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Artificial drainage canals promote habitat-specific dominance of the invasive mussel Sinanodonta woodiana Lea, 1834 in the Tisza River basin (Slovakia)

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Abstract

Artificial waterways are increasingly recognised as facilitators of freshwater biological invasions, yet their role as habitats promoting invasive dominance remains insufficiently quantified. We investigated the occurrence, density, and shell length structure of the Chinese pond mussel (*Sinanodonta woodiana*) within artificial drainage canals, natural river sections, and reservoir habitats in the Slovak section of the Tisza River basin. For contextual comparison, we additionally documented the occurrence of Asian freshwater clam (*Corbicula fluminea*), representing the first recorded occurrence within the Tisa River basin in Slovakia, and Zebra mussel (*Dreissena polymorpha*). *S. woodiana* was recorded at more than 58% sites and occurred across all habitat types. However, pronounced habitat-related differences were observed. Artificial drainage canals supported densities reaching 43.8 individuals per m², whereas densities in river and reservoir habitats were markedly lower. The most abundant canal populations also exhibited larger median shell length, with the largest recorded individual reaching 229 mm. In contrast, *C. fluminea* and *D. polymorpha* were primarily associated with riverine and reservoir habitats and did not reach comparable densities in canal systems. These findings suggest habitat-specific concentration of *S. woodiana* within artificial drainage networks. Our results indicate that artificial canal systems may function not only as dispersal corridors but also as habitats capable of sustaining dense and demographically structured populations of invasive unionids. Such systems may therefore represent overlooked invasion hotspots in artificial habitat of Tisza river basins.

Introduction

Invasive species are among the most serious ecological threats to freshwater ecosystems. Their spread accelerated in Europe during the late nineteenth century with the construction of canals connecting major lowland rivers. In the second half of the twentieth century, the expansion of aquaculture and increasing trade with East Asia further contributed to the introduction of non-native aquatic organisms. Aquatic ecosystems are particularly vulnerable to biological invasions and have historically been colonised by numerous non-native species (Cohen & Carlton 1998; Kolar & Lodge 2002; Strayer 2010). Hydrological alteration, artificial connectivity among river basins, and aquaculture-mediated translocations have substantially increased propagule pressure and facilitated the secondary spread of aquatic invaders across Europe (Bij de Vaate et al. 2002; Hulme 2009; Lockwood et al. 2005). Artificial waterways may therefore act not only as dispersal corridors but also as habitats that favour the establishment and growth of non-native species.

Non-native freshwater bivalves represent a particularly successful group of aquatic invaders. They can colonise a wide range of habitats and can significantly influence hydrological processes, nutrient cycling, and biotic interactions (Sousa et al. 2014). Many invasive bivalves function as ecosystem engineers. By filtering large volumes of water and modifying sediment structure, they can alter benthic communities and affect competitive relationships within native assemblages (Karatayev et al. 2007; Sousa et al. 2014).

Chinese pond mussel (*S. woodiana*) is currently the largest freshwater bivalve species in continental Europe. Its average shell length ranges from 150 to 170 mm, although individuals exceeding 200 mm have been recorded (Tej et al. 2024). The species is native to Southeast Asia and the Amur Basin but has been unintentionally introduced to many parts of Europe (Watters 1997; Graf 2007; Benkő-Kiss 2013). It was most likely introduced through fish stocking and aquaculture activities (Watters 1997). In Slovakia, *S. woodiana* was first recorded in 1995 (Košel 1995; Šteffek et al. 2005), and in eastern Slovakia in 2004 (Nagel & Šteffek 2005; Šteffek et al. 2006, 2008; Čejka & Černecký 2021). Unlike dreissenids, which disperse via planktonic larvae, *S. woodiana* has parasitic glochidia that attach to fish hosts. This life-history strategy links its dispersal directly to fish movements and aquaculture practices (Konečný et al.

2018). It may therefore enhance long-distance spread and increase propagule pressure in hydrologically modified landscapes (Lockwood et al. 2005; Simberloff 2009).

In several European regions, *S. woodiana* has established dense populations and often exceeds native unionids in both size and biomass (Benkő-Kiss 2013; Tej et al. 2024). As a large benthic species, it may compete for space and resources and modify sediment characteristics. However, despite its expanding distribution in Central Europe, habitat-specific patterns of its dominance remain insufficiently quantified.

The Tisza River basin in the Eastern Slovak Lowland represents a hydrologically modified landscape characterised by an extensive network of artificial drainage canals constructed during large-scale wetland transformation in the twentieth century. These canals are interconnected with natural rivers, a reservoir, and aquaculture facilities. Artificial drainage systems often differ from natural aquatic habitats, especially in sediment composition and flow regime. Such modified habitats may reduce native species richness and weaken biotic resistance against invasive taxa (Mack et al. 2000; Didham et al. 2007). The unoccupied spatial niche and nutrient availability in modified habitats may provide favourable conditions for invasive unionids to attain high densities and substantial body size.

In addition, we recorded two other non-native bivalves occur within the sampling localities: *C. fluminea* and *D. polymorpha*. Both species are well established in Europe and are strongly associated with artificial waterways and major invasion corridors (Bij de Vaate et al. 2002; Karatayev et al. 2007; Sousa et al. 2008). *D. polymorpha* is an epibenthic species that attaches to hard substrates and disperses through planktonic larvae, whereas *C. fluminea* is a smaller infaunal species capable of rapid reproduction. In comparison, *S. woodiana* represents a large-bodied sediment-dwelling unionid. These functional differences suggest that artificial canal systems may selectively favour invasive strategies.

The aim of this study was to: i) evaluate the occurrence, abundance, and length structure of *S. woodiana* across artificial canals, natural rivers, and reservoir habitats within the Slovak section of the Tisza River basin. For contextual comparison, we also documented the distribution of other two species (*C. fluminea* and *D. polymorpha*) in relationship with habitat type and number of native molluscs.

We tested the hypotheses that (i) artificial drainage canals host higher densities of *S. woodiana* than natural river and reservoir habitats, and (ii) individuals inhabiting canals attain larger shell sizes, indicating habitat-specific dominance potentially facilitated by favourable sediment conditions or reduced interspecific competition.

Material and Methods

Study area

The study area consists mainly of the Eastern Slovak Plain (Tisza River basin), which forms part of the Alpine–Himalayan system, the Pannonian Basin subsystem, and the East Pannonian Basin province. Overall, it belongs to the Greater Danube Basin (Kočický & Ivanič 2011). The region consists of a dense mosaic of agricultural fields, remnant wetlands, and xerothermic meadows. In recent decades, it has undergone extensive drainage, resulting in a dense network of artificial channels flowing into major lowland rivers. Among large water bodies, the area includes the Zemplínska šírava reservoir and the Senné system of aquaculture ponds.

Malacological surveys were conducted in 2024 and 2025 at multiple sites within the study area. All sampling sites were in Slovakia, except for one site situated in the Hungarian border area for comparison of the opposite banks of the Tisza River.

Seventeen sites (Fig. 1) were selected to represent three main habitat categories: (i) artificial drainage canals, (ii) natural river sections, and (iii) reservoir shoreline habitats. Site selection aimed to ensure representation of the dominant hydromorphological conditions within the basin.

Field sampling and identification

Sampling followed standard malacological methods for aquatic mollusc collection as described by Ložek (1956) and Horsák et al. (2013). At each site, a total area of 30 m² was surveyed by random sampling of different microhabitats within the watercourse. Specimens were collected by hand-picking and by sieving bottom substrates using a D-shaped benthic net.

In two drainage channels (Iňačovce and Stretávka), sampling was conducted over a reduced area of 6 m² due to site-specific constraints. At these sites, exceptionally high densities of *S. woodiana* required reduction of the effective sampling area to ensure accurate counting and measurement of individuals. Population density was subsequently standardised to individuals per m².

The specimens were identified in the field, as no other morphologically similar species occur in the study area. For *D. polymorpha*, we used the diagnostic features described by Horsák et al. (2013) to distinguish it from *D. rostriformis*. All live individuals of *S. woodiana* were counted. Empty shells were recorded separately but excluded from statistical analyses. Shell length (maximum anterior–posterior dimension) was measured to the nearest millimetre using digital callipers.

For contextual comparison of abundance and habitat preferences, the presence and abundance of *C. fluminea* and *D. polymorpha* were recorded at each site.

Data analysis

Analyses focused primarily on *S. woodiana*. Population density (individuals per m²) was calculated for each site by standardising counts to the surveyed area (Table 1).

Differences in density among habitat categories were evaluated using non-parametric methods, due to the small number of sites (n = 10) and the non-normal distribution of density (occurrence of zero values and extreme values) the non-parametric statistical methods were used. Differences in the density of the *S. woodiana* species between habitat types (reservoir, river, channel) were visually assessed using boxplots supplemented with individual values (jitter). For better visualization of variability and reduction of the influence of extreme values, the density was transformed using logarithmic transformation (log + 1). Statistical significance of differences in abundances between habitats was tested using the Kruskal-Wallis test. In case of demonstrating a significant difference, pairwise comparisons were performed using Dunn's post-hoc test with BH correction for multiple comparisons.

The relationship between the presence of *S. woodiana* and the number of native species was analyzed using the Mann–Whitney U test. As the data did not meet the assumption of normal distribution, differences in shell length of *S. woodiana* among the ten habitats were evaluated using the non-parametric Kruskal–Wallis test. Subsequent pairwise comparisons were performed using Dunn’s test with Benjamini–Hochberg (BH) correction for multiple comparisons.

All statistical analyses were performed using R Statistical Software (v 4.5.2; R Core Team, 2025). The statistical significance level was set at $\alpha = 0.05$. Graphical outputs were created with the using of ggplot2 (Wickham 2016)

Table 1
List of sampled sites indicating the sites where we considered the density and length structure of Chinese pond mussel (*S. woodiana*)

Locality		GPS	Type of habitat	*S. woodiana*	*C. fluminea*	*D. polymorpha*	Density	*Length structure*
1	Zemplínska šírava (Vinné)	48.779492, 21.952504	reservoir	3	65	x	x	x
2	Zemplínska šírava (Paľkov)	48.808998, 22.040962	reservoir	7	70	X	x	x
3	Zemplínska šírava (Jovsa)	48.814855, 22.073439	reservoir	4	29	2	x	x
4	Zemplínska šírava (Lúčky)	48.777231, 22.040531	reservoir	0	84	50	-	-
5	Zemplínska šírava (Zalužice)	48.763884, 21.975110	reservoir	0	1	7	-	-
6	Iňačovce	48.683112, 22.062017	channel	33	0	0	x	x
7	Pavlovce nad Uhom (Čierna voda)	48.645054, 22.010906	channel	4	0	0	x	x
8	Stretávka (Čierna voda)	48.607463, 21.994325	channel	263	0	0	x	x
9	Čičarovce (Udoč)	48.539456, 22.038457	channel	0	0	0	-	-
10	Latorica (Leles)	48.500113, 22.051899	river	0	0	0	-	-
11	Hraň (Trnávka)	48.539409, 21.803304	channel	9	0	0	x	x
12	Hraň (Ondava)	48.535685, 21.805877	river	5	16	0	x	x
13	Streda nad Bodrogom (Somotorský kanál)	48.396200, 21.765962	channel	23	0	0	x	x
14	Streda nad Bodrogom (Veľká Krčava)	48.348624, 21.740569	channel	0	0	0	-	-
15	Svätá Mária	48.433415, 21.853690	channel	0	0	0	-	-
16	Malé Trakany	48.394141, 22.143032	river	0	11	0	-	-

Locality		GPS	Type of habitat	*S. woodiana*	*C. fluminea*	*D. polymorpha*	Density	*Length structure*
	(Tisza)							
17	Győröcske (Tisza)	48.392891, 22.144020	river	18	175	0	x	x

Results

Occurrence of non-native bivalves

The investigated sites represented a mosaic of artificial and natural aquatic habitats within the Eastern Slovak Lowland. Artificial drainage canals constituted the most frequent habitat type and were typically characterised by slow flow, fine sediments, and simplified channel morphology. Natural river sites were represented by sections of the Tisza, Ondava, and Latorica rivers, while reservoir habitats were located along the shoreline of Zemplínska šírava.

Non-native bivalves were recorded at 13 from 17 investigated sites within the study area. *S. woodiana* was present at ten sites, including artificial channels, rivers, and reservoir habitats. *C. fluminea* was recorded at six sites, while *D. polymorpha* occurred at four sites. All three species co-occurred at three localities situated in reservoir and major river sections. In contrast, artificial drainage canals were predominantly occupied by *S. woodiana*, with only sporadic or no records of the other two invasive species.

The number of native species did not differ statistically significantly between sites with and without the presence of *S. woodiana* (Mann–Whitney U test, W = 17.5, p = 0.774). The lack of statistical significance may also be related to the low number of sites monitored (17) and the high variability of the data.

Habitat-specific abundance of S. woodiana

S. woodiana density differed significantly among habitats (Kruskal–Wallis rank sum test: $\chi^2(2) = 6.58$, p = 0.037) (Fig. 2).

Post-hoc Dunn´s test with BH correction showed significantly higher density in channel habitats compared to river habitats (p = 0.044). The difference between channel and reservoir was at the marginal significance (p = 0.079), while no significant difference was found between reservoir and river (p = 0.928) (Table 2).

Table 2
Post-hoc Dunn´s test with Benjamini-Hochberg (B-H) correction showed pairwise comparison of abundances between habitat types

Comparison	Z	P (unadj.)	P (adj.)
channel – reservoir	2.219	0.026	0.079
channel – river	2.182	0.029	0.044
reservoir – river	0.090	0.928	0.928

The highest abundances of *S. woodiana* were recorded in drainage channels. At the Stretávka site (Čierna Voda channel), 263 live individuals were recorded within a 6 m² sampling area. At Iňačovce, 33 individuals were recorded within 6 m².

After standardisation to individuals per m², these values correspond to densities of 43.8 individuals per m² at Stretávka and 5.5 individuals per m² at Iňačovce. This density was more than forty times higher than the highest densities recorded in river habitats.

In natural river sections, abundances were lower. At the Hungarian section of the Tisza River (Győröcske), 18 individuals were recorded within 30 m². At other river sites, only isolated individuals were found.

In reservoir habitats, the abundance of *S. woodiana* ranged from 0 to 7 individuals per 30 m². Overall, artificial habitats like channels exhibited markedly higher densities of *S. woodiana* compared to natural river and reservoir habitats.

Shell length variation among habitat types

Shell length differed significantly among habitats (Kruskal–Wallis H test, χ^2 (9) = 83.34, $p < 0.001$; (Fig. 3).

Post hoc pairwise comparisons using Dunn's test with BH correction identified several significant differences among habitats. The highest median shell length was recorded in channel_8 (180 mm, IQR 151–198), followed by channel_6 (170 mm, IQR 160–183). The lowest median values were observed in reservoir_1 (96 mm, IQR 92.5–97) and river_17 (104 mm, IQR 90.8–114) (note: Values are presented as median (Q1–Q3). Overall, the strongest differences were observed between channel habitats (particularly channel_6 and channel_8) and river_17, as well as reservoir_2 (Table 3).

Table 3
Chinese pond mussel (*S. woodiana*) shell length (mm) across habitats with significant pairwise differences. Significant pairwise differences were identified using Dunn's test with BH correction.

Habitat	n	Median (Q1–Q3)	Significant differences (BH-adjusted p </> 0.05)
channel_8	50	180 (151–198)	> channel_11, channel_13, reservoir_1, reservoir_2, reservoir_3, river_17
channel_6	33	170 (160–183)	> channel_11, channel_13, reservoir_1, reservoir_2, reservoir_3, river_17
channel_13	22	148 (138–154)	> reservoir_2, river_17
channel_7	4	129 (104–157)	–
channel_3	4	118 (110–124)	< channel_6, channel_8
channel_11	9	117 (112–126)	< channel_6, channel_8
river_12	2	114 (110–119)	–
reservoir_2	7	108 (94.5–110)	< channel_6, channel_8, channel_13
river_17	18	104 (90.8–114)	< channel_6, channel_8, channel_13
reservoir_2	3	96 (92.5–97)	< channel_6, channel_8

Median shell length was highest in artificial canals, followed by river habitats, and lowest in reservoir sites.

Pairwise comparisons using Dunn's post hoc test revealed a significant difference between canal and river habitats (adjusted p = 0.044), whereas differences between river and reservoir habitats were not statistically significant (adjusted p = 0.928).

Occurrence of other non-native bivalves

Asian freshwater clam (*C. fluminea*) was recorded primarily in natural river sections and reservoir habitats. The highest abundance was observed at Győröcske, where 175 individuals were recorded within 30 m².

Zebra mussel (*D. polymorpha*) was recorded exclusively in reservoir habitats. At certain reservoir sites, densities were high and difficult to quantify due to clustering.

Neither *C. fluminea* nor *D. polymorpha* reached comparable densities to *S. woodiana* in artificial canal habitats.

Discussion

Our results confirm the established presence of *S. woodiana* within the Slovak section of the Tisza River basin. The species was recorded across artificial canals, natural river sections, and reservoir habitats, demonstrating broad ecological tolerance and continued expansion in the region.

However, the magnitude of habitat-related differences observed in this study is particularly notable. Artificial drainage canals supported densities reaching 43.8 individuals per m², whereas densities in river and reservoir habitats rarely exceeded 1 individual per m². This represents a marked contrast between artificial and natural systems and indicates that canals may promote local concentration rather than merely supporting incidental presence.

High-density populations of invasive bivalves can substantially modify benthic structure and ecosystem processes, including sediment stability, nutrient cycling, and competitive interactions (Karatayev et al. 2007; Sousa et al. 2014). Where densities exceed 40 individuals per m², *S. woodiana* may represent a dominant component of benthic biomass, potentially influencing native unionids and associated invertebrate communities.

Although *S. woodiana* has been reported from a wide range of European habitats, published population densities vary considerably depending on environmental conditions and habitat type (Andrzejewski et al. 2013). The density recorded in the Stretávka canal represents a pronounced local aggregation within an artificial drainage system. Rather than simply confirming occurrence, this finding suggests strong establishment and habitat-specific concentration.

Shell length analyses revealed that individuals from canal habitats reached the largest sizes observed in this study, including a maximum of 229 mm. Median shell length was also higher in canal populations compared to river and reservoir sites. Reported maximum shell lengths for *S. woodiana* in European populations generally range up to approximately 200–250 mm (Protasov et al. 1993). The maximum size recorded in the present study therefore falls within the upper range of documented values.

Body size in unionids is influenced by multiple factors, including sediment stability, hydrological disturbance, temperature, and resource availability. Habitat-specific differences in size structure may therefore reflect environmental conditions rather than intrinsic species traits alone. Larger median size in canal populations may indicate favourable growth conditions, reduced disturbance, or prolonged survival (Negishi et al. 2008a,b; Nakano et al. 2017).

The coexistence of high density and large body size in canal habitats suggests a well-established and demographically structured population. Such a pattern is consistent with later stages of invasion, in which initial colonisation is followed by population expansion and stabilisation (Berryman 1999, Arim et al. 2006). However, long-term demographic monitoring would be necessary to confirm persistence and growth dynamics.

Although *S. woodiana* is frequently described as a thermophilic species preferring lentic or slow-flowing environments (Kraszewski 2006), our results demonstrate that artificial drainage canals may provide functionally comparable

conditions. Drainage canals in lowland agricultural landscapes often accumulate fine sediments and experience reduced flow variability. These characteristics may create stable depositional environments that favour large sediment-dwelling unionids (Nakano et al. 2015). Habitat simplification associated with anthropogenic modification has been linked to enhanced invasion success in other systems (Mack et al. 2000; Didham et al. 2007).

The contrasting distribution patterns of *C. fluminea* and *D. polymorpha* provide additional ecological context. *C. fluminea* was primarily associated with riverine and reservoir habitats, while *D. polymorpha* occurred exclusively in reservoir environments. Neither species achieved comparable densities within canal habitats. This pattern suggests functional segregation among invasive bivalves and indicates that artificial canal systems may act as habitat filters favouring large sediment-dwelling unionids over epibenthic or rapidly reproducing taxa (Nakano & Morii 2019).

Artificial waterways are increasingly recognised not only as invasion corridors but also as novel ecosystems shaped by anthropogenic modification (Hulme 2009). Our findings support the hypothesis that such systems may create environmental conditions that enhance establishment success and promote habitat-specific dominance. In this context, drainage canals should not be regarded solely as passive conduits of spread, but as potential invasion hotspots capable of sustaining dense and demographically robust populations.

From a broader invasion ecology perspective, the observed pattern aligns with theoretical frameworks linking propagule pressure, habitat disturbance, and establishment success (Lockwood et al. 2005; Simberloff 2009). The hydrological modification of the Eastern Slovak Lowland, combined with aquaculture activities and fish-mediated dispersal, likely increases propagule supply to canal systems. Once established, reduced interspecific competition and favourable sediment conditions may enable rapid population growth and long-term persistence.

Although this study was conducted at a regional scale, the implications may extend to other lowland basins characterised by extensive drainage infrastructure. If similar habitat-mediated dominance occurs elsewhere, artificial canal networks may represent underappreciated drivers of unionid invasions at the landscape scale.

Future research should focus on long-term demographic monitoring, growth rates, and potential competitive interactions with native unionids to assess displacement risk and ecosystem consequences.

Conclusion

This study demonstrates that *S. woodiana* is well established within the Tisza River basin and exhibits pronounced habitat-specific differences in density and size structure. Artificial drainage canals supported substantially higher densities and larger individuals compared to natural river and reservoir habitats.

These findings suggest that artificial canal systems may provide favourable environmental conditions for the establishment and local dominance of invasive unionids. Rather than functioning solely as dispersal corridors, such systems may represent habitats that actively promote population expansion.

Although the present study was conducted at a regional scale, the observed pattern highlights the need to consider artificial drainage infrastructure in invasion risk assessments. Further research integrating long-term demographic data and interactions with native unionids will be necessary to evaluate potential ecosystem consequences.

Declarations

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Author Contribution

B.T. wrote the main manuscript text, prepared tables and map of research sitesA.C. edited the manuscript's style and checked the grammarJ.F. performed data analyses and prepared graph figuresJ.K. edited the content page with a grammar check

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Figures

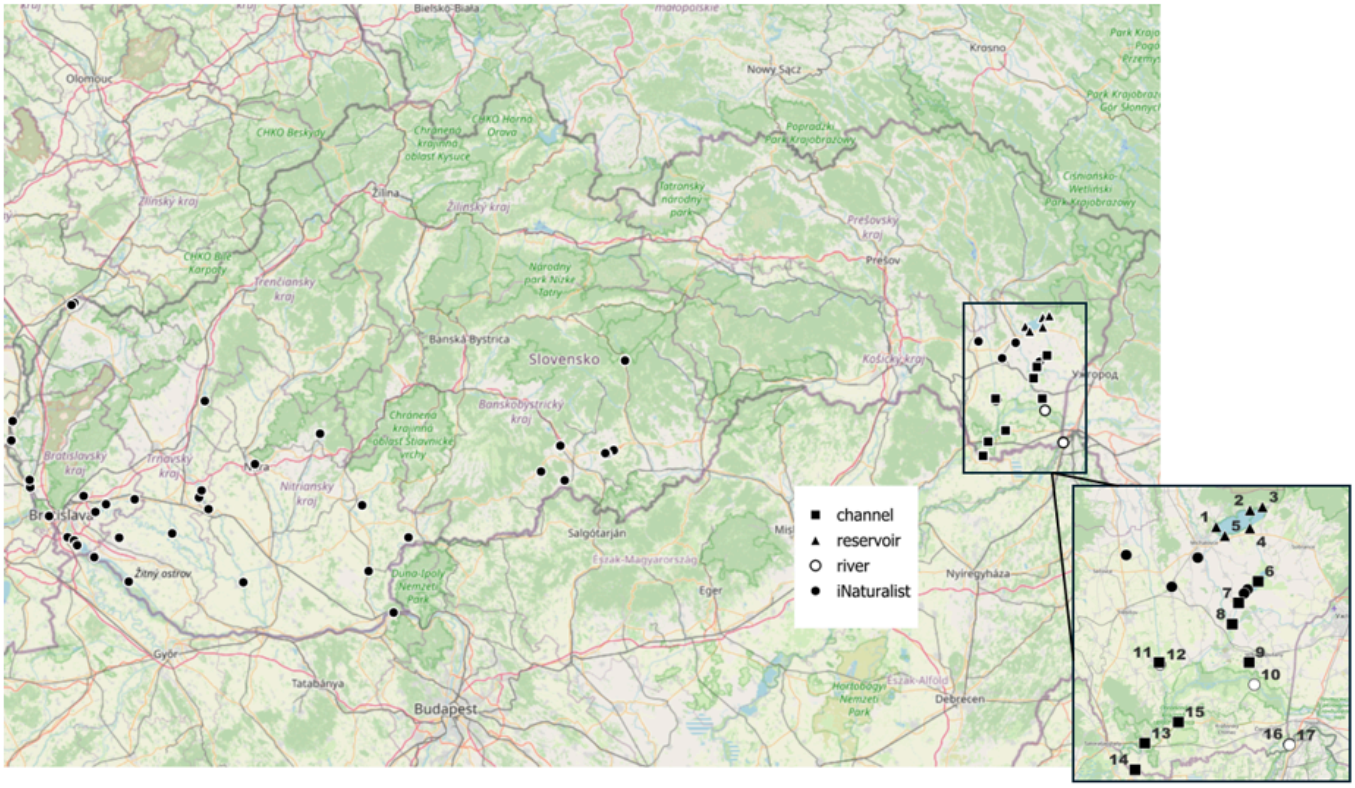


Figure 1

Map of research sites (channel, reservoir, river) with added records of known localities of the Chinese pond mussel (*S. woodiana*) in Slovakia, based on data from the publicly available iNaturalist database.

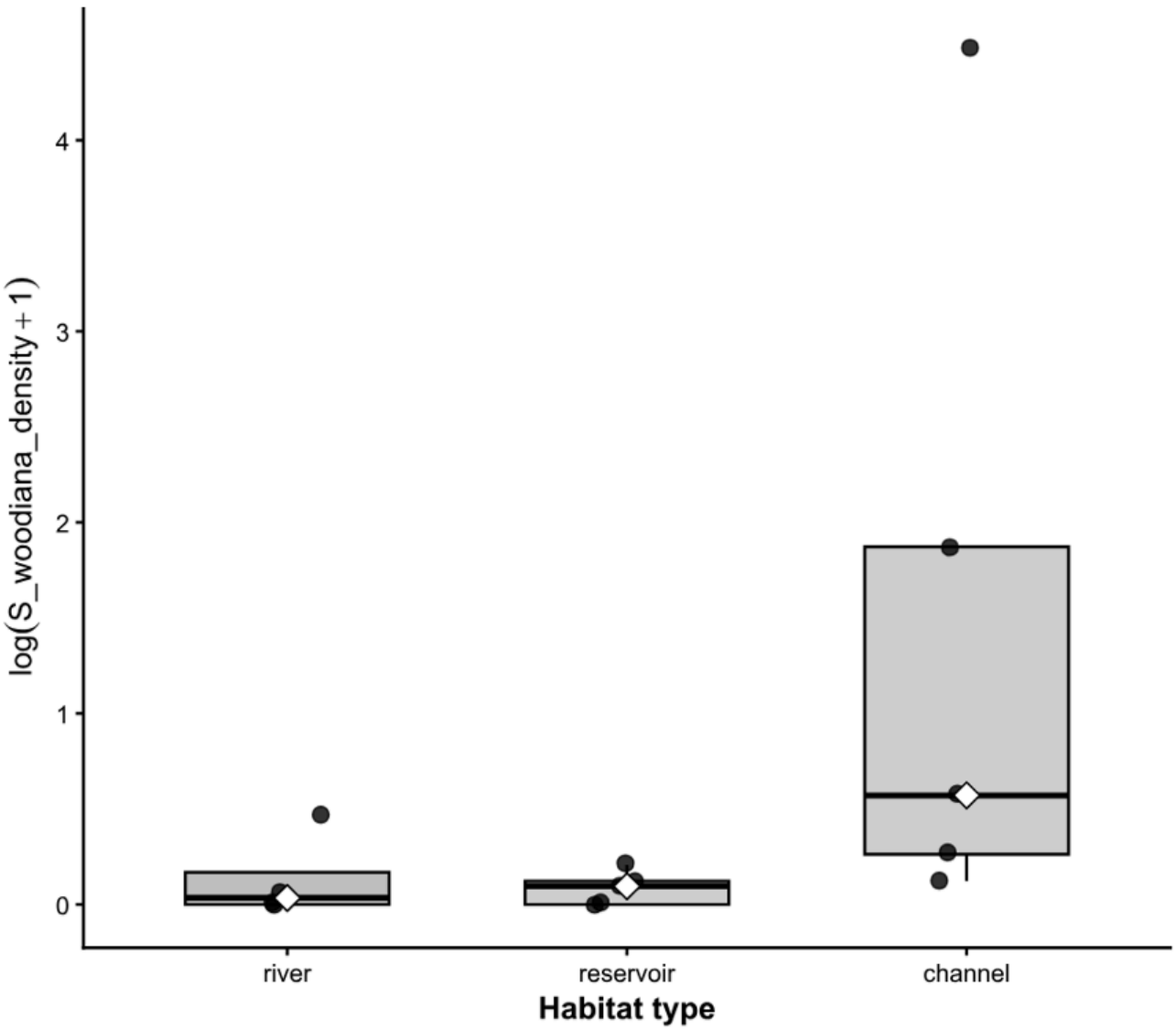


Figure 2

Plot of log transformed densities of Chinese pond mussel (*S. woodiana*) according to different type of habitat

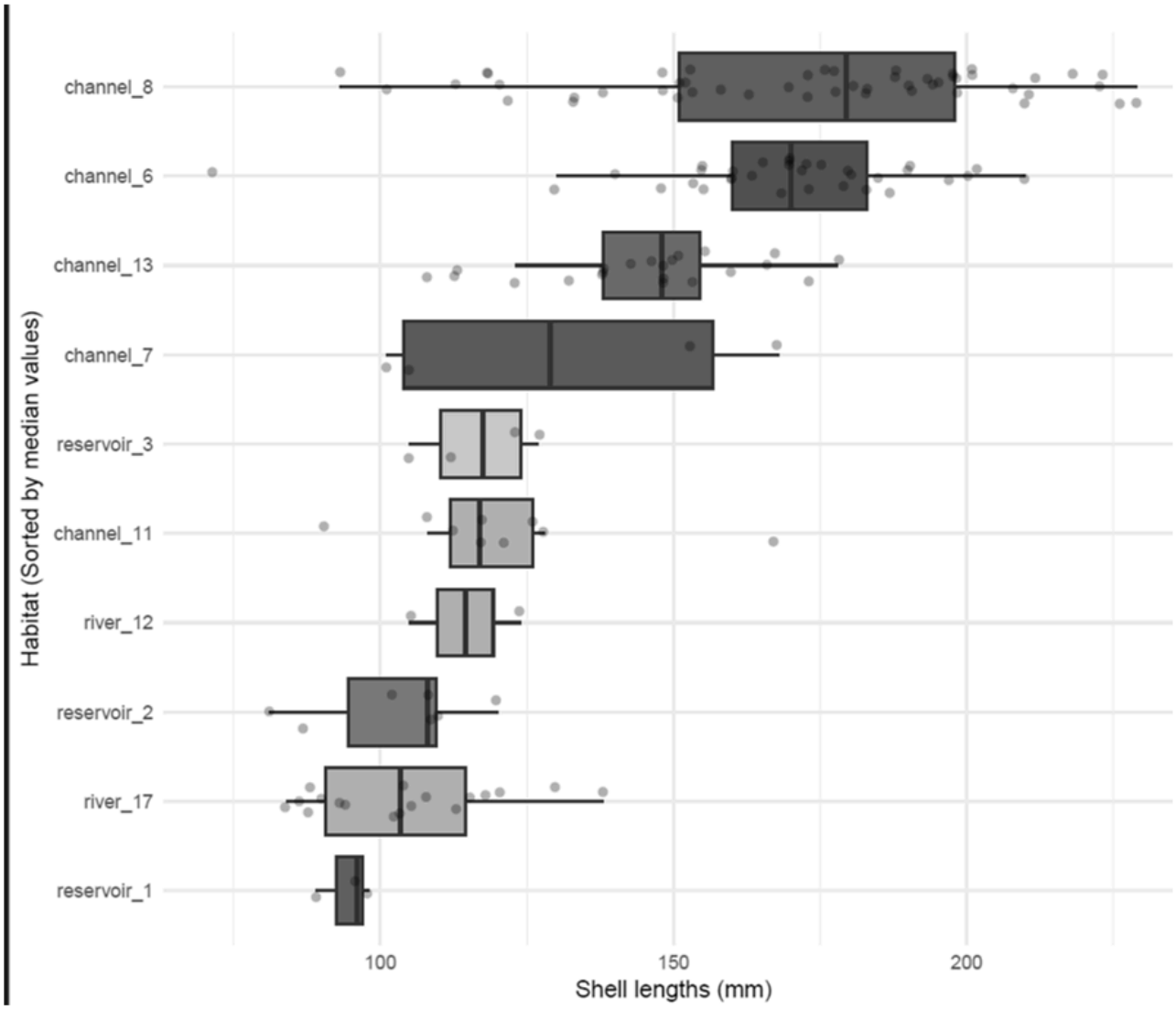


Figure 3

Chinese pond mussel (*S. woodiana*) shell length variation and median values among different type of habitat.