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Local and regional drivers of standing-water metacommunities on a riverine island

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Abstract

Small standing waters on large riverine islands provide a model system for evaluating how local environmental conditions and regional connectivity jointly shape biodiversity, extending beyond species richness to community composition. We surveyed 42 artificial and reference standing waters on Europe's largest riverine island in Slovakia, comparing richness and multivariate community structure of zooplankton and molluscs (taxa with contrasting dispersal capacities) across gradients of area, nutrients, and distance to the Danube and Little Danube.

Artificial waters were significantly larger and more nutrient-enriched, with higher N:P ratios, whereas reference waters retained distinct hydrochemical conditions. Mollusc richness responded strongly to habitat type, area, and Danube proximity, reflecting sensitivity to hydrological connectivity, while zooplankton richness increased only with area, consistent with high dispersal and near-saturation of regional species pools. Species–area and species–distance predictors significantly explained richness in both groups but accounted for only a modest, non-negligible fraction of multivariate community variation; nonetheless, artificial and reference waters differed in composition.

These results show that small standing waters function as metacommunities structured primarily by local environmental gradients and regional species pools rather than spatial configuration alone. The contrasting responses indicate that molluscs are more effective indicators for studies of hydrological connectivity and long-term landscape processes, whereas zooplankton patterns better reflect regional dispersal dynamics. Our findings offer a framework for identifying which water bodies contribute most to regional biodiversity and underscore that preserving natural hydrochemical gradients and reference water bodies is essential for sustaining multi-taxonomic diversity in extensively modified floodplain landscapes.

Keywords zooplankton, Mollusca, ponds, species–area relationship, hydrological connectivity

Introduction

Patterns of biodiversity among discrete habitat patches can be interpreted through both the theory of island biogeography (TIB) and metacommunity theory. The TIB predicts local species richness from the balance between immigration and extinction, with habitat area and isolation representing its principal spatial determinants (MacArthur and Wilson 1963, 1967). Metacommunity theory extends this perspective from species richness to community composition by considering sets of local communities linked by dispersal and jointly structured by local environmental conditions and regional spatial processes (Leibold et al. 2004; Cottenie 2005; Logue et al. 2011). In networks of small standing waters, island biogeography therefore provides specific predictions concerning species–area and species–isolation relationships, whereas the metacommunity framework is more appropriate for evaluating how environmental filtering and dispersal interact to structure assemblages.

Although initially developed for terrestrial systems, the TIB has been applied to various freshwater environments, such as coastal rivers (Sepkoski and Rex 1974), dendrothelms (Oboňa and Svitok 2012), and city fountains (Hamerlík and Brodersen 2010), but lakes and ponds have been the most studied habitats for decades (e.g. Aho 1978; Browne 1981; Jenkins and Buikema 1998; Oertli et al. 2002; Samways et al. 2020). Freshwater habitats that are not connected to other water bodies are the perfect counterparts to islands surrounded by the sea (Warren et al. 2015). It has been shown that these habitats can function as ecological islands, but responses can vary with habitat type, the taxon involved, and the geographical area. Naturally formed lakes, tarns, wetlands, and dissected river meanders or side-arms can be considered the origin, i.e. reference waters, in contrast to relatively recently created artificial waters. Ponds created by gravel mining, filled with groundwater and lacking a direct connection to other water bodies, meet the physical requirements of newly created islands. These water bodies are usually up to 50 ha in size, categorising them as small biotopes (Céréghino et al. 2008). Moreover, these biotopes are recognised for their biodiversity conservation potential (Thornhill et al. 2017; Oertli 2018).

Several studies have examined species–area and species–isolation relationships in ponds and lakes (Bosiacka and Pieńkowski 2012; Várbíró et al. 2017). More recent work has increasingly integrated patch configuration with local environmental variation and whole-community composition (Hill et al. 2019; Meland et al. 2020). This distinction is important because similar levels of species richness may conceal markedly different assemblages (Sun et al. 2019), while local environmental differences may generate compositional turnover beyond that associated with patch area or spatial isolation (Hill et al. 2019). Comparing artificial and reference standing waters within the same floodplain landscape therefore allows classical island-biogeographic predictions concerning area and isolation to be evaluated within a broader metacommunity framework that integrates local environmental filtering and regional dispersal processes (Chase et al. 2020; Chanut et al. 2023).

In aquatic environments, TIB patterns have been clearly observed in water insects and non-insects, with molluscs and zooplankton showing the strongest responses (Lassen 1975; Aho 1978; Dodson 1992; Declerck et al. 2011). Two groups of invertebrates with different dispersal abilities and habitats, zooplankton (Cladocera and Copepoda) and molluscs (Gastropoda and Bivalvia), were selected as models to investigate the application of TIB to the studied standing waters. Zooplankton and molluscs are bound to aquatic habitats, so their dispersal capacity is low compared to insects with active dispersal. For both groups, occasional passive dispersal between sites is facilitated by animal vectors, usually waterfowl (Bilton et al. 2001). Among all macroinvertebrate groups, molluscs are among the most diverse, with the highest species richness but low abundance in natural or artificial ponds (Hill et al. 2016). In contrast, zooplankton community structure and abundance can be highly variable as they depend on the colonisation history of a pond, refuting previously known distribution patterns (Jenkins and Buikema 1998). In general, studies on freshwater mollusc or zooplankton fauna in relation to TIB are scarce and outdated, although they contain valuable knowledge (e.g. Lassen 1975; Dodson 1992).

Planktonic species show high variability in dispersal due to differences in vagility and viability (Bohonak and Jenkins 2003). Cladocera species generally exhibit high genetic variability with confirmed crypticity over short distances, demonstrating their low dispersal capacity (e.g. Hebert and Finston 1996). De Bie et al.

(2012) found an increasing influence of body size on dispersal limitation, with zooplankton favoured over molluscs. In addition to the dispersal limitations of both groups, their life history habitat requirements could also be responsible for their success in colonising nearby waters. In this study, we focused not only on the distribution pattern of quantitative information (species richness), but also on the qualitative structure of the studied communities using the same data. This represents a unique and innovative extension of TIB principles that has rarely been tested before (Hamerlík and Brodersen 2010).

This study examined how local habitat conditions and regional connectivity shape the richness and composition of zooplankton and mollusc metacommunities in artificial and reference standing waters on a large riverine island. Specifically, we asked: (1) whether local species richness is related to patch area and isolation from potential colonisation sources; (2) whether community composition differs between habitat types and is associated with local environmental conditions and regional connectivity; and (3) whether these relationships differ between zooplankton and molluscs because of their contrasting dispersal capacities. We predicted that: (H1) species richness would increase with water-surface area in both taxonomic groups; (H2) mollusc richness and composition would decline or become increasingly differentiated with distance from the Danube and other potential source habitats, whereas zooplankton would show weaker spatial responses; (H3) artificial and reference waters would support compositionally distinct assemblages because their contrasting hydrological histories and nutrient regimes impose different local filters. As the study was conducted on a riverine island, we assumed a significant influence of the Danube as the primary source of diversity. For the study, the distance to the nearest source of diversity, the nearest pond, and to a point in the Danube and the Little Danube was measured to determine the main pattern of colonisation. We used total nitrogen, total phosphorus, and their stoichiometric relationship as indicators of local environmental conditions that may indirectly influence the studied assemblages through productivity, food-resource composition, and habitat quality. These variables were contrasted with spatial measures of connectivity to evaluate the relative contributions of local and regional drivers.

Material and methods

Study area and sampling sites

The research area covered the south-western part of the Danube lowlands (Slovakia), known as Žitný ostrov (Rye Island), the most significant parallel riverine island in Europe (Fig. 1). This area is bordered to the south-west and south by the Danube, to the north-west and north by the Little Danube, and to the east by a short section of the Váh River. Rye Island is the warmest area in Slovakia, with the longest growing season, where agriculture often suffers from drought and therefore requires irrigation (Kandra and Gomboš 2020; Jurík et al. 2019).

Of the 42 sites selected for the study, 22 gravel pits are of artificial origin, created by gravel mining and filled with groundwater. The remaining 20 standing waters are of a near-natural character. These include old river channels, side arms, or lakes located in the floodplain and formed during river regulation, the construction of flood defence walls, or extensive land improvement in the second half of the 20th century. The basic characteristics of the sites are listed in Appendix 1.

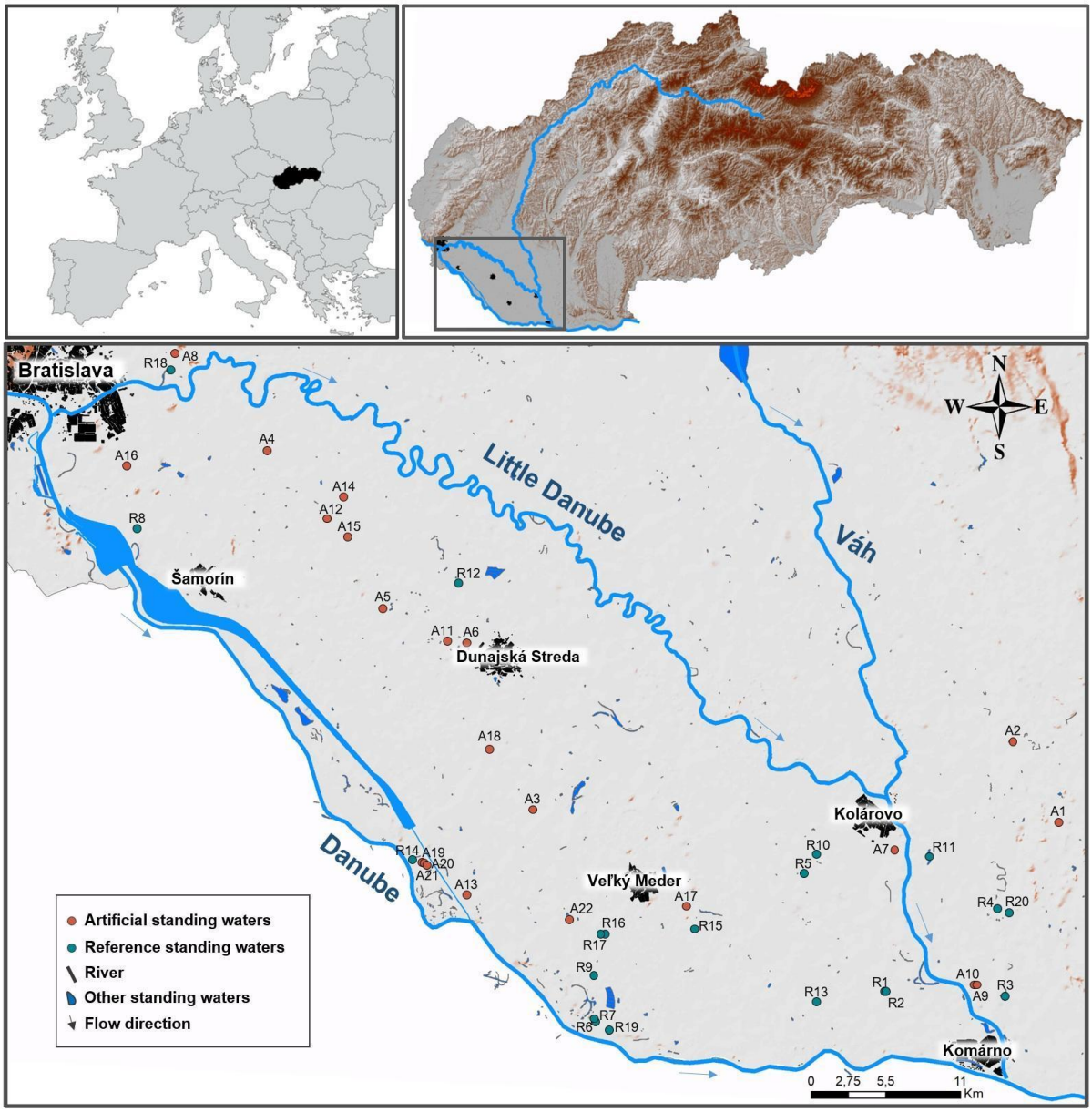


Fig. 1 Map of the study area. Explanatory notes: Red circles indicate artificial standing waters, while green circles denote reference standing waters. Other water types are shown in blue. The black arrow indicates the direction of flow

Environmental measurements

The wet surface area of all sites was accurately measured using the ZBGIS web application (GCCAS 2024) on an orthophotographic map with a measurement function. The distance from each site to the nearest pond, the nearest source (canal, ditch, pond, lake, stream), and the nearest point of the Danube and the Little Danube was measured with a ruler in the Google Earth application (Google 2025).

Sampling methodology

Samples of biological material and measurements of environmental variables were collected in 2015. Each sampling site was sampled twice during the study, in spring and autumn, to record changes in community composition caused by the different life strategies of the species. Total nitrogen and phosphorus were determined using the methods described by Hrbáček (1972).

Qualitative zooplankton samples were collected in the pelagic and littoral zones of each water body by vertical and horizontal trawling with a plankton net (mesh size 70 μm). The material was preserved in 4% formaldehyde solution in plastic bottles. In the laboratory, samples were sorted into two groups, Cladocera and Copepoda, and identified to species level using a LEICA DMLB stereomicroscope and the identification keys of Hudec (2010) and Einsle (1993, 1996). Only adult stages were considered for further analyses.

Mollusc samples were collected along a 20-metre section of each standing water body. Individuals were collected at four randomly selected sites along the sampling route, chosen at random from distances between 0.5 and 2.0 metres from the bank. Each sample consisted of a vigorous sweep over a length of 5 m, parallel to the bank and including sediment, vegetation, and the water surface, using a 200 mm diameter, 1 mm mesh sieve net (modified according to Watson and Ormerod 2004). Samples were stored in 70% denatured ethanol. In the laboratory, samples were washed through a 0.5 mm mesh sieve, and molluscs were removed and identified by eye and under a light microscope according to Glöer and Meier-Brook (2003).

Statistical analyses

The total nitrogen–phosphorus relationship was analysed using log–log linear regression separately for artificial and reference standing waters. Confidence intervals for the fitted slopes were used to assess overlap between groups. Differences in N:P molar ratios were tested using a Wilcoxon rank-sum test, as the data did not meet the assumptions of normality, as evidenced by a Shapiro–Wilk test.

Differences in TIB predictors between artificial and reference standing waters were assessed using Wilcoxon rank-sum tests. This non-parametric approach was chosen because all predictors exhibited non-normal distributions, identified by a Shapiro–Wilk test.

To compare species richness between artificial and reference waters while accounting for unequal sampling effort, sample-size-based and coverage-based rarefaction and extrapolation of Hill numbers were used. Rarefaction standardised richness estimates to a standard sample size, while extrapolation assessed expected richness beyond the observed sampling effort. As the data contained binary occurrences, the input data type was set as a species-by-sampling-units incidence matrix (raw incidence). Confidence intervals (95%) were calculated using bootstrap resampling. These analyses were performed separately for molluscs and zooplankton using the iNEXT package (Hsieh et al. 2025).

Generalised linear mixed models (GLMMs) were used to analyse species richness for molluscs and zooplankton. As the response variables were counts and showed overdispersion, all models were fitted using a negative binomial distribution with a log link function. For each taxonomic group, the initial complete model included habitat type, area, and distances to significant sources of species diversity (distance to the Danube, the Little Danube, nearest pond, and nearest source). To account for potential spatial clustering of sampling sites, geographic coordinates (latitude and longitude) were included as a random intercept. The effect of the random intercept was assessed by checking the variance of the random effect and was removed from the model formula if it was low. The model was simplified by eliminating variables with insignificant effects. The complete model was compared to reduced models using Akaike's Information Criterion (AIC), and the model with the lowest AIC was retained as the most parsimonious. For each reduced model, pseudo-R^2 values were calculated, including McFadden's R^2 and variance-based indices (marginal and conditional R^2), to quantify the proportion of variation explained by fixed effects and by the whole model structure. We also evaluated whether including a zero-inflation component improved model performance. These analyses were performed using the glmmTMB (Brooks et al. 2017) and pscl (Jackman 2024) packages.

Simulated residuals were examined for deviations from expected distributions, over- or under-dispersion, and the presence of outliers in the reduced models. Residuals were plotted against fitted values to assess potential non-linear patterns. Spatial autocorrelation in residuals of the reduced model was evaluated using Moran's I test based on geographic distances between sampling sites. Model diagnostics were performed using the DHARMa package (Hartig 2025).

Distance-based redundancy analysis (dbRDA) was used to quantify the relationships between community composition of both groups and TIB predictors, taking into account the similarity between communities and not just the number of species. The measured distances to sources, as well as the water surface area, were logarithmically transformed ($\log x + 1$) before analysis. Species data were transformed into a Bray–Curtis dissimilarity matrix based on presence–absence (Sørensen index), which is appropriate for community datasets dominated by zeros. Variable selection within each group was carried out using the ordiR2step procedure. This method performs stepwise selection based on adjusted R^2 while simultaneously applying the specified permutation scheme, ensuring that both model building and statistical inference follow the same constraints. The adjusted R^2 of the whole model was used as the upper limit for model complexity, and only predictors that improved model fit without exceeding this threshold were retained. The significance of the final dbRDA models and individual predictors was assessed using permutation tests ($n = 1999$). Because

sampling sites belonged to two habitat types (reference vs artificial), all permutation tests were conducted using a blocked permutation design to preserve this grouping structure. This approach ensured that statistical inference respected the sampling design and prevented inflation of Type I error rates. These analyses were performed using the packages vegan (Oksanen et al. 2025) and adespatial (Dray et al. 2025).
Graphical outputs were constructed using the packages ggplot2 (Wickham 2016), ggeffects (Lüdecke 2018), tidyr (Wickham et al. 2024), and dplyr (Wickham et al. 2023). Statistical analysis and plots were conducted in the R environment (R Core Team 2025).

Results

Nutrient relationships and N:P stoichiometry

The relationship between total nitrogen (TN) and total phosphorus (TP) showed a clear positive trend in both types of standing waters (Fig. 2). Log–log linear regressions fitted separately for artificial and reference waters had similar slopes, with overlapping confidence intervals across the observed nutrient range, indicating comparable variability in TN–TP relationships.
The N:P molar ratio differed significantly between the two waterbody types (W = 304, p = 0.036). Artificial waters had higher median N:P values than reference waters, and both groups showed substantial variability in the ratio. Despite this variability, the central tendency of N:P values remained consistently higher in artificial systems.

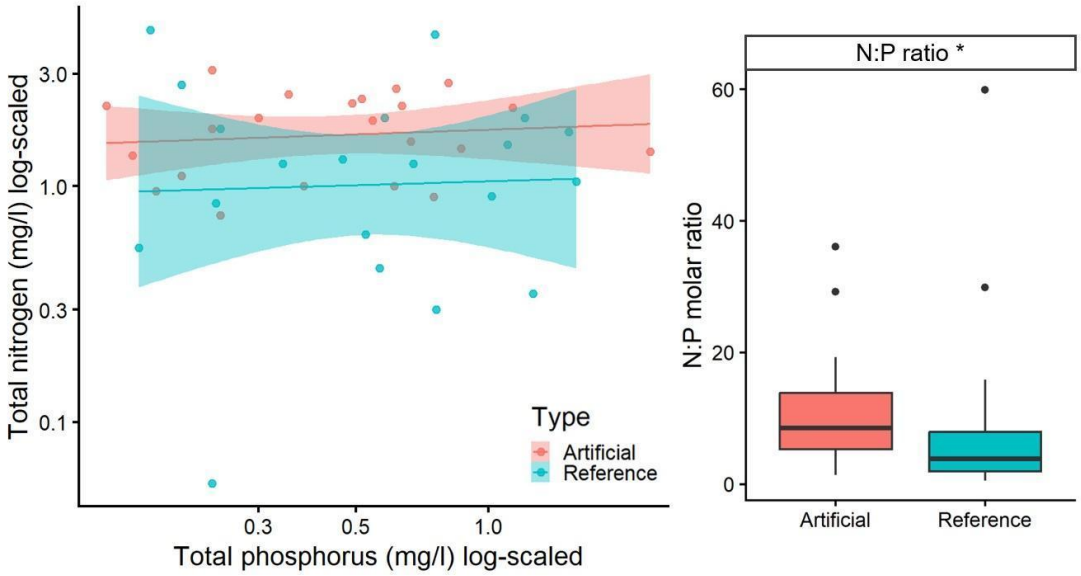


Fig. 2 Log–log relationship between total nitrogen (TN) and total phosphorus (TP) in artificial gravel pits and reference oxbows and wetlands (left), with separate linear regressions and 95% confidence intervals shown for each waterbody type. The N:P molar ratio for both categories of standing waters is presented on the right as boxplots illustrating median values, interquartile ranges, and data dispersion.

Spatial attributes of study waters

Wilcoxon rank-sum tests revealed that area differed significantly between the two habitat types (W = 363.0, p < 0.001), with artificial waters generally being larger (Fig. 3). Distance from source also showed a significant difference (W = 300.5, p = 0.044), indicating that artificial waters tended to be located farther from the nearest colonisation source. Distance to the Danube did not differ between reference and artificial standing waters (W = 283.0, p = 0.115). No significant difference was found in the distances to the nearest pond (W = 266.0, p = 0.251) or to the Little Danube (W = 208.5, p = 0.782).

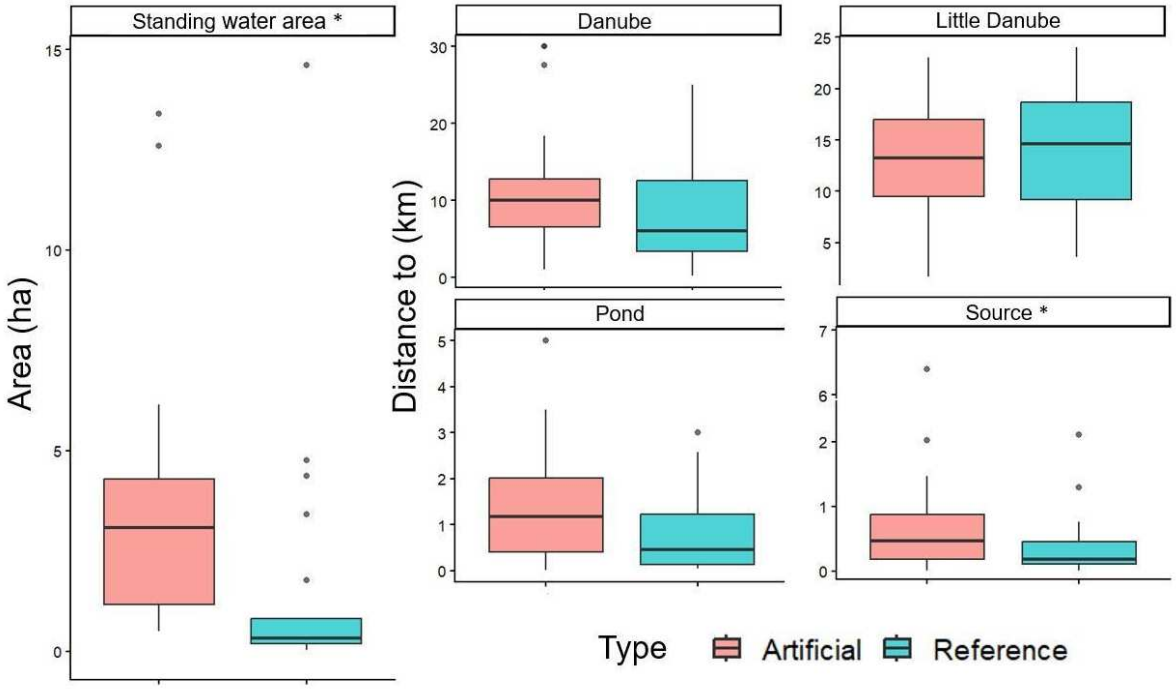


Fig. 3 Boxplots showing the difference in area and distances to colonisation sources (Danube, Little Danube, nearest pond and nearest source) between artificial and reference waters; significant differences ($p < 0.05$) are marked with * after the variable name

Species richness patterns

In summary, 39 mollusc and 95 zooplankton species were identified across all sites during the study period (Appendices 2 and 3). Sample-size-based rarefaction and extrapolation curves revealed apparent differences in species richness between standing water types for molluscs. In contrast, zooplankton communities displayed broadly similar patterns (Fig. 4). For molluscs, artificial waters exhibited higher estimated species richness than reference waters at both rarefied and extrapolated sample sizes (Fig. 4a, c). In contrast, zooplankton richness showed minimal differences between artificial and reference standing waters, although species richness in reference waters tended to be lower (Fig. 4b, d). Rarefaction and extrapolation curves for both groups converged towards similar asymptotes, and coverage-based analyses confirmed that sampling completeness approached 100% in both types with a relatively small number of sites.

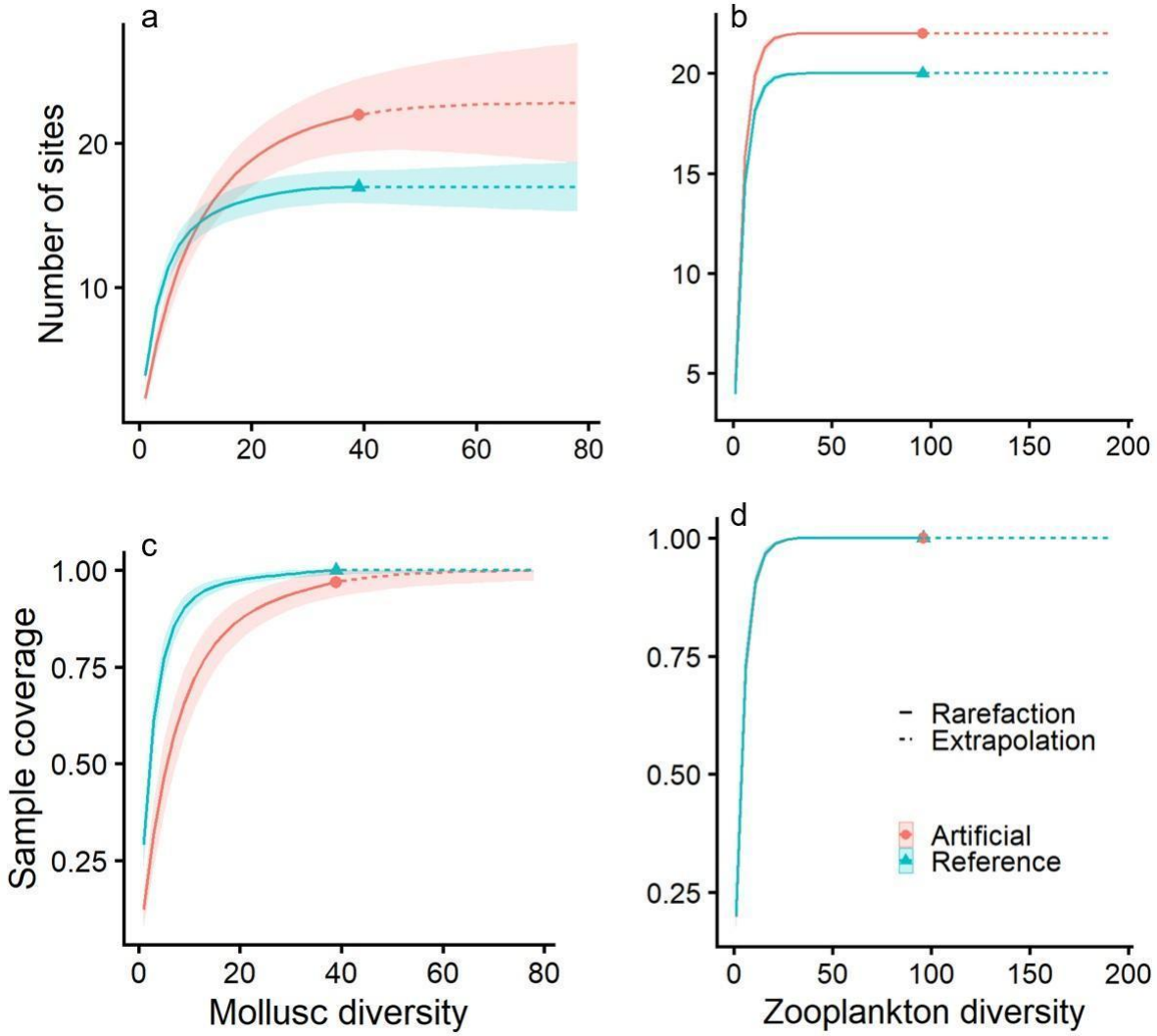


Fig. 4 Rarefaction and extrapolation curves comparing mollusc and zooplankton diversity between artificial (red) and reference (blue) standing waters. Panels (a) and (b) show sample-size-based rarefaction and extrapolation, while panels (c) and (d) present coverage-based estimates. Panels (a) and (c) show mollusc richness, and panels (b) and (d) show zooplankton richness. Shaded areas indicate 95% confidence intervals.

Mollusc richness response to TIB

Analysis of mollusc species richness using a GLMM identified type, area, and distance to the Danube as significant predictors (Table 1). Species richness was significantly higher in artificial waters than in reference waters (Fig. 5a). Area had a significant positive effect (Fig. 5b), indicating that larger standing waters supported more species. This effect was more pronounced in reference waters. In contrast, distance to the Danube had a significant adverse effect, indicating that waters farther from the Danube harboured fewer mollusc species. As with area, the impact of distance to the Danube was more pronounced in reference waters than in artificial waters (Fig. 5c). Figure 6, which illustrates predicted mollusc species richness across a two-dimensional environmental gradient of the significant predictors, shows a consistent decrease in mollusc richness with increasing area but decreasing distance to the Danube. Reference waters exhibit markedly higher richness, particularly in larger ones located closer to the Danube.

Model simplification showed that a reduced model including only statistically significant variables provided a better and more parsimonious fit. The reduced model indicated significant zero inflation; therefore, the zero-inflated structure in the model was defined (zi = 1) (Table 1). McFadden's pseudo-R^2 value indicated that the reduced model explained a moderate proportion of the variation. At the same time, variance-based indices showed that approximately one-third of the variability was accounted for by the fixed effects (Table 2). Residual diagnostics showed no violations of model assumptions. DHARMa tests indicated no deviation from expected residual distributions, no overdispersion or underdispersion, and no outliers (Appendix 4a).

The Moran's I test revealed no spatial autocorrelation in the residuals (observed Moran's I = 0.014; p = 0.616), confirming that the model adequately accounted for spatial structure.

Table 1 Summary of the GLMM full and reduced models for mollusc richness, showing model fit statistics: AIC – Akaike Information Criterion, BIC – Bayesian Information Criterion, df.resid – residual degrees of freedom, McFadden R^2 – McFadden pseudo-R^2, ML R^2 – marginal R^2, CU R^2 – conditional R^2. The table also presents the variance of the random effect (conditional model) and the test statistics of the reduced model, including estimated coefficient, standard error (SE), z-value, and p-value.

Mollusca							
Full model	Mol_sr ~ type + area + d_danube + d_littled + d_pond + d_source + (1|coordinates)						
		AIC	BIC	df.resid	McFadden R^2	ML R^2	CU R^2
		229.1	244.7	33	0.084	0.368	0.370
	group	variance	SE				
Conditional model	coordinates	1.23e-8	1.11e-4				
Reduced model	Mol_sr ~ type + area + d_danube, zi = 1						
		AIC	BIC	df.resid	McFadden R^2	ML R^2	CU R^2
		223.3	233.7	36	0.083	0.365	0.366
Summary							
	Variable	Estimate	SE	z-value	p-value		
	type	0.599	0.206	2.908	**0.004**		
	area	0.060	0.028	2.146	**0.032**		
	d_danube	-0.049	0.018	-2.801	**0.005**		
Zero-inflation	intercept	-3.288	1.177	-2.794	**0.005**		

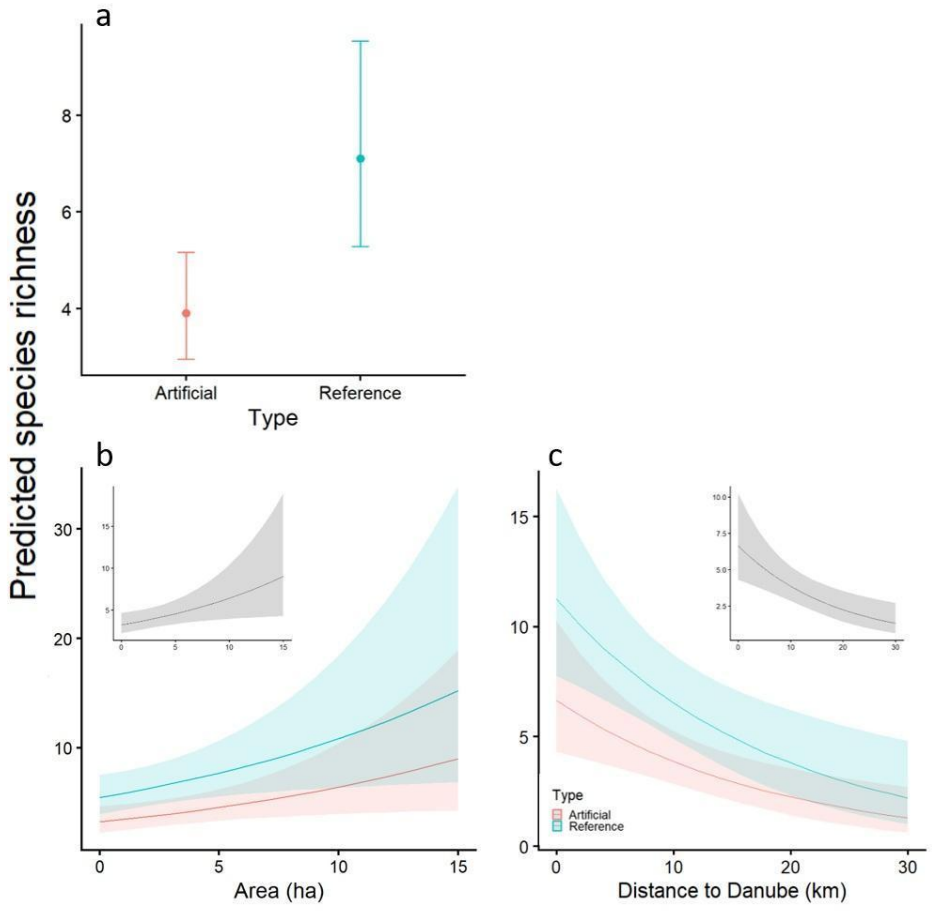


Fig. 5 Graphical representation of the models showing the effect of type (a), area (b), and distance from the Danube (c) on the species richness of molluscs in reference (blue) and artificial (red) standing waters.

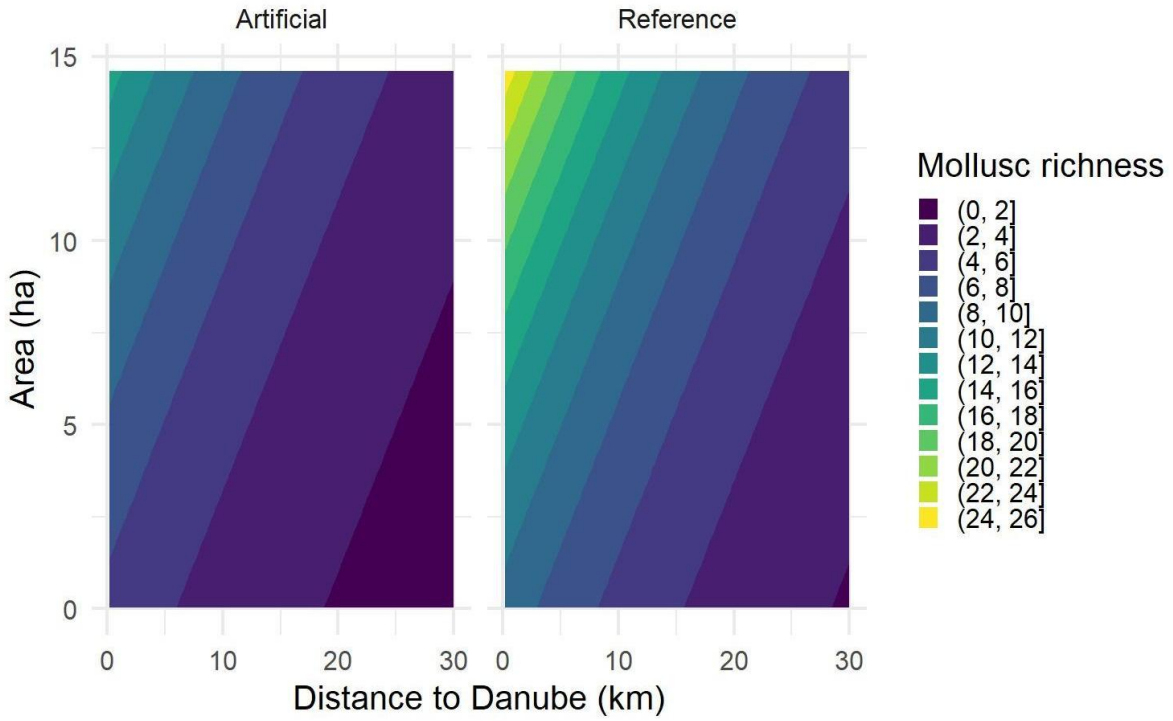


Fig. 6 Predicted mollusc species richness across gradients of area (ha) and distance to the Danube River (km) for artificial (left) and reference standing waters (right). The colour scale indicates predicted richness, with darker shades representing low and lighter shades representing high species richness.

Zooplankton richness response to TIB

GLMM analysis identified area as the only significant predictor of zooplankton species richness (Table 2), indicating that larger waters supported greater diversity (Fig. 7a). Distance to the nearest pond showed a marginally non-significant positive trend ($p = 0.053$), suggesting a tendency for higher zooplankton richness in more isolated waters (Fig. 7b). As predicted zooplankton richness increased continuously with area and distance to the nearest pond, species diversity in more isolated waters increased with size, favouring larger waters (Fig. 8).

The reduced model provided a better and more parsimonious fit than the complete model, including all TIB predictors (Table 2). Zero-inflated structure did not show a significant effect, so it was excluded from the model. McFadden's pseudo-R^2 values were low, suggesting that the model captured only a limited amount of the variation in species richness. Residual diagnostics using DHARMA tests confirmed that the model met all key assumptions (Appendix 4b). Moran's I test indicated no spatial autocorrelation in residuals ($p = 0.207$), confirming that the model adequately accounted for spatial structure.

Table 2 Summary of the GLMM full and reduced models for zooplankton richness, showing model fit statistics: AIC – Akaike Information Criterion, BIC – Bayesian Information Criterion, df.resid – residual degrees of freedom, McFadden R^2 – McFadden pseudo-R^2, ML R^2 – marginal R^2, CU R^2 – conditional R^2, + – marginally significant. The table also presents the variance of the random effect (conditional model) and the test statistics of the reduced model, including the estimated coefficient, standard error (SE), z-value, and p-value.

Zooplankton							
Full model	Zoo_sr ~ type + area + d_danube + d_littled + d_pond + d_source + (1|coordinates)						
		AIC	BIC	df.resid	McFadden R^2	ML R^2	CU R^2
		249.6	265.2	33	0.048	0.244	0.245
	group	variance	SE				

Conditional model	coordinates	3.85e-9	6.20e-5				
Reduced model	Zoo_sr ~ area + d_pond, zi = 0						
		AIC	BIC	df.resid	McFadden R^2	ML R^2	CU R^2
		242.5	249.4	38	0.039	0.190	0.191
Summary							
	Variable	Estimate	SE	z-value	p-value		
	area	0.019	0.009	3.06	**0.039**		
	d_pond	0.058	0.030	1.93	0.053+		
Zero-inflation	intercept	-18.64	1718.36	-0.011	0.991		

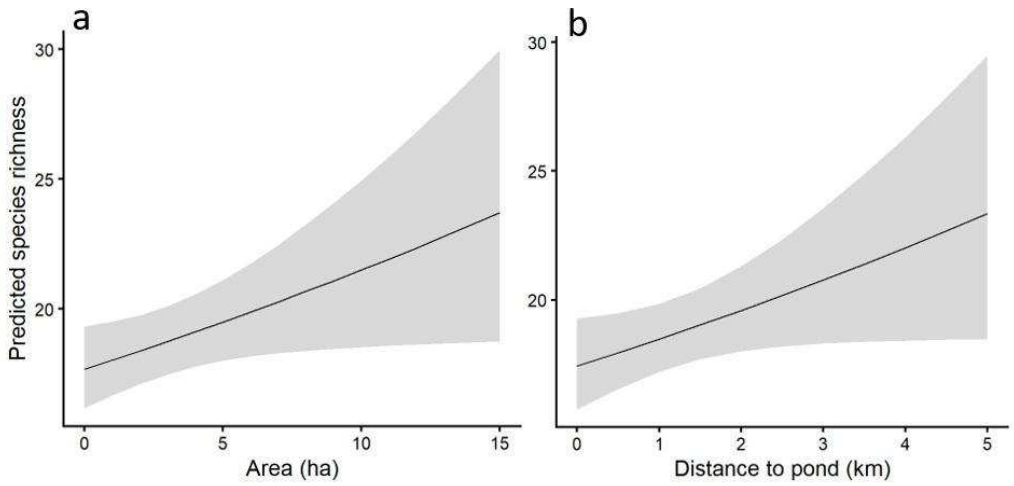


Fig. 7 Graphical representation of the models showing the effect of area (a) and distance from the nearest pond (b) on zooplankton species richness in the studied standing waters.

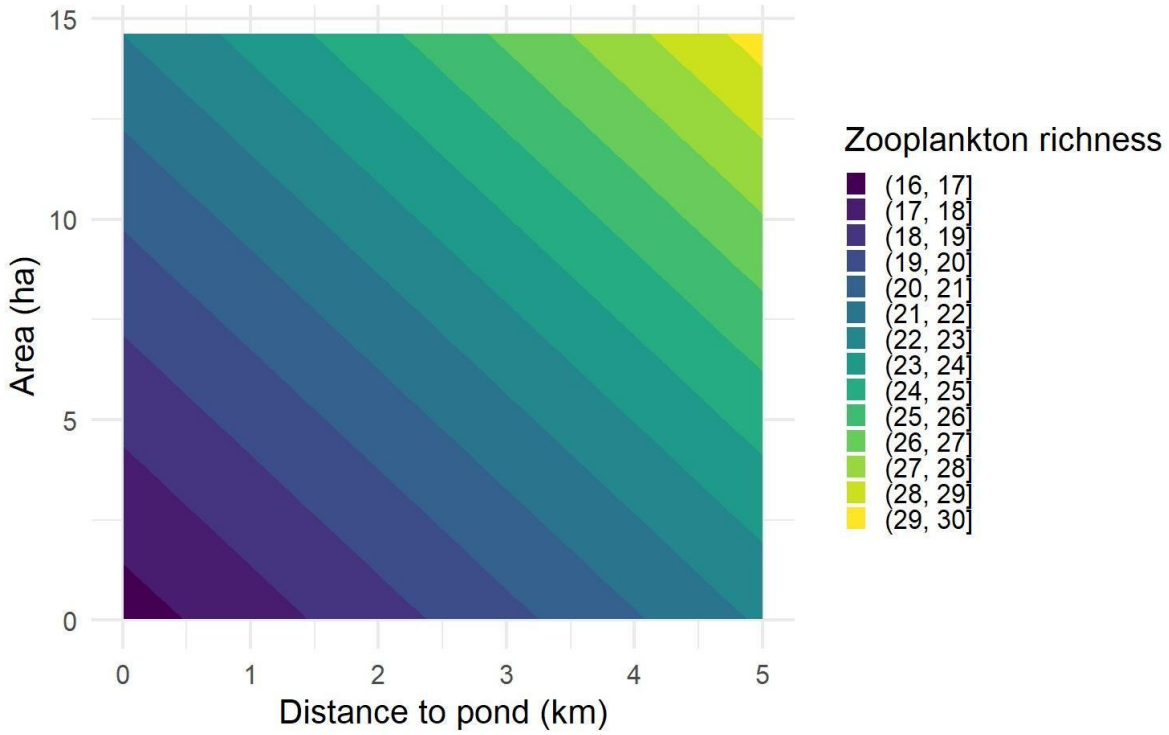


Figure 8. Predicted zooplankton species richness across gradients of area (ha) and distance to the nearest pond (km) for the studied standing waters. The colour scale indicates predicted richness, with darker shades representing low and lighter shades representing high species richness.

Community structure and TIB predictors

Spatial autocorrelation of community datasets was evaluated using Moran's I with inverse distance weights. The mollusc community had an observed Moran's I of 0.062, which was not significant ($p = 0.260$). Similarly, the zooplankton community had a Moran's I of 0.050 with a non-significant p-value ($p = 0.321$). These results indicate no detectable spatial autocorrelation in the distribution of either organism group; therefore, no spatial correction or spatial eigenvector filtering was required in subsequent analyses. However, the dbRDA variable selection performed with ordiR2step did not retain any TIB predictor for the mollusc community. The null model (adjusted $R^2 = 0$) was not improved by adding any variable from the TIB set, as none produced a statistically significant increase in explained variation under the blocked permutation scheme ($p = 0.068$ for the strongest candidate, d_source). The complete TIB model explained only a small proportion of community variation (adjusted $R^2 = 0.036$). Nevertheless, gradients of all TIB predictors were plotted in the ordination diagram to examine the distribution of the studied standing waters in relation to their community similarity (Fig. 9). The difference in mollusc species richness between the two habitat types is evident, as most of the most diverse waters belong to the reference type. The diagram also revealed considerable differences in community structure, as the types formed almost separate groups. The effect of significant predictors, area and distance to the Danube, is also apparent, as their gradients increased with species richness in the waters.

Similarly, the selection procedure did not identify any TIB variable for the zooplankton community. Although distance to the nearest source had the highest explanatory potential, its inclusion did not improve the adjusted R^2 beyond the null model. It remained below the adjusted R^2 of the complete TIB model (0.016). All other TIB variables produced even lower adjusted R^2 values, and none met the criteria for inclusion under the permutation-based selection procedure. The complete TIB model for zooplankton explained only a tiny fraction of the variation (adjusted $R^2 = 0.026$). The ordination diagram of site distribution according to community structure indicated high similarity in species richness. Still, community structure differed, with only a minority of reference waters sharing the same species as artificial waters (Fig. 10). The majority of reference waters have a completely different species composition, which could be linked to shorter distances to the source water bodies.

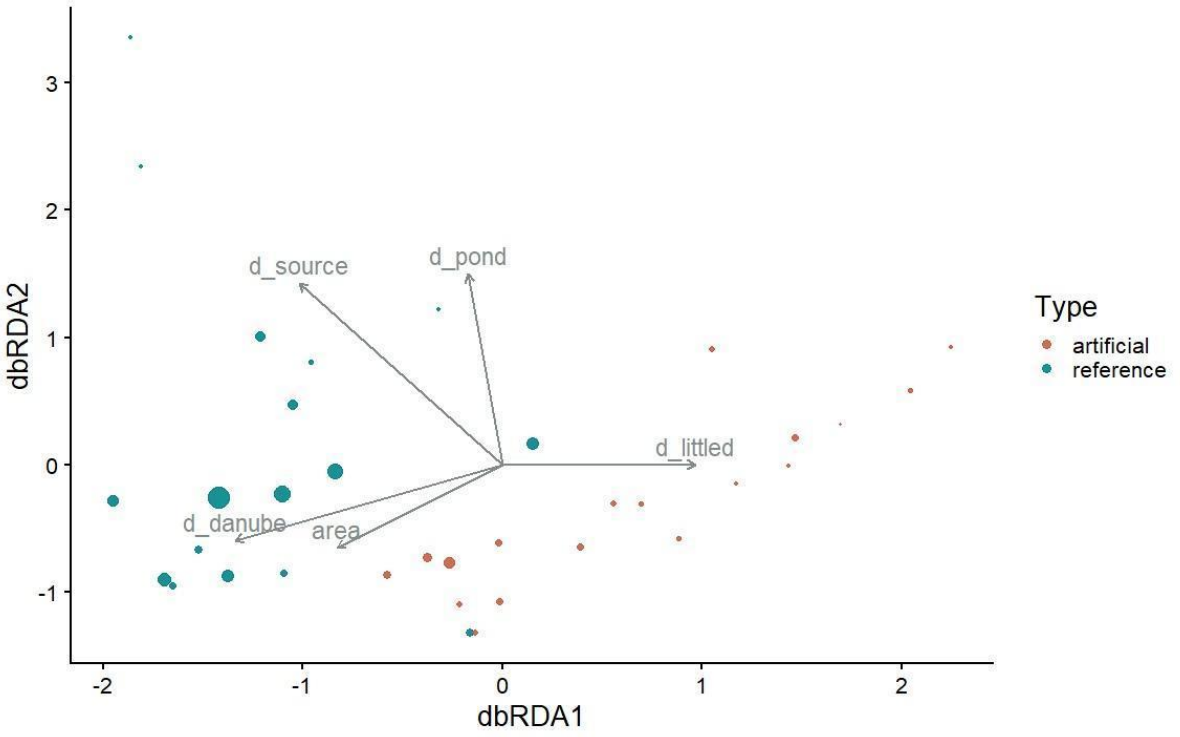


Fig. 9 Ordination biplot of the db-RDA analysis showing the distribution of studied artificial (red) and reference (blue) waters according to the mollusc community; point size represents species richness.

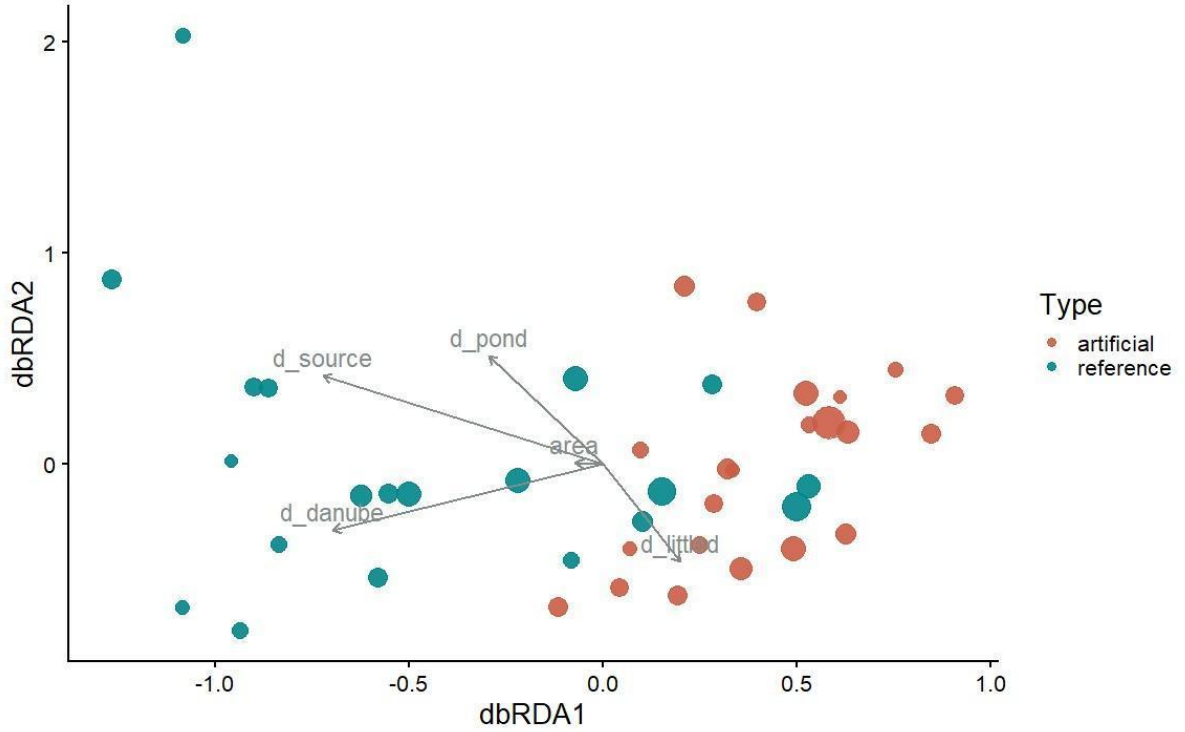


Fig. 10 Ordination biplot of the db-RDA analysis showing the distribution of artificial (red) and reference (blue) standing waters according to zooplankton community composition; dot size represents species richness.

Discussion

Nutrient dynamics at the studied sites

Although total phosphorus and total nitrogen concentrations were similar between artificial and reference waters, their nutrient stoichiometry differed markedly. Reference sites exhibited low N:P ratios, consistent with substantial nitrogen limitation typically observed in less impacted systems. In contrast, artificial waters had substantially higher N:P ratios, indicating a shift towards mixed or even phosphorus-limited conditions. These patterns align with global evidence that low N:P ratios reflect nitrogen limitation, whereas higher ratios are associated with mixed or phosphorus-limited nutrient regimes (Redfield 1958; Guildford and Hecky 2000; Elser et al. 2007). Altered nutrient stoichiometry in artificial water bodies has been reported elsewhere (Søndergaard et al. 2005), and variation in elemental ratios is known to affect both phytoplankton composition and zooplankton responses (Sterner and Elser 2002; Hessen et al. 2013).

Species richness vs area

The TIB hypothesis posits that the area of an island or island-like system is a key determinant of species richness, which is one of the oldest principles in ecology (Drakare et al. 2006). The general observation that species richness increases with area has often been confirmed in studies of freshwater habitats, with larger areas supporting more species than smaller ones (Allen et al. 1999; Bilton et al. 2001; Oertli et al. 2002). However, this relationship appears limited, as Aho (1978) found little evidence that TIB applies to lakes larger than 840 ha. Nevertheless, small water bodies such as ponds and small lakes up to 50 ha in area can contribute significantly to regional biodiversity (Williams et al. 2004; Biggs et al. 2017).
In line with this, we hypothesised that species richness in both habitat types increases with water surface area. This was confirmed for both invertebrate groups, although molluscs exhibited a more specific response. A clear positive relationship between mollusc species richness and area is well established (Aho 1978; Lassen 1975). However, the strength of this relationship may be directly influenced by trophic status (Lassen

1975) and altitude (Oertli et al. 2002). Other studies indicate that nutrient conditions, water quality, or habitat heterogeneity affect species composition rather than the species–area relationship itself (Pip 1986; Sanderson et al. 2005; Stendera et al. 2012; Lewin 2014).

Trophic status may therefore partly explain the difference in species richness between reference and artificial lakes observed in our study, but we did not assess it. Instead, the contrasting nutrient regimes indicated by our analyses provide a more plausible explanation. Artificial waters exhibited consistently higher N:P molar ratios, suggesting a shift towards mixed or phosphorus-limited conditions, whereas reference waters showed lower N:P ratios indicative of more substantial nitrogen limitation. These differences in nutrient stoichiometry and overall nutrient dynamics may influence primary producer composition and periphyton, thereby shaping zooplankton community structure and contributing to the observed variation in species richness between the two habitat types.

The steeper species–area gradient observed in artificial waters is consistent with the idea that spatial factors can explain a larger proportion of variation in species richness when underlying environmental conditions differ systematically between sites (Aho 1978). Altitude cannot explain the differences between the two habitat types, as all sites were situated within the same riverine island and therefore shared an identical geographical context. Consequently, spatial location is unlikely to contribute to the observed variation in species richness, as demonstrated by our results. Moreover, our results support the view that small water bodies (< 2 ha) can act as biodiversity hotspots (Williams et al. 2004). In line with this expectation, the smaller reference waters in our study hosted significantly more mollusc species than the larger artificial waters.

In general, larger lakes have higher zooplankton species richness than smaller water bodies (Gooriah et al. 2020). This has been attributed to a more heterogeneous environment and larger catchment areas. Larger waters are also less susceptible to local stress events and desiccation (De Bie et al. 2008). Our results are consistent with this expectation, as we detected a significant positive relationship between zooplankton species richness and area. Zooplankton richness in standing waters is shaped by a combination of geographical, habitat-related, biotic, and dispersal-related factors, many of which can influence the species–area relationship (Hobæk et al. 2002; Kuczyńska-Kippen and Joniak 2016).

Unlike molluscs, zooplankton showed no significant difference in species richness between artificial and reference sites. The similar patterns observed in both waterbody types likely reflect the fact that all sites shared the same geographical context, including altitude, climatic conditions, regional species pool, and similar levels of isolation. Moreover, spatial dependence was not significant in our results. These factors are known to influence zooplankton richness strongly and can homogenise species–area responses across habitat types (Dodson 1992).

Importantly, this pattern is also consistent with our findings on nutrient stoichiometry. Although artificial and reference waters differed significantly in their N:P molar ratios, these differences did not result in detectable changes in zooplankton species richness. Zooplankton communities are generally less sensitive to nutrient stoichiometry and respond more strongly to overall productivity or trophic status (Hoffmann and Dodson 2005), which our data did not indicate. Thus, the absence of a richness difference between habitat types likely reflects both the shared geographical setting and the limited influence of the observed N:P variation on zooplankton assemblages.

Species richness vs distance from source

Regarding the TIB (MacArthur and Wilson 1963, 1967), it was hypothesised that species richness on islands decreases with increasing distance from the source of colonisation. This TIB assumption was confirmed in our study and applies to both groups, though with different responses.

Remnants of the former Danube floodplain, now preserved as standing waters classified as “reference”, may serve as important refuges for the original malacofauna. In a relatively short section of the river influenced by a large hydropower plant, 40 species were recorded (Beracko et al. 2016), and a detailed survey documented 67 aquatic mollusc species in the Danube basin, representing the current species pool of the Danube lowland (Čejka et al. 2015). The Danube river system hosts one of the most diverse molluscan faunas among European rivers, partly due to the presence of numerous Ponto-Caspian species (Ketelaars 2004). In this context, the 39 species recorded in our study represent a substantial proportion of the regional species pool, underscoring the strong influence of the Danube as a source of colonists.

Distance to the Danube emerged as a significant predictor of mollusc species richness. This pattern suggests that the Danube acts as a significant regional species source and that dispersal limitation increases with distance. Dispersal processes are particularly relevant for molluscs, which rely mainly on passive transport via animals or human activities (Bilton et al. 2001; Kappes and Haase 2012). Previous studies have reported mixed evidence regarding the importance of area and distance to source populations for mollusc richness. Some found weak support for island-biogeographic predictions (e.g. Harris et al. 2011), whereas others demonstrated apparent distance-related effects (e.g. Browne 1981). Brönmark (1985) showed that species richness in only a few nearby ponds could explain mollusc distributions across a much larger landscape, and Dodson (1992) identified the number of lakes within 20 km as a key driver of diversity, highlighting the importance of immigration sources. The absence of a proximity effect reported in some earlier studies was therefore not supported here. Instead, our findings indicate that spatial connectivity to the Danube, even without direct hydrological connection, plays a crucial role in shaping mollusc assemblages across the studied standing waters.

Distance to colonisation sources is often considered a key factor determining dispersal success and colonisation rates in cladoceran and copepod communities, although spatial and temporal scales can modulate these effects (Frisch et al. 2012).

In our study, zooplankton species richness showed a marginally non-significant positive trend with increasing distance from the nearest pond, suggesting that isolation did not constrain dispersal and may even weakly favour higher richness. This pattern is consistent with the high dispersal capacity of zooplankton, which can rapidly colonise new habitats through passive aerial transport or rain-mediated dispersal (Cáceres and Soluk 2002; Cohen and Shurin 2003).

Despite the considerable reduction of the Danube floodplain (Eder et al. 2022), the remaining network of side arms still provides diverse habitats for lowland invertebrates. Reference waters within the study area, formerly part of an extensive floodplain, may therefore act as reservoirs of the original biodiversity. Long-term monitoring has documented more than 120 zooplankton species in this system, including 71 cladocerans (Illýová and Matečný 2014) and 50 copepods (Illýová et al. 2017), indicating a rich regional species pool capable of supplying colonists to nearby ponds. In this context, the 95 zooplankton species recorded in our study represent a substantial portion of the regional species pool, indicating that the surrounding floodplain habitats provide a rich and readily accessible source of colonists for nearby ponds. These habitats can serve as effective sources of zooplankton species, as dispersal is primarily mediated by resting eggs capable of surviving desiccation and transport outside water (Louette and De Meester 2005). Resting eggs are typically produced in macrophyte-rich littoral zones of potamal habitats, oxbow lakes, wetlands and fishponds (Gabaldón et al. 2018), all of which are widespread in the Danube floodplain. In addition to wind-driven dispersal, waterbirds represent essential vectors for the spread of aquatic organisms (Havel and Shurin 2004). Endozoochory can facilitate long-distance dispersal over hundreds of kilometres (Santamaría et al. 2023), and the Danube lies along major migratory routes where standing waters provide suitable resting and feeding habitats for waterbirds (Santoul et al. 2010). These mechanisms collectively explain why zooplankton richness was not reduced in more isolated standing waters and why distance to the nearest pond showed only a weak positive trend.

Metacommunity framework

The dbRDA results showed that TIB predictors explained only a tiny proportion of community variation in both organism groups, indicating that classical island biogeographic variables were poor descriptors of multivariate community structure. This is consistent with the idea that species diversity in standing waters is shaped by a combination of local and regional processes rather than by spatial configuration alone (Shurin 2000; Stendera and Johnson 2005). Although no TIB variable significantly improved the null model, the ordination diagrams revealed clear ecological patterns.

Mollusc communities formed almost distinct clusters between reference and artificial waters, reflecting big differences in community structure and the influence of regional gradients such as distance to the Danube. This supports the view that regional species pools and hydrological history can shape local assemblages, particularly in taxa with limited dispersal (Cornell 1999).

For zooplankton, the dbRDA also retained no TIB predictor, and the whole model explained only a negligible fraction of the variation. However, the ordination still showed compositional differences between

habitat types, despite similar species richness. The number of species recorded in our study represents a substantial portion of the regional pool, suggesting that dispersal processes and the availability of resting eggs across the floodplain landscape override spatial constraints. This is consistent with previous findings that zooplankton communities are often saturated and strongly influenced by regional species supply (Shurin 2000), resulting in more homogeneous assemblages compared to molluscs.

The greater heterogeneity of mollusc communities in ordination space, compared with the more compact zooplankton patterns, supports the idea that dispersal capacity shapes community variability (Hassall et al. 2011). While some zooplankton groups show preferences for larger standing waters (Fryer 1985), molluscs lack such clear habitat associations and may be more sensitive to historical connectivity and regional hydrology. The dbRDA therefore highlights that, although TIB variables alone do not explain community structure, local environmental gradients and regional species pools remain key drivers of differentiation between types of standing waters.

Conclusions and implications

Our study demonstrates that the interaction between local environmental conditions and the regional species pool shapes biodiversity patterns in small standing waters. Although species richness and species diversity are often used interchangeably, they represent distinct aspects of community organisation (Delang and Li 2013), and both are essential for understanding how immigration, extinction, and habitat saturation function in standing water ecosystems.

The Rye Island landscape, with its uniform geomorphological history and clear ecological boundaries, meets the criteria for a coherent biogeographical region (Cornell 1999), making it an appropriate system for evaluating the relative roles of local and regional drivers. Our results indicate that mollusc communities are more strongly structured by regional processes, particularly proximity to the Danube, whereas zooplankton richness is driven mainly by local factors such as area.

Multivariate analyses further showed that classical island biogeographic predictors explained only a small fraction of multivariate community variation in both groups, suggesting that dispersal capacity and species traits modulate the extent to which regional gradients influence community structure. The high number of zooplankton species recorded in our study indicates that regional propagule supply and strong dispersal capacity reduce the influence of spatial configuration. At the same time, mollusc assemblages remain more heterogeneous and sensitive to regional hydrological connectivity.

These findings have several implications. First, reference waters support distinct and diverse mollusc communities and should be prioritised in conservation planning, as they retain elements of the original floodplain fauna. Second, maintaining a network of natural and artificial water bodies can sustain high zooplankton diversity if environmental conditions remain suitable, reflecting the importance of regional species pools for unsaturated communities (Huston 1994). Third, the weak explanatory power of TIB variables highlights the need to incorporate species traits, hydrological history, and regional context into biodiversity assessments of landscapes. Finally, the potential for artificial waters to act as sources of non-native species (Oertli and Parris 2019) underscores the importance of monitoring and managing these habitats to prevent the spread of invasive taxa.

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Author contributions

M.I. and T.Č.—study conception and design, including site selection and survey methodology. I.K., M.I. and T.Č.—sample processing and identification, data collection, and analysis. I.K., T.Č. and M.I.—wrote the first draft of the manuscript, and all authors commented on previous versions of the manuscript. I.K. and T.Č.—read and approved the final manuscript.

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Data availability
All data supporting the findings of this study are available within the paper. The tables and figures present original results included in this paper.

Declarations

Consent to publish
Authors confirm that the work contains original research carried out by the authors; the manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal.

Conflict of interests
The authors have no competing interests to declare that are relevant to the content of this article.

References

Aho J (1978) Freshwater snail populations and the equilibrium theory of island biogeography. I. A case study in southern Finland. Ann Zool Fenn 15:146-154

Allen AP, Whittier TR, Kaufmann PR, Larsen DP, O'Connor RJ, Hughes RM, Paulsen SG (1999) Concordance of taxonomic richness patterns across multiple assemblages in lakes of the northeastern United States. Can J Fish Aquat Sci 56:739-747

Beracko P, Matečný I, Košel V (2016) Long-term changes in freshwater molluscan communities in the middle stretch of the Danube River (Slovakia) over a 23-year period. Fund Appl Limnol 187:263-280. https://doi.org/10.1127/fal/2016/0824

Biggs J, von Fumetti S, Kelly-Quinn M (2017) The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. Hydrobiologia 793:3-39. https://doi.org/10.1007/s10750-016-3007-0

Bilton DT, Freeland JR, Okamura B (2001) Dispersal in freshwater invertebrates. Annu Rev Ecol Syst 32:159-181

Bohonak AJ, Jenkins DG (2003) Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecol Lett 6:783-796. https://doi.org/10.1046/j.1461-0248.2003.00486.x

Bosiacka B, Pieńkowski P (2012) Do biogeographic parameters matter? Plant species richness and distribution of macrophytes in relation to area and isolation of ponds in NW Polish agricultural landscape. Hydrobiologia 689:79-90. https://doi.org/10.1007/s10750-011-0850-x

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378-400. https://doi.org/10.32614/RJ-2017-066

Browne RA (1981) Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. J Biogeogr 8:75-83. https://doi.org/10.2307/2844594

Brönmark C (1985) Freshwater snail diversity: effects of pond area, habitat heterogeneity and isolation. Oecologia 67:127-131

Cáceres CE, Soluk DA (2002) Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131:402-408. https://doi.org/10.1007/s00442-002-0897-5

Céréghino R, Biggs J, Oertli B, Declerck S (2008) The ecology of European ponds: defining the characteristics of a neglected freshwater habitat. Hydrobiologia 597:1-6. https://doi.org/10.1007/s10750-007-9225-8
Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. Ecol Lett 8:1175-1182. http://doi.org/10.1111/j.1461-0248.2005.00820.x

Čejka T, Čačaný J, Horsák M, Juřičková L, Buďová J, Duda M, Holubová A, Horsáková V, Jansová A, Kocurková A, Korábek O, Maňas M, Říhová D, Šizling AL (2015) Freshwater molluscs of water bodies with a high conservation value in the Danubian Lowland (SW Slovakia). Malacologica Bohemoslovaca 14:5-16. https://doi.org/10.5817/MaB2015-14-5

Chanut PCM, Burdon FJ, Datry T (2023) Convergence in floodplain pond communities indicates different pathways to community assembly. Aquat Sci 85:59. https://doi.org/10.1007/s00027-023-00957-9

Chase JM, Jeliazkov A, Ladouceur E, Viana DS (2020) Biodiversity conservation through the lens of metacommunity ecology. Ann NY Acad Sci 1469:86-104. https://doi.org/10.1111/nyas.14378
Cohen GM, Shurin JB (2003) Scale-dependence and mechanisms of dispersal in freshwater zooplankton. Oikos 103:603-617. https://doi.org/10.1034/j.1600-0706.2003.12660.x
Cornell HV (1999) Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. Ecoscience 6:303-315. https://doi.org/10.1080/11956860.1999.11682532
De Bie T, Declerck S, Martens K, De Meester L, Brendonck L (2008) A comparative analysis of cladoceran communities from different water body types: patterns in community composition and diversity. Hydrobiologia 597:19-27. https://doi.org/10.1007/s10750-007-9222-y
De Bie T, De Meester L, Brendonck L, Martens K, Goddeeris B, Ercken D, Hampel H, Denys L, Vanhecke L, Van Der Gucht K (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecol Lett 15:740-747. https://doi.org/10.1111/j.1461-0248.2012.01794.x
Declerck SAJ, Coronel JS, Legendre P, Brendonck L (2011) Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. Ecography 34:296-305. https://doi.org/10.1111/j.1600-0587.2010.06462.x
Delang CO, Li WM (2013) Species richness and diversity. In: Ecological succession on followed shifting cultivation fields: a review of the literature. Nova Science Publishers, New York, pp 39-66
Dodson SI (1992) Predicting crustacean zooplankton species richness. Limnol Oceanogr 37:848-856. https://doi.org/10.4319/lo.1992.37.4.0848
Drakare S, Lennon JJ, Hillebrand H (2006) The imprint of the geographical, evolutionary and ecological context on species-area relationships. Ecol Lett 9:215-227. https://doi.org/10.1111/j.1461-0248.2005.00848.x
Dray S, Bauman D, Blanchet G, Borcard D, Clappe S, Guénard G (2025) adespatial: multivariate multiscale spatial analysis. R package version 0.3-28. https://CRAN.R-project.org/package=adespatial
Eder M, Perosa F, Hohensinner S, Tritthart M, Scheuer S, Gelhaus M, Cyffka B (2022) How can we identify active, former, and potential floodplains? Methods and lessons learned from the Danube River. Water 14:2295. https://doi.org/10.3390/w14152295
Einsle U (1993) Crustacea: Copepoda: Calanoida und Cyclopoida. In: Schwoerbel J, Zwick P (eds) Süßwasserfauna von Mitteleuropa, vol 8/4.1. Gustav Fischer Verlag, Stuttgart
Einsle U (1996) Copepoda: Cyclopoida. Genera Cyclops, Megacyclops, Acanthocyclops. In: Dumont HJ (ed) Guides to the identification of the microinvertebrates of the continental waters of the world, vol 10. SPB Academic Publishing, Amsterdam
Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135-1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x
Frisch D, Cottenie K, Badosa A, Green AJ (2012) Strong spatial influence on colonization rates in a pioneer zooplankton metacommunity. PLoS ONE 7:e40205. https://doi.org/10.1371/journal.pone.0040205
Fryer G (1985) The ecology and distribution of the genus Daphnia (Crustacea: Cladocera) in restricted areas: the pattern in Yorkshire. J Nat Hist 19:97-128. https://doi.org/10.1080/00222938500770051

Gabaldón C, Buseva Z, Illýová M, Seda J (2018) Littoral vegetation improves the productivity of drainable fish ponds: interactive effects of refuge for Daphnia individuals and resting eggs. Aquaculture 485:111-118. https://doi.org/10.1016/j.aquaculture.2017.11.027
GCCAS (Geodesy, Cartography and Catastre Authority of the Slovak Republic) (2024) ZBGIS [WWW document]. https://zbgis.sk. Accessed 20 May 2024
Glöer P, Meier-Brook C (2003) Süßwassermollusken. DJN, Hamburg
Google (2025) Google Earth (version 7.3.6.10441) [Computer software]. https://www.google.com/earth/
Gooriah LD, Davidar P, Chase JM (2020) Species-area relationships in the Andaman and Nicobar Islands emerge because rarer species are disproportionately favored on larger islands. Ecol Evol 10:7551-7559. https://doi.org/10.1002/ece3.6480
Guildford SJ, Hecky RE (2000) Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: is there a common relationship? Limnol Oceanogr 45:1213-1226. https://doi.org/10.4319/lo.2000.45.6.1213
Hamerlík L, Brodersen KP (2010) Non-biting midges (Diptera: Chironomidae) from fountains of two European cities: micro-scale island biogeography. Aquat Insects 32:67-79. https://doi.org/10.1080/01650420903397645
Harris AT, Woolnough DA, Zanatta DT (2011) Insular lake island biogeography: using lake metrics to predict diversity in littoral zone mollusk communities. J N Am Benthol Soc 30:997-1008. https://doi.org/10.1899/11-020.1
Hartig F (2025) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.7. https://github.com/florianhartig/dharma
Hassall C, Hollinshead J, Hull A (2011) Environmental correlates of plant and invertebrate species richness in ponds. Biodivers Conserv 20:3189-3222. https://doi.org/10.1007/s10531-011-0142-9
Havel JE, Shurin JB (2004) Mechanisms, effects, and scales of dispersal in freshwater zooplankton. Limnol Oceanogr 49:1229-1238. https://doi.org/10.4319/lo.2004.49.4_part_2.1229
Hebert PDN, Finston TL (1996) A taxonomic reevaluation of North American Daphnia (Crustacea: Cladocera). II. New species in the Daphnia pulex group from the south-central United States and Mexico. Can J Zool 74:632-653
Hessen DO, Elser JJ, Sterner RW, Urabe J (2013) Ecological stoichiometry: an elementary approach using basic principles. Limnol Oceanogr 58:2219-2236. https://doi.org/10.4319/lo.2013.58.6.2219
Hill MJ, Ryves DB, White JC, Wood PJ (2016) Macroinvertebrate diversity in urban and rural ponds: implications for freshwater biodiversity conservation. Biol Conserv 201:50-59. https://doi.org/10.1016/j.biocon.2016.06.027
Hill MJ, Heino J, White JC, Ryves DB, Wood PJ (2019) Environmental factors are primary determinants of different facets of pond macroinvertebrate alpha and beta diversity in a human-modified landscape. Biological Conservation 237:348-357. https://doi.org/10.1016/j.biocon.2019.07.015

Hobæk A, Manca M, Andersen T (2002) Factors influencing species richness in lacustrine zooplankton. Acta Oecol 23:155-163. https://doi.org/10.1016/S1146-609X(02)01147-5
Hoffmann MD, Dodson SI (2005) Land use, primary productivity, and lake area as descriptors of zooplankton diversity. Ecology 86:255-261. https://doi.org/10.1890/03-0833
Hrbáček J (1972) Limnologické metody. Státní pedagogické nakladatelství, Praha
Hsieh TC, Ma KH, Chao A (2025) iNEXT: interpolation and extrapolation for species diversity. R package version 3.0.2. https://chao.stat.nthu.edu.tw/wordpress/software_download/inext/
Hudec I (2010) Fauna Slovenska III: Anomopoda, Ctenopoda, Haplopoda, Onychopoda (Crustacea: Branchiopoda). VEDA, Bratislava
Huston MA (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge
Illýová M, Matečný I (2014) Ecological validity of river-floodplain system assessment by planktonic crustacean survey (Branchiata: Branchiopoda). Environ Monit Assess 186:4195-4208. https://doi.org/10.1007/s10661-014-3690-0
Illýová M, Beracko P, Vranovský M, Matečný I (2017) Long-term changes in copepods assemblages in the area of the Danube floodplain (Slovak-Hungarian stretch). Limnologica 65:22-33. https://doi.org/10.1016/j.limno.2017.05.001

Jackman S (2024) pscl: classes and methods for R developed in the Political Science Computational Laboratory. R package version 1.5.9. https://github.com/atahk/pscl/
Jenkins DG, Buikema AL Jr (1998) Do similar communities develop in similar sites? A test with zooplankton structure and function. Ecol Monogr 68:421-443. https://doi.org/10.1890/0012-9615(1998)068[0421:DSCDIS]2.0.CO;2
Jurík Ľ, Zeleňáková M, Kaletová T, Arifjanov A (2019) Small water reservoirs: sources of water for irrigation. In: Zeleňáková J (ed) Water resources in Slovakia: Part I. Springer, Cham, pp 115-131
Kandra B, Gomboš M (2020) The importance of volume changes in the determination of soil water retention curves on the East Slovakian Lowland. J Water Land Dev 45:1-10. https://doi.org/10.24425/jwld.2020.133045
Kappes H, Haase P (2012) Slow, but steady: dispersal of freshwater molluscs. Aquat Sci 74:1-14. https://doi.org/10.1007/s00027-011-0187-6
Ketelaars HAM (2004) Range extensions of Ponto-Caspian aquatic invertebrates in continental Europe. In: Dumont H (ed) Aquatic invasions in the Black, Caspian, and Mediterranean Seas. Springer, Dordrecht, pp 209-236. https://doi.org/10.1007/1-4020-2152-6_13
Kuczyńska-Kippen N, Joniak T (2016) Zooplankton diversity and macrophyte biometry in shallow water bodies of various trophic state. Hydrobiologia 774:39-51. https://doi.org/10.1007/s10750-015-2595-4
Lassen HH (1975) The diversity of freshwater snails in view of the equilibrium theory of island biogeography. Oecologia 19:1-8. https://doi.org/10.1007/BF00377585
Leibold, M. A. et al. (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters, 7, 601–613. http://doi.org/10.1111/j.1461-0248.2004.00608.x
Lewin I (2014) Mollusc communities of lowland rivers and oxbow lakes in agricultural areas with anthropogenically elevated nutrient concentration. Folia Malacol 22:127-138. https://doi.org/10.12657/folmal.022.012
Logue JB, Jürg B, Mouquet N, Hannes P, Hillebrand H, The Metacommunity Working Group (2011) Empirical approaches to metacommunities: a review and comparison with theory. Trends Ecol Evol 26:482-491. http://doi.org/10.1016/j.tree.2011.04.009
Louette G, De Meester L. 2005. High dispersal capacity of cladoceran zooplankton in newly founded communities. Ecology 86:353-359. https://doi.org/10.1890/04-0403

Lüdecke D (2018) ggeffects: tidy data frames of marginal effects from regression models. J Open Source Softw 3:772. https://doi.org/10.21105/joss.00772
MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. Evolution 17:373-387. https://doi.org/10.2307/2407089
MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton
Meland S, Sun Z, Sokolova E, Rauch S, Brittain JE (2020). A comparative study of macroinvertebrate biodiversity in highway stormwater ponds and natural ponds. Science of the Total Environment, 740, 140029. https://doi.org/10.1016/j.scitotenv.2020.140029

Oboňa J, Svitok M (2012) Dendrotelmy a ich miesto v ostrovnej ekológii. Limnologický spravodajca 6:11-15
Oertli B (2018) Freshwater biodiversity conservation: the role of artificial ponds in the 21st century. Aquat Conserv Mar Freshw Ecosyst 28:264-269. https://doi.org/10.1002/aqc.2902
Oertli B, Parris KM (2019) Toward management of urban ponds for freshwater biodiversity. Ecosphere 10:e02810. https://doi.org/10.1002/ecs2.2810
Oertli B, Joye DA, Castella E, Juge R, Cambin D, Lachavanne JB (2002) Does size matter? The relationship between pond area and biodiversity. Biol Conserv 104:59-70. https://doi.org/10.1016/S0006-3207(01)00154-9
Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista HB, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlinn D, Ouellette MH, Ribeiro ER, Smallwood MP, Roelandt R, Selemani S, Sharifian M, Staniaszek-Kik D (2025) vegan: community ecology package. R package version 2.7-2. https://CRAN.R-project.org/package=vegan

Pip E (1986) A study of pond colonization by freshwater molluscs. J Molluscan Stud 52:214-224. https://doi.org/10.1093/mollus/52.3.214
R Core Team (2025) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/
Redfield AC (1958) The biological control of chemical factors in the environment. Am Sci 46:205-221
Samways MJ, Deacon C, Kietzka GJ, Pryke JS, Vorster C, Simaika JP (2020) Value of artificial ponds for aquatic insects in drought-prone southern Africa: a review. Biodivers Conserv 29:3131-3150. https://doi.org/10.1007/s10531-020-02020-7
Sanderson RA, Eyre MD, Rushton SP (2005) Distribution of selected macroinvertebrates in a mosaic of temporary and permanent freshwater ponds as explained by autologistic models. Ecography 28:355-362. https://doi.org/10.1111/j.0906-7590.2005.04093.x
Santamaría L, Charalambidou I, Viana D, van Donk E (2023) Evidence that long-distance dispersal of aquatic invertebrates by ducks increases with propagule size. Freshw Biol 68:1530-1541. https://doi.org/10.1111/fwb.14146
Santoul F, Gaujard A, Angélibert S, Mastrorillo S, Céréghino R (2010) Gravel pits support waterbird diversity in an urban landscape. In: Oertli B, Céréghino R, Hull A, Miracle M (eds) Pond conservation in Europe. Springer, Dordrecht, pp 263-270
Sepkoski JJ Jr, Rex MA (1974) Distribution of freshwater mussels: coastal rivers as biogeographic islands. Syst Biol 23:165-188. https://doi.org/10.1093/sysbio/23.2.165
Shurin JB (2000) Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecology 81:3074-3086. https://doi.org/10.1890/0012-9658(2000)081[3074:DLIRAT]2.0.CO;2
Søndergaard M, Jensen JP, Jeppesen E (2005) Seasonal response of nutrients to reduced phosphorus loading in 12 Danish lakes. Freshw Biol 50:1605-1615. https://doi.org/10.1111/j.1365-2427.2005.01412.x
Stendera S, Johnson RK (2005) Does climate change confound lake recovery? AGU Spring Meeting Abstracts 2005:NB32D-04
Stendera S, Adrian R, Bonada N, Cañedo-Argüelles M, Hugueny B, Januschke K, Pletterbauer S, Hering D (2012) Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: a review. Hydrobiologia 696:1-28. https://doi.org/10.1007/s10750-012-1183-0
Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton

Sun Z, Sokolova E, Brittain JE (2019) Impact of environmental factors on aquatic biodiversity in roadside stormwater ponds. Sci Rep 9:5994. https://doi.org/10.1038/s41598-019-42497-z
Thornhill I, Batty L, Death RG, Friberg NR, Ledger ME (2017) Local and landscape scale determinants of macroinvertebrate assemblages and their conservation value in ponds across an urban land-use gradient. Biodivers Conserv 26:1065-1086. https://doi.org/10.1007/s10531-016-1286-4

Várbíró G, Görgényi J, Tóthmérész B, Padisák J, Hajnal É, Borics G (2017) Functional redundancy modifies species–area relationship for freshwater phytoplankton. Ecol Evol 23:9905-9913. https://doi.org/10.1002/ece3.3512
Warren BH, Simberloff D, Ricklefs RE, Aguilée R, Condamine FL, Gravel D, Morlon J, Mouquet N, Rosindell J, Casquet J, Conti E, Cornuault J, Fernández-Palacios JM, Hengl T, Norder SJ, Rijsdijk KF, Sanmartín I, Strasberg SP, Triantis KA, Valente LM, Whittaker RJ, Thébaud SP, Emerson BC (2015) Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. Ecol Lett 18:200-217. https://doi.org/10.1111/ele.12398
Watson AM, Ormerod SJ (2004) The distribution of three uncommon freshwater gastropods in the drainage ditches of British grazing marshes. Biol Conserv 118:455-466. https://doi.org/10.1016/j.biocon.2003.09.021
Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer, New York. https://doi.org/10.1007/978-3-319-24277-4
Wickham H, François R, Henry L, Müller K, Vaughan D (2023) dplyr: a grammar of data manipulation. R package version 1.1.4. https://CRAN.R-project.org/package=dplyr
Wickham H, Vaughan D, Girlich M (2024) tidyr: tidy messy data. R package version 1.3.1. https://CRAN.R-project.org/package=tidyr

Williams P, Whitfield M, Biggs J, Bray S, Fox G, Nicolet P, Sear D (2004) Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. Biol Conserv 115:329-341. https://doi.org/10.1016/S0006-3207(03)00153-8

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