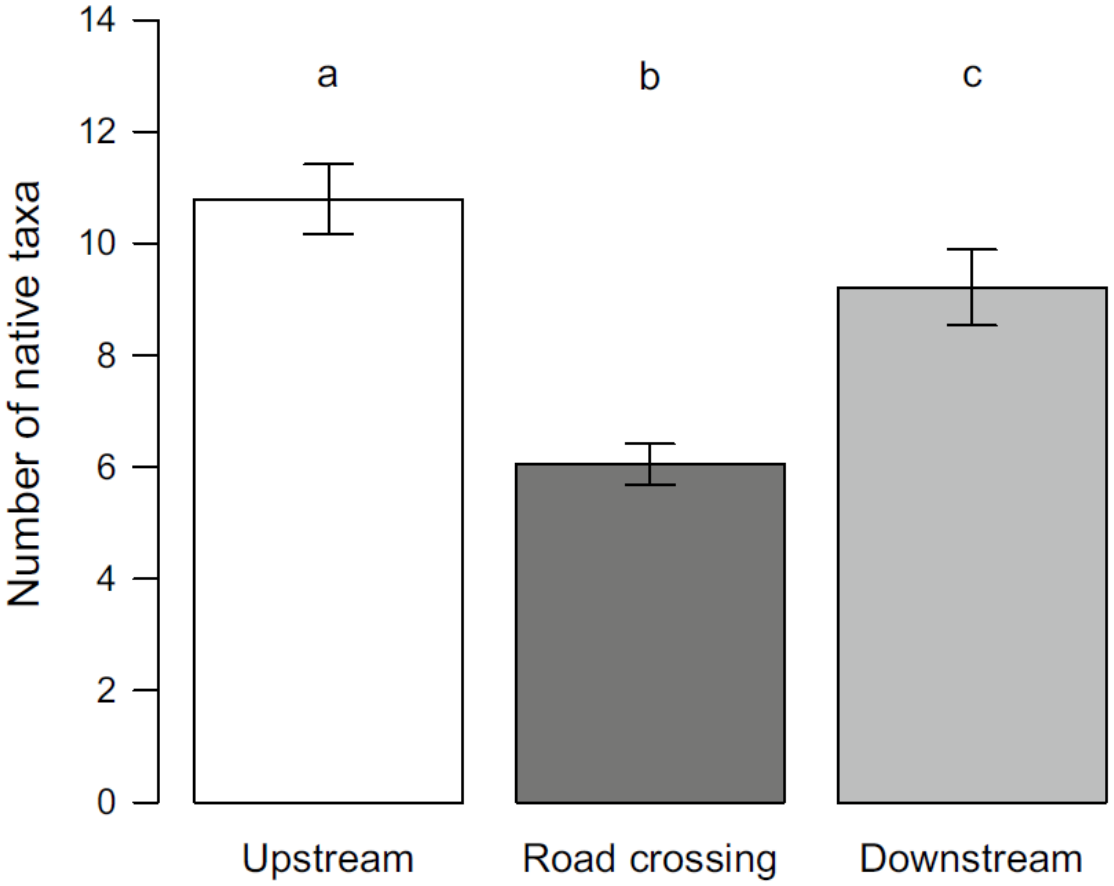

Fig. 2: Effetc os stream section (upstream [white], road crossing [dark grey] and downstream [light grey] on the number of native macroinvertebrate taxa. Different letters indicate differences by Tukey test. Bars indicate mean values, whiskers standard errors.

Controlled experiments are among the most frequently applied approaches in ecology. Compared to observational studies, where researchers merely describe what is happening, in experiments researchers have the ability to control most of the variables and manipulate one or more factors of specific interest. As a result, experimental studies are founded on the principles of cause and effect, specifically examining relationships that cannot be demonstrated via observational studies. It follows that experiments, among others, provide the possibility of examining the effects of anthropogenic disturbances on freshwater biodiversity. To open the possibility of performing such studies, we reviewed the facilities, protocols and studied questions related to experimental streams (Menczelesz et al. 2020).

We focused on how information from community data can be extracted (Schmera et al. 2020). As a novel concept, we suggested pairwise pattern components (PPCs), which can be efficiently used to identify response types of communities (Fig. 3). Then, we argued that the conceptual distinction among community patterns (on which inference is made), pairwise pattern components (PPCs, which reflect the unique response of communities for pairs of sites), and measures (which quantify a relevant property of PPCs), liberates our field from the possible misinterpretation of results derived from existing approaches. In other words, the introduction of PPCs supports the analysis of real data sets and links patterns to ecological hypotheses. Based on PPCs, we proposed a new partitioning of beta diversity, called SET framework. The SET framework partition beta diversity into intersection (I) of nestedness and beta diversity and the

relative complement (RC) of nestedness in beta diversity. We performed an algebraic assessment of three existing partitioning frameworks of beta diversity: the BAS (published by Andrés Baselga), POD (published by Podani & Schmera) and SET. We found that when a community pattern is anti-nested, which is characterized by the presence of both Replacement and Richness difference PPCs, the BAS framework falsely indicates a 100% share of replacement from beta diversity. In contrast, the POD and SET partitioning procedures detect the presence and the proper size of PPCs for all types of community patterns. In conclusion, we found that breaking down community patterns into PPCs and then quantifying the importance of these PPCs form a straightforward strategy to extract information from community data under a broad range of circumstances.

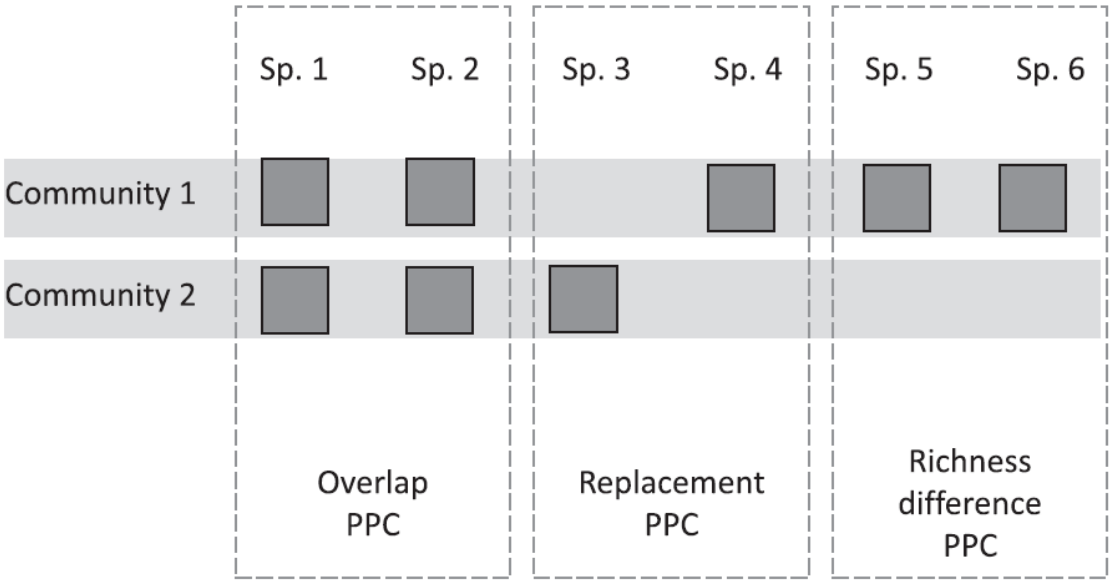

Fig. 3: Schematic representation of pairwise pattern components (Overlap, Replacement and Richness difference).

We examined the effects of recreational beaches on chironomid assemblages of Lake Balaton (Árva et al. 2021). Taking into account the establishment of beaches, we examined natural reed vegetated shorelines (representing natural situation), open areas (representing areas, where reed has been removed), as well as beaches. We assessed the abiotic parameters as well as the chironomid assemblages of these habitats. We found that the transformation of reeds through open habitats to beaches is associated with multiple changes in environmental properties and with a decrease in habitat heterogeneity. We observed that the transformation of reeds to beaches caused an 18% reduction in chironomid taxa richness and a moderate drop in their abundance (Fig. 4). This reduction can be explained by the removal of reeds, because this action transforms a productive system to an unproductive one, and by the assumed dependence of chironomid richness and abundance to the organic-matter content of the sediment. Our analyses showed that the composition of chironomids was sensitive to the transformation of the habitats, and to the natural differences in the northern and southern shorelines of the lake. These findings suggest that the establishment and use of recreational beaches had a negative effect on local biodiversity. Although beaches can promote diversified societal and economic benefits, our results show that they can also generate conservation issues related to biodiversity loss. Consequently, action plans focusing on the maintenance and the establishment of recreational beaches should carefully consider both economic and conservation aspects.

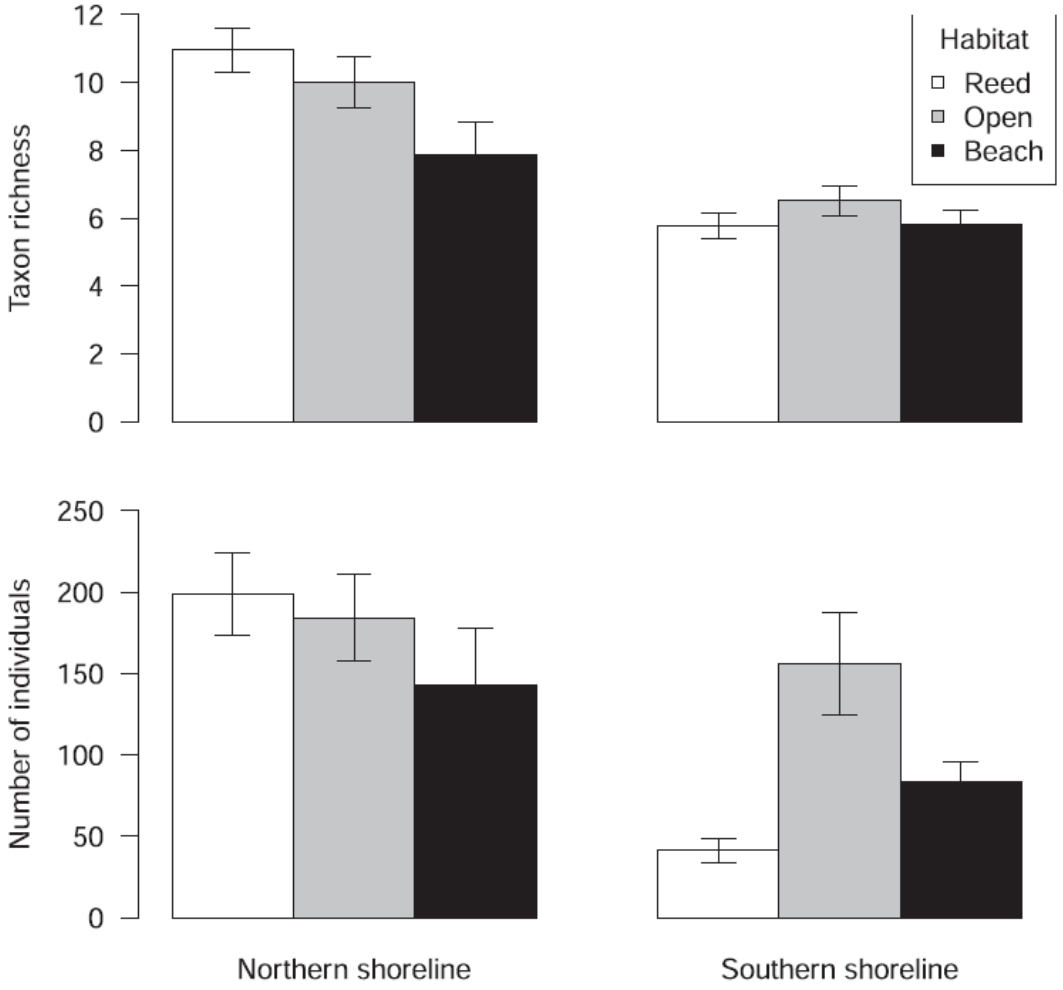

Fig. 4: Response of taxon richness (top) and number of individuals (bottom) on the transformation of reed-covered shoreline (reed) to open habitat (open) and to recreational beaches (beach) in the northern (left) and southern (right) shorelines of Lake Balaton. Bars show mean values and whiskers are standard errors.

We examined also the effects of roads on amphibian abundance in ponds across a fragmented landscape (Hamer et al. 2021). We examined whether the combined effects of habitat loss and roads or railways (accessible habitat) was a better predictor of amphibian abundance than (1) the total amount of habitat surrounding ponds, (2) distance to a highway or railway, or (3) surrounding road cover. Aquatic surveys for amphibian larvae were conducted at 30 freshwater ponds over the breeding season in a mixed peri-urban/ agricultural landscape in Hungary. Landscape variables were quantified within a 1000-m radius surrounding ponds and habitat variables were measured at the local (pond) scale. The larvae of seven amphibian species were detected. There were strong relationships between the abundance of amphibian larvae and the distance to a highway and the proportion of road cover within 1000 m of ponds (Fig. 5). Relationships with accessible habitat and total habitat amount were uncertain, while there were no clear relationships with a major railway. Larval abundance increased with pond size, but there were mixed relationships with the presence of fish. Our results suggest that road effects were having a stronger impact on amphibian abundance than the combined effects of roads and habitat amount in the study area. Highways appeared to be negatively impacting amphibian communities within a wide road-effect zone up to 1 km from ponds. However, our results were obtained from a single-season snap-shot study and multi-season surveys are likely required to

reduce uncertainty in the model predictions. Our analysis suggests that road mitigation projects for amphibians should create large ponds in areas with no highways and low road density, and with connectivity to surrounding habitats.

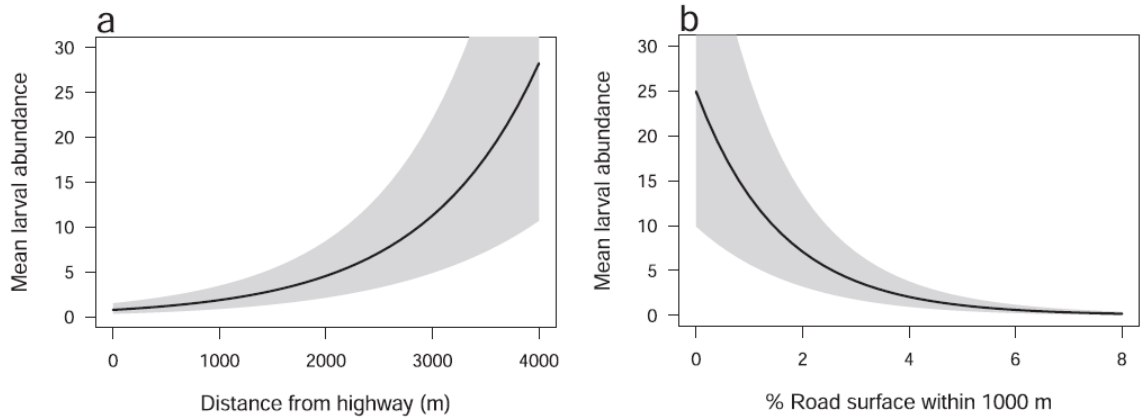

Fig. 5: Mean estimated larval abundance (line) and 95% Bayesian credible intervals (shaded area) across the amphibian community versus distance from highway (a) and % road surface within a 100-m radius (b).

We focused on how unintentional absence of values for some observations or variables influences the use of standard multivariate exploratory methods, such as principal component analysis (Podani et al. 2021). It is a problem especially for biologists, who are often faced with high percentages of values lacking from their data set for various reasons. This issue may be handled in very different ways. The most radical – and common – solution is to delete as many variables and/or objects from the data as necessary to reach completeness. Deletion always involves undesirable loss of information and does not work when too many rows and columns of the matrix have unknown values. The second possibility is imputation: the unknown scores are substituted by the mean of existing values for each variable or estimated through regression analysis. Some entries may also be lacking for logical reasons, however. Morphometric data matrices used in biological taxonomy, or tables of functional traits in ecology may include variables that do not apply to all observations. For example, the value of "seed size" for ferns in a large plant trait database is not simply missing, but biologically meaningless and therefore cannot be imputed. We described a minor modification of eigenanalysis-based PCA in which correlations or covariances are calculated using different numbers of observations for each pair of variables, and the resulting eigenvalues and eigenvectors are used to calculate component scores such that missing values are skipped. This procedure avoids artificial data imputation, exhausts all information from the data and allows the preparation of biplots for the simultaneous display of the ordination of variables and observations.

Although there exist a few resemblance functions that allow missing scores, there is no theoretical background and software support for most distance and similarity coefficients potentially applied in multivariate data analysis. We provided a general framework for a precise mathematical redefinition of a large set of resemblance functions originally developed for complete data sets with presence-absence (binary) or ratio-scale variables (Podani & Schmera 2021). Included are coefficients which consider double absences in abundance data. Potential problems with the use of these functions are discussed, with the conclusion that incompleteness of data would rarely if ever influence greatly the interpretability of ordinations and classifications.

We used analysis of similarities and classification strength analysis to examine if the Broad River Types delineate distinct macroinvertebrate communities across Europe and whether they outperform two ecoregional approaches: the European Biogeographical Regions and Illies' Freshwater Ecoregions (Jupke et al. 2022). We determined indicator and typical taxa for the types of all three typology systems and evaluated their distinctiveness. All three typology systems captured more variation in macroinvertebrate communities than random combinations of sites. The results were similar among typology systems, but the Broad River Types always performed worse than either the Biogeographic Regions or Illies' Freshwater Ecoregions. Despite reaching statistical significance, the statistics of analysis of similarity and classification strength were low in all tests indicating substantial overlap among the macroinvertebrate communities of different types. We conclude that the Broad River Types do not represent an improvement upon existing freshwater typologies when used to delineate macroinvertebrate communities and we propose future avenues for advancement: regionally constrained types, better recognition of intermittent rivers, and consideration of biotic communities.

We applied also our methodology on terrestrial spider communities (Samu et al. 2021). Analyses showed that beta diversity increased only moderately in time (from 2014 to 2018) and that species replacement and richness difference contributed equally to beta diversity.

We examined the functional strategies and the trait space of 596 European taxa of freshwater macroinvertebrates characterized by 63 fuzzy coded traits belonging to 11 trait groups (Schmera et al. 2022a). Principal component analysis was used to reduce trait dimensionality, to explain ecological strategies, and to quantify the trait space occupied by taxa. Null models were used to compare observed occupancy with theoretical models, and randomization-based analyses were performed to test whether taxonomic relatedness, a proxy of phylogenetic signal, constrains the functional trait space of freshwater macroinvertebrates. We identified four major strategies along which functional traits of the taxa examined show trade-offs. In agreement with expectations and in contrast to existing evidence we found that life cycles and aquatic strategies are important in shaping functional structure of freshwater macroinvertebrates. Our results showed that the taxonomic groups examined fill remarkably different niches in the functional trait space. We found that the functional trait space of freshwater macroinvertebrates is reduced compared to the range of possibilities that would exist if traits varied independently. The observed decrease was between 23.44 and 44.61% depending on the formulation of the null expectations. We demonstrated also that taxonomic relatedness constrains the functional trait space of macroinvertebrates.

We focused on how to quantify directional changes in presence-absence community data (Schmera et al. 2022). Variation in community composition and species turnover are different types of beta diversity, expressing nondirectional and directional changes, respectively. While directional changes (e.g. turnover) along geographic gradients can be studied in any direction depending on the hypothesis of interest to researchers, temporal changes can only be meaningfully studied from past to present. Although a wide variety of methods exist for partitioning variation and related community-level phenomena such as similarity, richness difference and nestedness, approaches evaluating species turnover along geographic or temporal gradients, based on an analogous conceptual framework, are rare. We therefore look into the possibilities for examining different aspects of directional changes along a gradient when presence-absence community data are available. Measures of community overlap, as well as species loss and gain from one sampling unit to another along a gradient are combined to define a variety of turnover and nestedness concepts and to derive functions for their quantification. Each concept represents an ecological phenomenon to be indicated

(indicandum), whereas measures (indicators) quantify relevant properties of these concepts. The measures use the raw number of species as well as relativized forms in accordance with the well-known Jaccard and Sørensen indices. The main innovation is the development of new measures of directional community change. We demonstrate differences between traditional nondirectional and the new directional measures and use several examples to show that actual communities display directional responses to a particular ecological gradient. The Fossil chironomid data set was obtained from the sediment of Lake Brazi, Retezat Mountains, Romania. Community changes in relation to the age of the sediment (expressed in years before present, hereafter yr BP) were analysed. The analysis of the Fossil chironomid data set reveals high overlap (>0.5) of the species composition of neighbouring sampling units, resulting in a moderate value of turnover (<0.5) and a high value of nestedness (>0.5). This means that when only presence/absence is considered, then the chironomid assemblages show relative stability (expressed by overlap) with age. In contrast to this high average value of overlap, the loss and gain components reflect remarkable community change between 15,000 and 14,000yr BP.

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