BIOLOGICA NYSSANA
16 (1) June 2025: 297-305

DOI: 10.46793/BiolNyss.16.1.17SP

The impact of pond origin on species and functional diversity of fish communities

Original Article

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Received: *March 24, 2025*
Revised: *April 18, 2025*
Accepted: *April 22, 2025*

Abstract:

Ponds are standing freshwater ecosystems, that play a significant role in supporting biodiversity and ecological functions. Despite their small size, they support high species diversity, particularly fish communities, that are influenced by variations in environmental factors such as hydroperiod, size of the pond, and water quality. This study investigates the differences in fish species composition and functional diversity between natural and artificial ponds in southeastern Serbia. The research reveals that functional diversity is more sensitive indicator of ecological differences between these ponds than species diversity. Artificial ponds, formed through human activity, tend to harbor opportunistic fish species, often resulting in lower functional diversity, while natural ponds exhibit greater species richness and more specialized fish communities. The findings underscore the importance of functional diversity in maintaining ecosystem health and highlight the distinct ecological roles played by ponds of different origins in sustaining freshwater biodiversity. Understanding these dynamics is essential for effective conservation and management strategies.

Key words:
fish community, natural ponds, artificial ponds, species richness, functional diversity

Apstrakt:

Uticaj porekla bara na specijski i funkcionalni diverzitet ribljih zajednica

Bare predstavljaju stajaće slatkovodne ekosisteme koji imaju značajnu ulogu u očuvanju biodiverziteta i ekoloških funkcija. Iako su male površine, karakteriše ih visoka raznovrsnost vrsta, posebno ribljih zajednica, koje su pod uticajem različitih ekoloških faktora kao što su hidroperiod, veličina bare i kvalitet vode. Ovo istraživanje se bavi ispitivanjem razlike u sastavu ribljih vrsta i funkcionalnom diverzitetu između prirodnih i veštačkih bara u jugoistočnoj Srbiji. Rezultati ukazuju na to da je funkcionalni diverzitet bolji pokazatelj ekoloških razlika između ovih tipova bara u poređenju sa specijskim diverzitetom. Veštačke bare, nastale pod uticajem ljudskih aktivnosti, često sadrže oportunističke riblje vrste, što dovodi do nižeg funkcionalnog diverziteta, dok prirodne bare karakteriše veće bogatstvo vrsta i prisustvo specijalizovanijih zajednica. Dobijeni rezultati ističu značaj funkcionalnog diverziteta za očuvanje vodenih ekosistema i ukazuju na različite ekološke uloge koje bare različitog porekla imaju u očuvanju slatkovodnog biodiverziteta. Razumevanje ove dinamike od suštinskog je značaja za efikasno planiranje strategija očuvanja i upravljanja vodenim ekosistemima.

Ključne reči:
riblje zajednice, prirodne bare, veštačke bare, bogatstvo vrsta, funkcionalni diverzitet

Introduction

Ponds are small, standing aquatic ecosystems that play a critical role in supporting biodiversity and ecological processes such as nutrient cycling, primary production, water purification, and habitat provision. These ecosystems are characterized by their relatively small size, shallow depths, and the absence of significant water flow. Although ponds are relatively small in size, they are highly productive environments that host a variety of organisms, including aquatic plants, invertebrates, amphibians, fish, and birds (Biggs et al., 2005). Ponds play a crucial role in regional biodiversity, particularly in supporting diverse and often rare fish communities (Wezel et al., 2014). The high β diversity of ponds, driven by variations in features such as hydroperiod, size, origin, and physical and chemical properties, creates a mosaic of habitats that support a diverse array of aquatic life (De Meester et al., 2005). These unique environmental conditions foster complex fish communities, often characterized by species that are adapted to the specific conditions of pond ecosystems (Wezel et al., 2014). As such, ponds are not only essential for freshwater biodiversity but also serve as critical habitats for maintaining and enhancing the resilience of fish populations in fragmented landscapes (Wetzel, 2001).

Ponds can vary significantly in terms of their origin, and these variations influence the biological communities that inhabit them (Biggs et al., 2005). The formation process of a pond influences its physical and chemical properties, such as water depth, temperature, and nutrient levels, which in turn affect the types of species that can thrive in it. Natural ponds are typically formed through geological or climatic processes over long periods. They vary in origin depending on local geography, climate, and ecological interactions (Brönmark & Hansson, 2017). Artificial ponds are created by human activity, and their biological communities can differ considerably from those of natural ponds. The way they are constructed and their intended use (e.g., ornamental, agricultural, or stormwater management) influence key aspects of their biological structure, including species richness, community composition, and the presence of sensitive or specialist species (Oertli et al., 2005). It has been shown that ponds differ significantly in terms of species richness and composition, meaning they possess high β biodiversity, thereby making a disproportionate contribution to regional biodiversity (Oertli et al., 2002; Williams et al., 2004). This is, of course, facilitated by their high variability in physicochemical properties and hydroperiod duration, which causes even spatially close ponds to exhibit unique flora and fauna (De Meester et al., 2005).

Recent studies propose two main approaches for the evaluation ecosystem health, stability, and resilience using aquatic communities (Pease et al., 2012; Villéger et al., 2017; Martini et al., 2021). One approach focuses on the taxonomic composition of the community and associated metrics, while the other emphasizes the functional characteristics of the observed community. According to the first approach, changes in water quality can lead to a noticeable shift in the taxonomic structure of aquatic communities, with only a limited number of tolerant species from the local pool likely to persist (Blonder et al., 2014). This shift in taxonomic composition, and the subsequent simplification of community structure, can further drive alterations in functional diversity (Petchey and Gaston, 2002). Functional diversity offers valuable insights into changes in the functional niches of species, as organisms are selected based on traits such as feeding behavior, physiology, and ecological role.

Bearing all this in mind, the objectives of our study were to: (i) test the differences between artificial and natural ponds in terms of fish species and functional diversity, and (ii) examine how environmental factors influence species and functional diversity in ponds of different origins.

Materials and Methods

Study area

The investigation was conducted in southeastern Serbia, around 10 kilometers west of the city of Niš (coordinates: 43°29′–43°30′N, 21°79–21°80′E). The study area includes six ponds, located along the South Morava River, between the villages of Batušinac and Mramor.

Two sets of ponds were included in the study, each composed of three ponds, differing in terms of origin (natural and artificial) (**Fig. 1**). Artificial ponds are located along the right bank (pond 1, 2, 3) of the South Morava River and were created by excavating sand and gravel during highway construction in the 1980s. On the other side, the set of ponds of the left side of the river (ponds 4, 5, 6) are natural and represent the remains of the former river channel. The bottoms of all three natural ponds are covered with submerged macrophytes, with significantly greater coverage in comparison to artificial ponds. In addition, littoral zone and shallower parts of the natural ponds are covered with emergent vegetation, which is, on the other hand, negligibly developed in the ponds created by gravel excavation. The sediment of natural ponds was dominated by a muddy substrate with organic material, while the substrate in the artificial ponds was mainly composed of gravel.

Sampling

Field work was performed during September 2016. Fish communities were surveyed using the EN 14011:2003 (EC, 2003) methodology. Fish were sampled from a boat on three transect per each pond, using a DC Aquatech IG 1300 electrofisher (2.6 kW, 80–470 V). The constant catch-per-unit-effort (CPUE) of time (10 min) was provided. The fish density is expressed as the number of individuals caught per 1 min. Each individual fish was identified to the species level according to its relevant morphological and anatomic features (Kottelat and Freyhof, 2007).

Water quality was assessed using the basic water quality parameters. Dissolved Oxygen Content (DO),

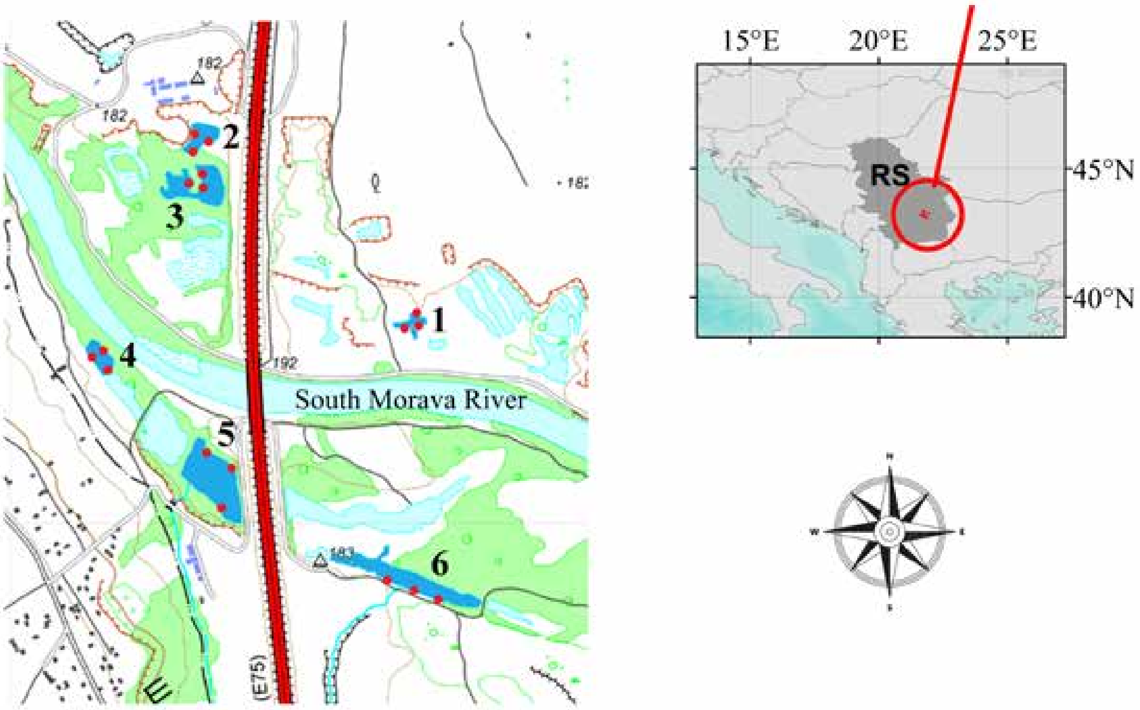


Fig. 1. Map of the study area with the position of the study sites. Arabic numbers indicate artificial (1-3) and natural ponds (4-6). RS stands for Republic of Serbia

Oxygen Saturation (DO%), Electroconductivity (EC), and Temperature (T) were measured by a WTW multi 340i probe. The concentrations of ammonia nitrogen, nitrate nitrogen and orthophosphates were estimated using the Spectrophotometer Shimatzu UV–Vis, while biological oxygen demand (BOD) was measured using standard methods (APHA, 1999). Finally, the percentage of the total organic matter in the sediment (C-TOT) was measured according to standard methodology given by Walkley and Black (1934).

Data analysis

To assess differences between artificial and natural ponds in terms of fish species and functional diversity, specific diversity metrics were established. First, each fish species found in the present study is categorized with regard to trophic and reproductive guilds. The assignment of fish species into ecological guilds was based on the data developed for the EFI (FAME Consortium, 2004), as well as our own observations (**Tab. 1**). The proportional abundance for each group of fish was calculated as the number of individuals within this group divided by the number of all individuals in the sample. We constructed a functional guild matrix assigning each taxon to their associated reproductive (lithophils, phytophils, phyto-lithophils, ostracophils) and trophic group (omnivores, insectivores, or carnivores). Based on the data regarding trophic and reproductive requrements, we assessed functional diversity (FD), functional evenness (Feve), and functional dispersion (Fdis) using the BAT package (Mammola and Cardoso, 2020). Following the methodology of Mammola and Cardoso (2020), we constructed a community functional hypervolume for each sample using the hypervolume package (Blonder et al., 2014). Alpha functional diversity was determined using the "kernel.alpha" function, which calculates the total volume of the functional hyperspace occupied by the species in the community (Mammola and Cardoso, 2020). Functional evenness was evaluated with the "kernel.evenness" function, which measures the regularity in the distribution of functional elements across the guild space (Mammola and Cardoso, 2020; Mason et al., 2005). We calculated functional dispersion using the "kernel.dispersion" function to determine the average distance between the guild space centroid and randomly chosen points within the hypervolume. Functional dispersion serves as a measure of functional divergence, indicating how species abundance is distributed in niche space, and reflects the degree of divergence in the community's functional guilds (Mason et al., 2005). Finally, six species richness/diversity measures were calculated to estimate differences between groups of ponds: total taxa richness, number of individuals, Margalef diversity index, Evenness, Shannon and Simpson index (Magurran, 2003).

As the normality assumption was not met for

Table 1. Fish species classification into ecological guilds according to their origin, trophic group and reproduction strategy

Family	Species	Origin	Trophic group	Reproduction strategy
Cyprinidae	*Alburnus alburnus* (Linnaeus, 1758)	Native	Omnivore	Phyto-lithophilic
	Carassius gibelio (Bloch, 1782)	Invasive	Omnivore	Phytophilic
	Chondrostoma nasus (Linnaeus, 1758)	Native		Lithophilic
	Cyprinus carpio Linnaeus, 1758	Native	Omnivore	Phytophilic
	Squalius cephalus (Linnaeus, 1758)	Native	Omnivore	Lithophilic
	Pseudorasbora parva (Temminck & Schlegel, 1846)	Invasive	Omnivore	Phytophilic
	Rhodeus amarus (Bloch, 1782)	Native	Omnivore	Ostacophilic
	Rutilus rutilus (Linnaeus, 1758)	Native	Omnivore	Phyto-lithophilic
Cobitidae	*Cobitis taenia* Linnaeus, 1758	Native		Phytophilic
Centrarchidae	*Lepomis gibbosus* (Linnaeus, 1758)	Invasive	Insectivore	Phyto-lithophilic
Esocidae	*Esox lucius* Linnaeus, 1758	Native	Carnivore	Phytophilic
Percidae	*Perca fluviatilis* Linnaeus, 1758	Native	Omnivore	Phyto-lithophilic
Siluridae	*Silurus glanis* Linnaeus, 1758	Native	Carnivore	Phytophilic
Ictaluridae	*Ameiurus nebulosus* (Lesueur, 1819)	Invasive	Omnivore	Lithophilic

tested parameters, we applied the Mann-Whitney post hoc test to compare whether the parameters differed across the pre-defined groups of ponds.

A distance-based redundancy analysis (dbRDA; Anderson et al., 2008) was conducted to examine the relationships between the fish community, represented by 1) species diversity and 2) functional diversity, and relevant environmental variables at the investigated groups of ponds. Before performing the dbRDA, Bray-Curtis similarity matrices were generated for both the species and functional diversity datasets. Environmental variables were tested for normality and log-transformed when necessary to meet normality assumptions.

Functional diversity and related parameters were calculated using R version 4.1.1 (R Core Team, 2016). Univariate tests were conducted using the software SPSS version 19.0, while multivariate analyses (dbRDA) ware carried out with PRIMER version 6 and the PERMANOVA+ for PRIMER package (Anderson et al., 2008).

Results

During the sampling campaign, a total of 372 individuals were collected from 6 surveyed ponds, represented by 7 families, 14 genera, and 14 species (**Tab. 1**). The highest diversity was recorded within the family Cyprinidae (8 species), while only one species was recorded within the other families. Out of total number of species, four invasive fish species were detected.

A total of 10 species and functional diversity measures were tested (**Fig. 2**). Mann–Whitney tests confirmed that the medians of all tested parameters, except for the number of individuals, differed significantly between the previously defined pond groups **(Tab. 2, Fig. 2).** Specifically, both functional and species diversity measures were significantly higher in natural ponds compared to artificial ones. In contrast, the only measure found to be higher in artificial ponds than in natural ones was the number of invasive species.

The dbRDA ordination plots clearly demonstrated that the separation of groups based on the functional diversity of the fish community was considerably more pronounced than that based on species diversity. Specifically, the dbRDA analysis of species diversity explained 73.5% of the variation in the fitted model and 57.4% of the total variation. In contrast, the dbRDA analysis of functional diversity explained 91.1% of the variation in the fitted model and 70.6% of the total variation (**Fig. 3a**, **Fig. 3b**).

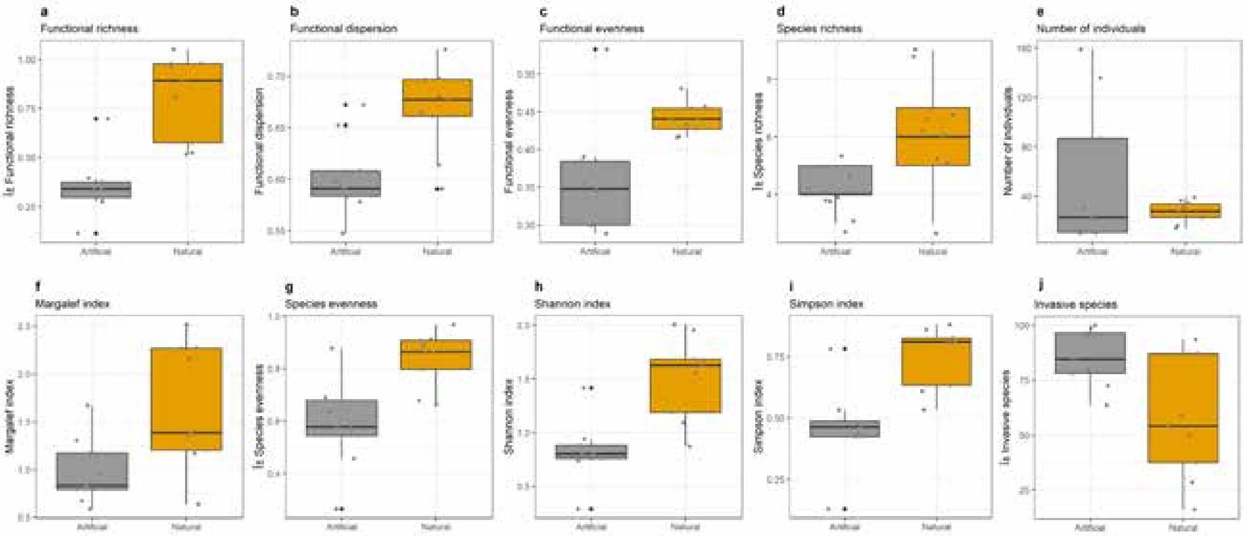


Fig. 2. Box plots of species and functional diversity parameters. The middle solid lines in boxes are medians, box ends are first and third quartiles, whiskers represent maximum and minimum values

Table 2. Medians (ranges) of selected species and functional diversity measures. Asterisks in the column "U test" indicate significant result of Mann-Whitney U test for comparison of variables (*$p<0.05$, **$p<0.01$, ***$p<0.001$, ns=non-significant difference)

Measured parameter	Artifical ponds	Natural ponds	U test
Functional richness	0.340 (0.1121-0.6975)	0.892 (0.5160-1.0525)	***
Functional dispersion	0.590 (0.5473-0.6721)	0.677 (0.5905-0.7262)	**
Functional evenness	0.347 (0.2886-0.5328)	0.440 (0.4160-0.4808)	**
Species richness	4 (3-5)	6 (3-9)	**
Number of individuals	23 (10-159)	28 (14-39)	ns
Margalef index	0.834 (0.5880-1.6681)	1.384 (0.6379-2.5173)	*
Species eveness	0.577 (0.2650-0.8787)	0.863 (0.6629-0.9687)	**
Shannon diversity	0.800 (0.2911-1.4143)	1.624 (0.8762-2.0046)	***
Simpson diversity	0.462 (0.1310-0.7818)	0.809 (0.5336-0.8804)	***
% of invasive species	84.61 (63.6364-100)	54.16 (16.2162-93.5484)	*

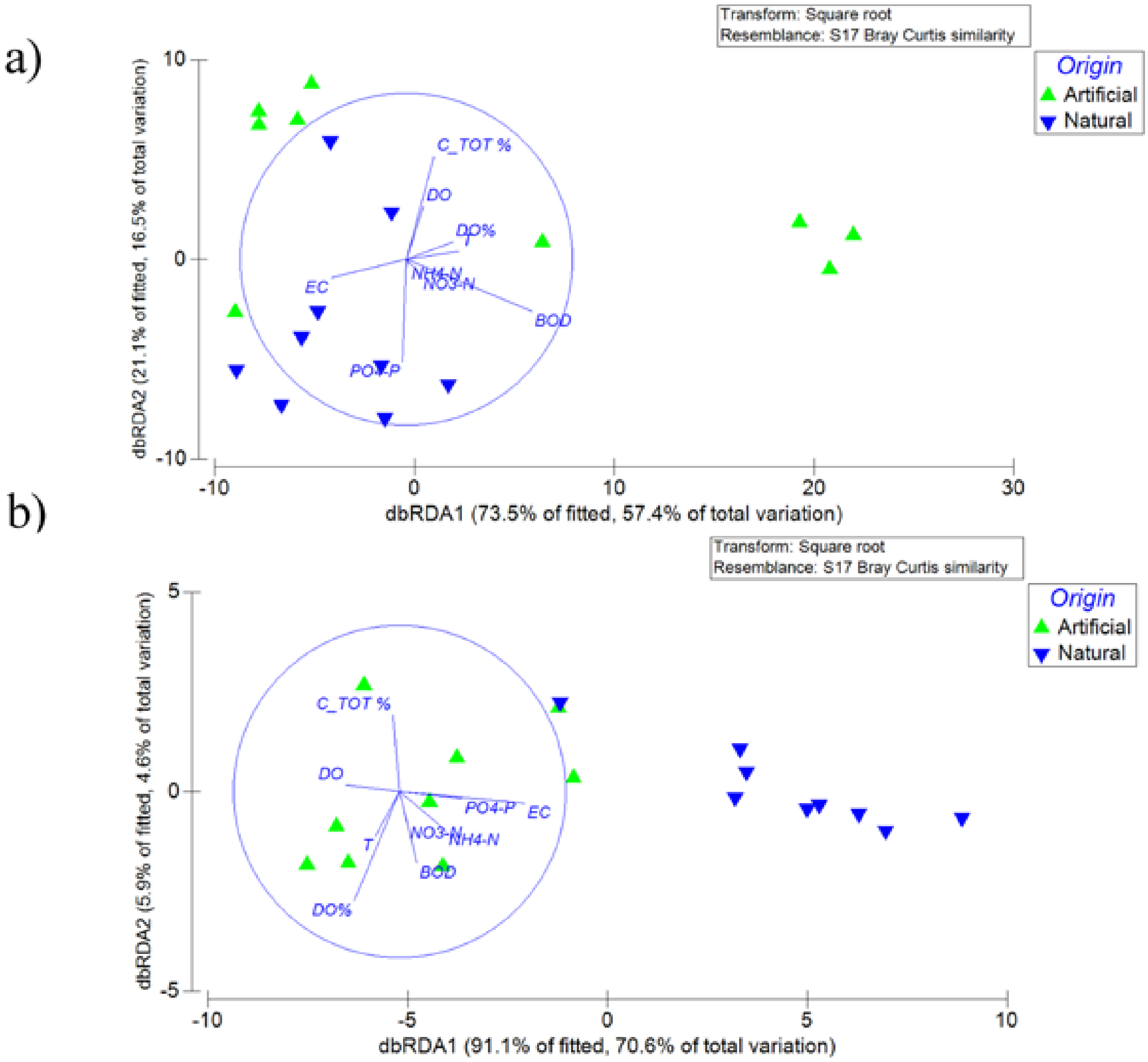
Discussion

Our findings indicate clear difference in species and functional diversity of fish assemblages in two groups of ponds differing in origin (natural and artificial) (**Tab. 2, Fig. 2**). Indeed, artificial ponds, that appears after excavating gravel or other materials are usually colonized by fish species with opportunistic strategies (Maday et al., 2023). Early colonizers tend to be species that are highly adaptable to changing environmental conditions and capable of exploiting the newly available resources. These species are often r-strategists, characterized by high reproductive rates, short life spans, and a capacity to rapidly populate available habitats. They thrive in disturbed or unstable environments, where the competition is low, and conditions are unpredictable (Begon et al., 2006).

Among the first to colonize are typically generalist species that can survive a range of conditions, including variable oxygen levels, temperature fluctuations, and the presence of few other competitors. Opportunistic species, such as small cyprinids or livebearers, can quickly establish themselves due to their high reproductive output and ability to tolerate environmental variability (Ricklefs & Schluter, 1993).

Ultimately, the diversity of fish in newly excavated ponds is shaped by a combination of colonization events, environmental conditions, and species' life history traits, with opportunistic species playing a crucial role in the early stages of ecological succession (Connell & Slatyer, 1977). For instance, the Prussian carp is an opportunistic species known

Fig. 3. Ordination plots of distance-based redundancy analysis (dbRDA) of **A**) species and **B**) functional diversity parameters of fish community



for its rapid reproduction and ability to expand into available niches. Its gynogenetic reproduction allows it to thrive in environments with low genetic diversity, and it can adapt to conditions like low oxygen, high pollution, and fluctuating temperatures (Tomljanović et al., 2012). This adaptability, combined with its high reproductive rate, enables the Prussian carp to quickly colonize new habitats, often outcompeting native species and causing ecological damage (Tomljanović et al., 2012). Thus, the absolute constancy and high abundance of this species at all sites withing group of artificail ponds, contributed to the significantly higher abundance of invasive species as well as total number of individuals in comparison to natural ponds **(Fig. 2)**.

The diversity of ponds that have formed as remaining of old river channels is often characterized by fish community structure shaped by the historical connection to the river system. These ponds are usually dynamic environments with a variety of fish species due to their physical and hydrological connection to the main river. Over time, these habitats develop their own ecological characteristics, often containing a suit of species that are adapted to both the slow-moving waters of the pond and the more turbulent conditions of the river that once fed them (Junk et al., 1989). Those communities often include both riverine species that are capable of adapting to lentic ecosystems, as well as species that are typically found in standing waters. Our results are consistent with this, since significantly higher species and functional richness were observed on sited from the natural ponds (**Tab. 2, Fig. 2**). Common fish found in these habitats may include species such as cyprinids, perch, and catfish, which are well-adapted to both slow-flowing and still waters. These species are often more tolerant of changes in water quality, temperature fluctuations, and lower oxygen levels compared to those in more stable riverine habitats (Junk et al., 1989; Penczak et al., 2000).

From a functional perspective, the fish community in natural ponds typically includes a combination of opportunistic species and specialist species. Opportunistic species - such as small cyprinids and livebearers - tend to dominate during the early stages of succession, rapidly exploiting the available resources and reproducing in abundance. Over time, however, the pond may support a more diverse functional community, including predators (e.g., larger piscivorous fish) and detritivores (e.g., bottom-feeding species), which contribute to the cycling of nutrients and the overall health of the ecosystem (Penczak et al., 2000).

Species diversity indices describe the structure of an assemblage, but their connection to ecological functions, such as productivity or stability, are still not well understood (Kwak & Peterson, 2007). Species diversity indices have been criticized for their limited biological relevance and should be seen as just one of many tools for describing assemblage structure - they are not a replacement for thorough analysis. Nevertheless, Cardinale et al. (2012) emphasized that increased species diversity in freshwater ecosystems may lead to the enhanced ecosystem stability. Despite the fact that some authors encourage the utility of species diversity indices, functional diversity has been considered to be the most effective measure of diversity for detecting the positive impact of biodiversity on ecosystem functioning and services (Balvanera et al., 2006; Díaz et al., 2006). Indeed, the results of this study shows that functional structure of fish community appears to be more sensitive and robust in discriminating origin-divided pond groups, in comparison to species diversity measures (**Fig. 3a, b**).

Conclusion

In conclusion, functional diversity is critically important for maintaining ecosystem functioning and services. The complex relationship between species traits and ecosystem services demonstrates that the loss of species with specific functional traits can lead to biased impacts on ecosystem processes. Given that species with certain traits are more vulnerable to biodiversity loss, conserving functional diversity is essential to preserving the integrity and resilience of ecosystems.

The origin of a pond profoundly shapes the biological communities within it. Natural ponds tend to support diverse, often specialized species that have adapted to the particular conditions of the pond, such as floodplain ponds that support species adapted to fluctuating water levels. Artificial ponds, on the other hand, tend to have a more controlled ecosystem, which can limit biodiversity but allows for human intervention in managing species and water quality. Understanding the origin of a pond is crucial for understanding its ecological function, biodiversity, and the challenges it faces in a changing environment.

Acknowledgements. This research was supported by the Ministry of Science, Technological Development and Innovations of the Republic of Serbia [Grant No.: 451-03-137/2025-03/200124].

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