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**Research Article**

# Invasion done: history and explanation of the spread of the river nerite (*Theodoxus fluviatilis* L., 1758) along the artificial shoreline of Lake Balaton

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## Abstract

Lakes and their catchment area, which are of great interest for tourism, are now heavily modified and subject to urbanisation and other forms of shoreline development. All these processes can contribute to the appearance and spread of non-native species. Although *Theodoxus fluviatilis* (L., 1758) appeared in Lake Balaton (Hungary) in 2013, we have limited information on the spread of the species as well as on the ecological preference of the species in the lake. To address these shortcomings, we surveyed the spatial distribution of the species, examined how land-use pressures along with the geographical location of sampling sites influence the abundance of *T. fluviatilis*, and investigated the depth preference of the species along the shoreline of the lake. We found that the species has successfully conquered the artificial rocky shoreline of Lake Balaton eight years after its first appearance. Our results indicate that the geographic location of the sampling sites had a significant role since the abundance of *T. fluviatilis* decreased from southwest to northeast, corresponds to the nutrient gradient in Lake Balaton. This result suggests that, beyond local factors like artificial rip-rap habitats, lake-level factors also significantly influence the distribution of the species. We observed that *T. fluviatilis* favours 70–80 cm water depth, which might be due to the decreasing rate of wave-induced disturbances along the depth gradient and the available food for the species. We argue that the occurrence and the spread of the species in the lake can be explained by the existence of shoreline modification and by the water management practice that maintains high water levels. These assumptions are consistent with literature evidence stating that the high water level can influence key environmental variables such as wind-induced turbidity, sediment resuspension, and underwater light conditions, which may affect the distribution of aquatic organisms in the littoral zone.

**Key words:** littoral zone, rip-rap, invasion, high water-level

## Introduction

The human-assisted dispersal of non-native species facilitates the disruption of “classical” biogeographic boundaries (Capinha et al. 2015). In the case of freshwater and marine ecosystems, shipping and channel construction are the most common human-related contributions for the invasions (Molnar et al. 2008). With these human contributions, the Ponto-Caspian region becomes one of the most significant donor regions for aquatic invasive species across Europe (Cuthbert et al. 2020), including the Lake Balaton (Balogh et al. 2018). Lake Balaton is the largest shallow lake in Central Europe and one of the most popular tourist destinations in Hungary. Since 1863, the water level of the lake has been controlled by the Sió Canal (Virág 1998), which creates access to the River Danube, and serves as the main invasion corridor of the lake (Takács et al. 2019). Approximately 45 percent of the lake shoreline has been modified into artificial rip-rap laying on concrete structure (Petrovszki et al. 2024), whereas the remaining natural shoreline is covered with reed patches and submerged macrovegetation and is characterised by silt and sand substrate (Balogh et al. 2008; Karádi-Kovács et al. 2023). The unified artificial shoreline creates opportunity for the establishment of numerous non-native species which origins are mostly Ponto-Caspian. According to Karádi-Kovács et al. (2023), the proportion of alien macroinvertebrate taxa was 89.2% in the artificial habitat in 2020. Together with crustaceans, freshwater molluscs are considered a relatively dominant group among alien freshwater taxa worldwide (Karatayev et al. 2009). These organisms can have significant ecological impacts on recipient communities and ecosystems (Devin et al. 2005; Preston et al. 2022; Yanai et al. 2017). As for the alien mollusc species in Lake Balaton, the first and most prevalent invader was the zebra mussel, *Dreissena polymorpha* (Pallas, 1771) in 1932 (Sebestyén 1938). Since then, the massive population of *Dressiena* has played a key role in the lakes' food web and enhancing water transparency by filtering planktonic algae (Balogh et al. 2008). The New Zealand mud snail *Potamopyrgus antipodarum* (J.E. Gray, 1843) successfully invaded fresh and brackish waters in Europe, Asia, North America, and Australia (Alonso and Castro-Díez 2008). The first record of *P. antipodarum* in Hungary as well as in the Lake Balaton dates back to 1977 (Pintér 1978). Five years after the first record, this gastropod species became very abundant (50 000–100 000 individuals/m$^2$) on the sandy bottom of the lake (Domokos and Kovács 1982) and subsequently invaded the Hungarian section of the River Danube and successfully spread in the freshwaters of Hungary. Today, *P. antipodarum* is present in relatively moderate abundance in Lake Balaton (Domokos 2013; Karádi-Kovács et al. 2023). In the 18th century, *Physa acuta* (Draparnaud, 1805), native to North America, colonised European freshwaters and became a globally cosmopolitan species worldwide due to its high ecological tolerance (Ebbs et al. 2018). Richnovszky and Pintér (1979) were among the first to mention its occurrence in Lake Balaton, and shortly thereafter the strong spread of the species on the northern side of the lake was reported (Domokos and Kovács 1982). The appearance of *P. acuta* in water bodies may affect the native fauna. Früh et al. (2017) revealed competitive interaction between *P. acuta* and the native *Physa fontinalis* (Linnaeus, 1758) at high temperatures, favouring the non-native species. This may exacerbate declines in *P. fontinalis* populations as summer temperatures increase due to climate change. In addition, the high densities of *P. acuta* may lead to competitive displacement of other native snail species and alter the structure of the native snail community (Cieplok and Spyra 2020). The Chinese pond mussel *Sinanodonta woodiana* (Lea, 1834), was first reported from Lake Balaton in 2006 (Majoros 2006), while it has been present in Hungarian waters since 1980 (Petró 1984). Fish carrying *S. woodiana* glochidia larvae from fishponds are believed to have been the primary route of introduction into the western part of the lake (Benkő-Kiss et al. 2013). *Sinanodonta woodiana* had rapidly developed high relative abundance and biomass, resulting in a serious threat to the native bivalve species *Anodonta anatina* (Benkő-Kiss et al. 2013). In 2008, further two non-native bivalve species were recorded in Lake Balaton: the Asian clam *Corbicula fluminea* (O.F. Müller, 1774) and the quagga mussel *Dreissena rostriformis bugensis* Andrusov, 1897 (Majoros 2009). The latter has completely outcompeted the earlier invader zebra mussel (*D. polymorpha*) in the eastern basin of the lake, while both species co-exist in the western part of the lake (Balogh et al. 2018).

*Theodoxus fluviatilis* (Linné, 1758) (river nerite, Gastropoda: Neritidae) is the latest detected alien mollusc species in Lake Balaton up to now. Within the family Neritidae, it is the most widely distributed species (Bunje 2005). *Theodoxus fluviatilis* is widespread in many European countries (e.g. Poland, Germany, Denmark, Italy, France) (Bunje 2005; Glöer and Pešić 2015; Zettler et al. 2004) and it is native to the Danube basin in the lower part of the River Danube (Čejka and Horsák 2002). This species prefers waters with a high calcium content and stony substrate (Dall et al. 1984). It is common in lotic waters and in the upper littoral zone of lakes, but also occurs in brackish coastal waters (Zettler et al. 2004). The first Hungarian record of *T. fluviatilis* was in the 1950s from the River Tisza, a tributary of the River Danube (Soós 1963) and in 1987 it was reported from the Hungarian stretch of the Danube (Csányi 1994; Frank 1988). Almost three decades later, in 2013, river nerite appeared for the first time in the middle section of Lake Balaton (Tihany Peninsula) (Takács et al. 2019). The first comprehensive survey of the species in autumn 2018 revealed that *T. fluviatilis* inhabited the central part of the lake (with population densities of approximately 4–5000 individuals/m$^2$), whereas the westernmost and easternmost parts of the lake were unoccupied (Takács et al. 2019). Later, Karádi-Kovács et al. (2023) found in a survey performed in 2020 that artificial rip-rap habitats harbour a higher proportion of alien taxa and that *T. fluviatilis* was consistently present in the rip-rap habitat of the lake. However, we did not know how environmental factors of the catchment and lake level variables affect the species in the lake. Land-use change such as urbanization and agriculture exerts pressure on the littoral zone leading to environmental contaminations (e.g. chemical pollution, nutrient input) increase sediment transport and cause habitat alteration (Grimm et al. 2008; Jennings et al. 1999; McGoff et al. 2013). As a result, urbanization and agricultural land use can change the ecological communities and may favour the proliferation of non-native species (Johnson et al. 2008; Schmidlin et al. 2012). Studying species-environment relationship can also help to distinguish the effects of human-induced disturbance from those of natural landscape features and help to prioritise management and restoration actions (Šiling and Urbanič 2016). Moreover, with increasing water depth, various factors such as water pressure, temperature, oxygen content, and the quantity and quality of food also change (Verhofstad et al. 2013). These factors can have a significant impact on the distribution of species. At present, our understanding of the species' subsequent territorial expansion is incomplete, and we are also unaware of the specific water depth preference of the species.

Therefore, our objectives were 1) to examine the past and present (year 2021) occurrence data of *T. fluviatilis* in order to reveal the dynamic of the spread of the species in Lake Balaton, 2) to investigate how land-use pressure (urban and agricultural) and the geographical location of the sampling sites (as a proxy for the natural trophic gradient of the lake) affect the abundance of *T. fluviatilis*, and 3) to estimate the abundance of *T. fluviatilis* at various depths in the littoral zone.

## Materials and methods

### Study area

The Lake Balaton is the largest shallow lake in Central Europe and one of the most popular tourist destinations in Hungary (Figure 1a). The water of the lake is calcareous with the dominant ions of $Ca^{2+}$, $Mg^{2+}$, and $HCO_3^-$ and slightly alkalic (pH 8.4–8.7) (Specziár and Bíró 1998). Almost half of the shoreline is highly modified since it was stabilised between the 1930s and 1965 with concrete and rip-rap structures (Balogh et al. 2008). Within the lake there is a difference between the northern and southern shorelines as a result of the dominant northern winds: the northern shoreline is exposed less to the wind and characterized by silty substrate, while the southern shoreline is unsheltered from the wind and characterized by intensive wave activity and sandy substrate (Árva et al. 2021). The Zala River enters the westernmost part of the lake and makes a major contribution to the nutrient input; thus, there is a trophic gradient from west to east in Lake Balaton (Farkas et al. 2020).

### Sampling and statistical method

To reveal the spatial distribution of river nerite, *T. fluviatilis* was sampled in July 2021 at 20 sites along the artificial rip-rap shoreline of the lake (Figure 1c, Supplementary material Table S1). We chose the same sampling

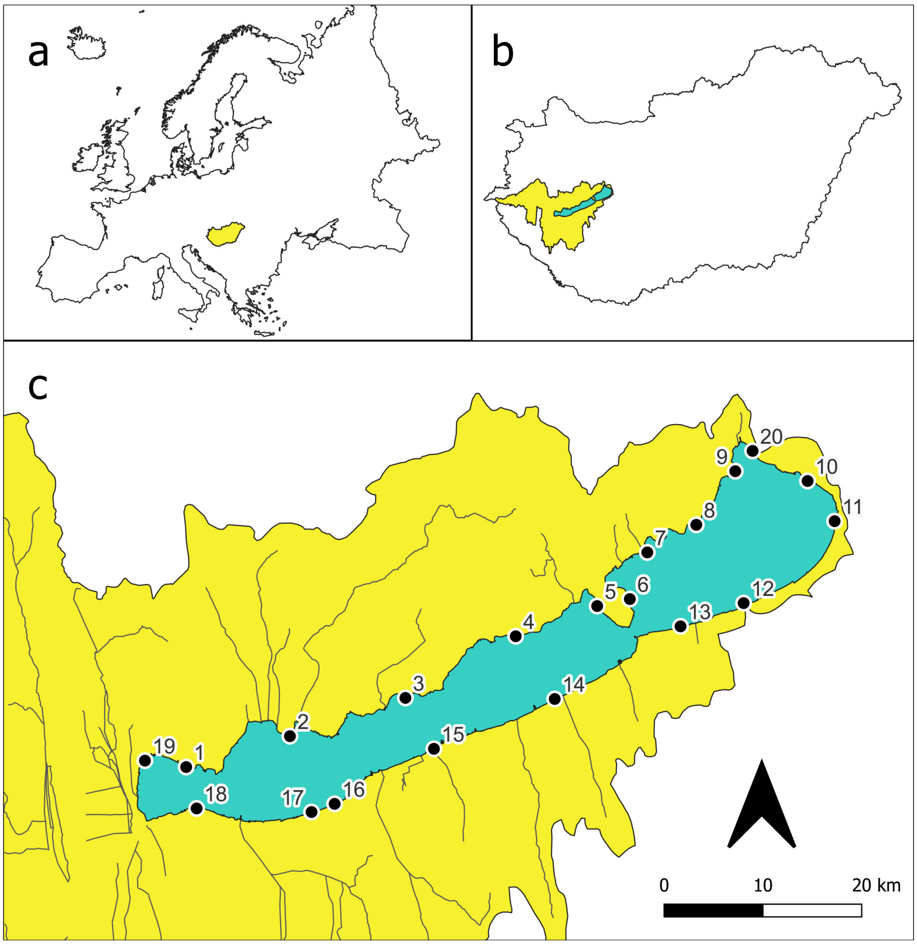

**Figure 1.** Study area and sampling sites. (a): The position of Hungary (yellow) in Europe. (b): Lake Balaton (blue) and its drainage area (yellow) in Hungary. (c): Sampling sites along the shoreline of lake Balaton, Hungary (1. Vonyarcvashegy, 2. Szigliget, 3. Pálköve, 4. Balatonakali, 5. Sajkod, 6. Tihany, 7. Balatonfüred, 8. Alsóörs, 9. Balatonalmádi, 10. Balatonkenese, 11. Balatonaliga, 12. Siófok, 13. Zamárdi, 14. Balatonőszöd, 15. Balatonboglár, 16. Balatonfenyves, 17. Balatonfenyves, 18. Balatonberény, 19. Keszthely, 20. Balatonfűzfő).

sites as Takács et al. (2019) (Sites 1–19) with one extra site (Site 20). This design allowed us to examine the spread of the species. At each site, 10 submerged pieces of stone were selected (length between 20 and 30 cm, height about 10 cm, width 10–20 cm) and carefully put on a tray. All *T. fluviatilis* individuals were removed by hand and counted. The length (L), high (H) and width (W) of each piece of stone were measured to estimate the stone surface area according to the formula: $\pi/3$ (LH+LW+HW) (Dall 1979).

To evaluate the aggregation patterns of *T. fluviatilis*, we used the Morisita index and Standardized Morisita index proposed by Morisita (1959) and Smith-Gill (1975), which estimate the degree of spatial dispersion and the degree of intraspecific aggregation of populations. The Morisita index values ranged from 0 to n (n = the number of samples) (between 0 and < 1: uniform; 1: random; between > 1 and n: aggregated). The Standardized Morisita index values ranged from −1 to 1 (<−0.5: uniform; −0.5 ≤ ≤ 0.5: random; > 0.5: aggregated). We used *dispindmorisita* function of the *vegan* package in R (Oksanen et al. 2020).

We used land-use variables in the proximity of the lake as an indicator of human-induced alteration (e.g. morphological alteration, nutrient enrichment) (McGoff et al. 2013). Urban, agricultural, and natural land-use variables were defined in $m^2$ for all sampling sites within 1000- and 500- meter buffers. Urban land-use included buildings, roads, artificially surfaced area and areas with vegetation within urban fabric like parks and camping grounds, sports grounds, leisure parks, beach, etc. Agricultural land-use included cultivated areas and pastures. Natural land-use included areas where vegetation formation consisted of trees, including shrub and bush understories, natural grasslands and reed vegetation within the lake. QGIS v.3.22.8 was used for all land-use calculations. In Lake Balaton, there are both longitudinal (west to east) and latitudinal (north to south) environmental gradients. To assess the effects of these gradients on the abundance, we used longitude (representing the west to east position) and latitude (representing the north to south position) GPS coordinates of the sites as the proxy of gradients.

Variance Inflation Factors (VIFs) were used to check for collinearity of land use variables, longitude, and the latitude coordinates (*vif* function of the *car* package). Longitude and latitude showed collinearity (Pearson $r = 0.908$, $P < 0.001$). To remove multicollinearity, we performed a Principal Component Analysis (PCA) of the longitude and latitude variables and used the first principal component, which captures the combined variance of the highly correlated variables, for the GLM models.

We used GLM models with negative binomial errors to assess the effects of land-use variables (natural, urban, and agricultural areas in $m^2$) of the 1000- and 500- meter buffer around the sampling sites and the geographical location (first principal component of the latitude and longitude) of the sampling sites on the abundance of *T. fluviatilis*. We used *glm.nb* function *MASS* package in R.

We collected individuals at the different water depths of the littoral rip-rap zone at 5 sites along the north shore of the lake to estimate the vertical distribution of the species. At each site, fully submerged stones were selected every 10 cm between the water depths of 10–160 cm. Individuals were collected from the stone surface, and stones were measured with the same method described above.

Water physicochemical parameters, e.g. temperature, pH, conductivity (μS/cm corrected to 25 °C), salinity (ppt-parts per thousand), and dissolved oxygen content, were measured at every site with an Aquameter AM-200 and Aquaprobe AP-2000 from Aquaread water monitoring instruments.

## Results

### *Present (2021) spatial distribution*

The results of the spatial distribution survey show that *T. fluviatilis* has colonized the entire shoreline except for two sampling sites (Sites 9 and 20)

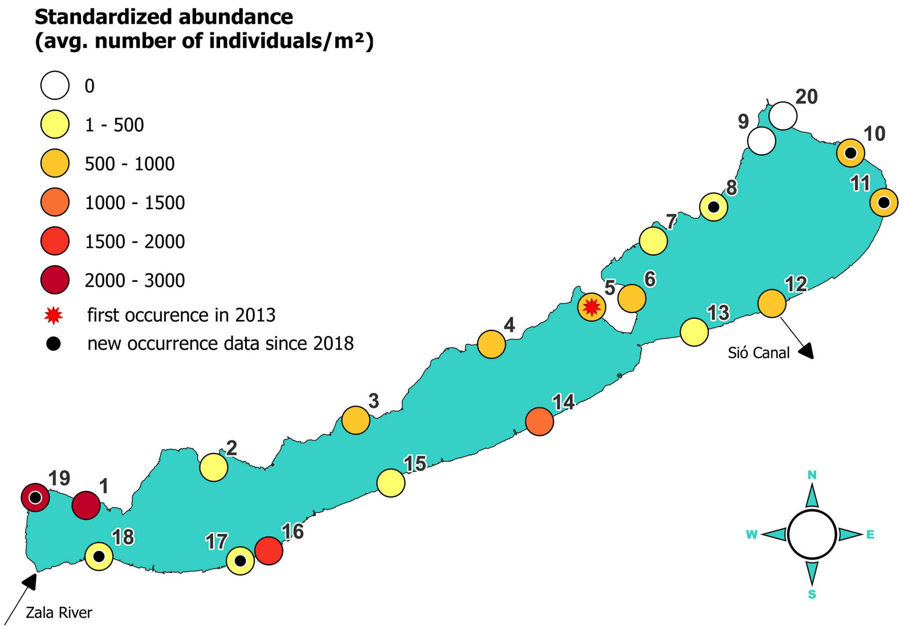

**Figure 2.** Spatial distribution of *Theodoxus fluviatilis* (avg. number of individuals/ m$^2$) on the shoreline of Lake Balaton. Standardized abundance is depicted as a colour gradient from yellow (low abundance) to dark red (high abundance). White colour indicates species absence. The red star indicates the first record of *T. fluviatilis* (Tihany Peninsula) and black circles indicate new occurrence data since 2018.

(Figure 2, Table S1). The density of *T. fluviatilis* was the highest at the northern shoreline, at Vonyarcvashegy (Site 1; 2570 avg. no. of ind./m$^2$) and at Keszthely (Site 19; 2072 avg. no. of ind./m$^2$). These sites are situated in the westernmost part of the lake (Figure 2). The lowest density was at Balatonberény (Site 18; 20.96 avg. no. of ind./m$^2$) which is located at the southern shoreline of the lake opposite to the densest sites (Sites 19 and 1).

### *Comparison of the present (2021) and past (2018) distribution*

We did not find any *T. fluviatilis* at the sampling site 9 as Takács et al. (2019) in 2018, and Site 20, (which was an extra site compared to Takács et al. 2019 sampling sites). Whereas we found *T. fluviatilis* at six more sites than Takács et al. (2019) in 2018 (at sites 8, 10, 11, 17, 18, 19).

### *Aggregation pattern*

The species examined consistently showed an aggregated pattern of dispersion between the sites and within every site (Morisita index > 1 with $p < 0.003$ and Standardized Morisita index > 0.5; Tables S2, S3).

### *The impacts of land-use variables and the geographical location of the sampling sites on the abundance of* T. fluviatilis

GLMs examining the effects of land-use variables and geographic location revealed that geographic location had a significant negative effect (Tables S4, S5), while urban, natural, and agricultural land use had no significant

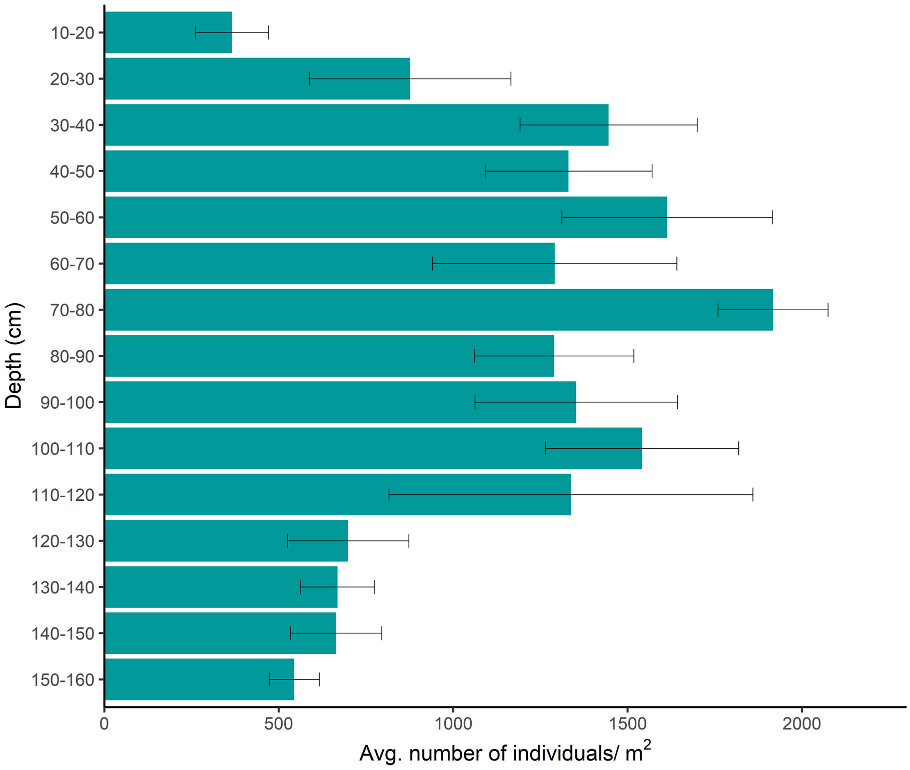

**Figure 3.** Standardized abundance of *T. fluviatilis* at various depths in the littoral zone of Lake Balaton.

effect on *T. fluviatilis* abundance at 500 (Table S4) and 1000 meters (Table S5) around the sampling sites. This result implies that the abundance of *T. fluviatilis* decreases from southwest to northeast, which corresponds to the nutrient gradient of Lake Balaton.

### *Vertical distribution*

The densities of *T. fluviatilis* were highest between 70 and 80 cm deep, followed by 50 and 60 cm and 100 and 110 cm (Figure 3). After 120 cm depth, the density decreased with the depth. The lowest density was between 10 and 20 cm and 150 and 160 cm.

## Discussion

The littoral zone of the lakes undergoes significant changes in land use over time, often driven by human development and recreation activities, and this process might significantly contribute to the spread of non-native species. This phenomenon is particularly pronounced in lakes with mass tourism, such as Lake Balaton. In the present study, we examined the current distribution of *T. fluviatilis* in Lake Balaton and compared this data with the results of previous surveys to infer the dynamic of its spread. In comparison with previous years, we found that *T. fluviatilis* successfully conquered almost the entire artificial shoreline zone of Lake Balaton. Our results suggest that the variation of *T. fluviatilis* abundance is mostly controlled by the geographical location and consequently by the trophic gradient of the lake. Furthermore, we investigated the vertical distribution of the species at different depths in the littoral zone. We found that *T. fluviatilis* prefers 70–80 cm of water depth, which might be related to the available food for the species and the substrate where the rate of wave-induced disturbances is less than in the upper zone of the depth gradient. We argue that the recent occurrence and successful spread of the species in the lake is due to the modified shoreline and indirectly to water management practices that ensure high water levels.

We assume that in 2018, the invasion process of *T. fluviatilis* in Lake Balaton was in the colonization stage. At this stage, invasive species attempt to overcome local barriers to colonize new habitats (Catford et al. 2009). This is confirmed by the study from Takács et al. (2019) which showed that the westernmost and easternmost parts of the lake were still unoccupied, while the highest density was found in the central part of the lake, from where the invasion originated (the western shore of the Tihany Peninsula). In addition, this study emphasized that the invasion was in progress in 2018 (Takács et al. 2019). On the other hand, during our survey in 2021, the colonization was already successful (we found *T. fluviatilis* at all but one sampling site as Takács in 2018). The invasion process might enter the establishment stage, where the major filters are the biotic ones that restrict population growth, while the population has to interact with local environmental conditions (Catford et al. 2009; Theoharides and Dukes 2007).

Our results showed that urban, agricultural, and natural land-use have no significant impact on the abundance of *T. fluviatilis*. On the other hand, geographical location had a significant negative effect on *T. fluviatilis* abundance, which means that the abundance decreased from southwest to northeast. The Zala River, which flows into the westernmost part of lake Balaton, serves as the main transporter of nutrients and contributes approximately half of the total phosphorus and nitrogen load of the lake (Farkas et al. 2020). This input contributes to a trophic gradient that extends from southwest to northeast across the lake. Thus, the spatial variation in abundance at the different sampling sites may have been driven by the trophic gradient of the lake. On the other hand, there is a difference between the northern and southern shorelines of the lake. The northern shoreline is sheltered from the wind and has steeper slopes, while the southern shoreline is shallow and more exposed to the wind and the resulting waves. The nutrient rich, wind-protected northern shoreline in the westernmost part of the lake can offer ideal habitat for *T. fluviatilis* and could favour the growth of periphyton on the artificial rocky shore, which provides food for the gastropods (Skoog 1978). On the contrary, the shallow, turbid, and wave exposed southern shoreline could negatively impact the abundance of *T. fluviatilis*. This is the reason why the highest density of the snail was observed along the northern shoreline of the lake, while we found a lower abundance of individuals at the southern shoreline in the westernmost part of the lake. Our results indicate that, in addition to local level factors (e.g. artificial rip-rap habitat), factors at lake level may also be important for the distribution of *T. fluviatilis*.

In terms of vertical distribution, we found that *T. fluviatilis* used all available hard surfaces on the artificial shoreline, colonizing rocks completely covered by water from the upper to the deepest zone (between 10–160 cm). However, they preferred 30 to 120 cm deep water, i.e. the middle of the artificial shoreline (max. avg. abundance was between 70 and 80 cm with 1917 ind./$m^2$), while above and below this middle section, more than half of the average numbers of individuals per $m^2$ decreased. The wind-induced water movements in Lake Balaton, including waves, currents, and regular fluctuations, affect the underwater cover of the rocks on the shoreline. As a result, the upper region of the artificial shoreline is one of the most disturbed habitats, alternating between periods of dryness and flooding, while the kinetic energy of waves is also a form of disturbance (G.-Tóth et al. 2011). Moreover, the top of the depth gradient can be an unfavourable habitat for *T. fluviatilis*, as waves can increase the rate of invertebrate detachment (Gabel et al. 2012) and in extreme cases such as storms and ice covers, it can lead to their mortality (Kirkegaard 2006). Consequently, these phenomena may lead to low abundance on the upper 30 centimetres. On the other hand, the benthic algae, which are the main food source of *T. fluviatilis* (Skoog 1978), are regulated by underwater light, with the result that in deeper water there is a lower biomass of benthic algae in Lake Balaton (Somogyi et al. 2024). Moreover, wind-induced sediment resuspension can influence the light climate under water (Istvánovics et al. 2007; Somlyódy and Koncsos 1991), which may affect negatively the benthic algae biomass as well (Somogyi et al. 2024). Consequently, the abundance of *T. fluviatilis* may be controlled by the limitation of food sources at the deepest section of the littoral zone. In addition to that, the wind can cause the resuspension of the natural sediments, such as fine sand and silt, and their deposition on the artificial rock surface in the deepest zone. This phenomenon can lead to unsuitable conditions there, resulting in lower abundance, as the species prefers primarily large stones with a clean surface (Bunje 2005).

Eight years after the first appearance of *T. fluviatilis*, we have found that the species has invaded the littoral zone of the largest shallow lake in Central Europe, Lake Balaton. Lake Balaton is intensively used by tourists for recreation purposes. The great interests of tourists influence the extent of urbanisation and other forms of land transformation (Petrovszki et al. 2024), which affects the lake's ecosystem as well. The increase of artificial surfaces along the shoreline favours non-native species (Karádi-Kovács et al. 2023). However, there is no information on how and why the appearance and spread of *T. fluviatilis* in Lake Balaton occurred just recently, which happened nearly three decades after its first appearance in the Hungarian section of the River Danube. We agree with Takács et al. (2019) that the late occurrence of the species cannot be explained by the spatial distance between the River Danube and Lake Balaton, and the ongoing change in the lake might be responsible for the recent spread of the species. Due to the water retention purposes, mass tourism and recreational activities, there is a strong societal demand to keep the water level high in the lake. There is evidence that wind-induced resuspension of sediments is the most important factor influencing underwater light conditions in Lake Balaton (Somlyódy and Koncsos 1991). The high water level makes the water column less susceptible to mixing by wind, and thus it can contribute to the better light availability at the bottom of the lake (Somogyi et al. 2024). According to Somogyi et al. (2024) the change in underwater light conditions influence zooplankton and phytoplankton dynamics and favour the biomass of benthic algae, shifting the planktonic life form to the benthic. Moreover, previously introduced invasive Dreissenidae species also contribute to the water transparency (Balogh et al. 2008). We argue that these phenomena might indirectly impact periphyton grazing gastropods such as *T. fluviatilis,* improving water quality and increasing food sources. This study is another example of how water management decisions or regulatory policies can lead to unaware consequences, as observed by Istvánovics et al. (2022) and Somogyi et al. (2024) in the case of an algal bloom and a shift in regime from planktonic to benthic algae in the lake. Given the increasing trend of the global spread of alien species and the increasing abundance of established alien species, we emphasise the importance of policymakers to managing and planning the further transformations of littoral zone and water management in terms of balancing ecological and social needs.

## Authors’ contribution

BG: research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, original draft, funding provision, BP: investigation and data collection, review, BZS: investigation and data collection, review, DS: research conceptualization, ethics approval, funding provision, review and editing.

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## Web sites, online databases and software

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**Supplementary material**

The following supplementary material is available for this article:

**Table S1.** The GPS coordinates and dates of the sampling sites.

**Table S2.** The result of Morisita and Standardized Morisita dispersion indexes of *T. fluviatilis* among sampling sites.

**Table S3.** The results of Morisita and Standardized Morisita dispersion indexes of *T. fluviatilis* at sampling sites.

**Table S4.** Results of generalized linear modelling (GLM) for analysing the impacts of land- use variables (within 500-meter buffer around the sampling sites) and the geographical location (PC1) of the sampling sites on the *T. fluviatilis* abundance.

**Table S5.** Results of generalized linear modelling (GLM) for analysing the impacts of land- use variables (within 1000-meter buffer around the sampling sites) and the geographical location (PC1) of the sampling sites on the *T. fluviatilis* abundance.

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