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Theodoxus transversalis (C. Pfeiffer, 1828) (Gastropoda: Neritidae) in the Western Balkans: an endangered freshwater snail bouncing back?

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Abstract. Populations of *Theodoxus transversalis*, striped nerite, have declined in recent decades, arguably due to negative anthropogenic impacts on their habitats. The species is classified as endangered by the International Union for Conservation of Nature, and there are generally few reports of its recent occurrence. This is especially true for the Western Balkans and Serbia, where data on the distribution of *T. transversalis* are more than a decade old. Herein, we present the latest data based on an extensive field study of this species conducted in 2023 and 2024. The Velika Morava-Južna Morava-Nišava catchment and ecoregion (ER) 5 were confirmed as the most important refugium for this rare snail in the investigated region. Of particular interest are the findings of an abundant population from the Drina River (where the species has not been reported for 15 years), from the lower Serbian section of the Danube (reports from the Danube are 30 years old), and the discovery of a new population from the Zapadna Morava River 100 km upstream from the nearest known population. Our results show considerable progress in the restoration of the former range of *T. transversalis* in the Western Balkans, although stable populations still appear to be localized. There is also a possibility that this species is spreading into new areas, which is a possibility for the Zapadna Morava River catchment. While it appears that *T. transversalis* is more resilient to negative anthropogenic impacts than previously described in the available literature, a more detailed ecological and genetic study should shed more light on the presence and prospects of the species in the region.

Key words. Striped nerite, geographic distribution, new findings, ecoregions, Serbia

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Introduction

Freshwater habitats are arguably among the most threatened habitats today (Dudgeon *et al.* 2006; Ritchie *et al.* 2024). The negative effects of increasing human activities over the last century have brought many new threats for freshwater species. Gastropods, which are among the most diverse groups of freshwater animals, are inevitably affected by these negative anthropogenic impacts, and it is not surprising that, according to recent estimates (Cuttelod *et al.* 2011), almost half of the freshwater gastropod species are threatened and endangered. The striped nerite, *Theodoxus transversalis* (C. Pfeiffer, 1828), is one of these endangered species of freshwater snails (Sólymos & Fehér 2011). Its remaining populations are rare, scattered, and almost exclusively within the borders of the Danube Basin. To make matters worse, the haplotype diversity of this species is estimated to be extremely low, which further limits the recovery potential of populations, especially in unstable and changing environments (Feher *et al.* 2012). The species is considered extinct in Austria and Slovakia, and it is probably extinct in Romania (Sîrbu & Benedek 2005; Cioboiu 2013), while only a single population is known in Germany (Duda *et al.* 2023). *Theodoxus transversalis* has been reported from Ukraine (upper Tisza; Afanasyev *et al.* 2020) and Moldova (lower Prut; Munjiu *et al.* 2014; Munjiu 2022). Currently, 48 Natura 2000 EU sites have been designated as habitats for *T. transversalis*; most of these sites are in Bulgaria (40), while seven

sites are in Hungary, and one site is in south-eastern Germany (European Environmental Agency 2024). Therefore, Bulgaria could be recognized as the hotspot for this species (Hubenov 2007; Georgiev & Hubenov 2013; Pavlova *et al.* 2013), but beyond Bulgaria, Hungary (Bódis *et al.* 2016) and Serbia (Marković 2014) have the remaining refugia for *T. transversalis*. Reports of this species outside of Danube Basin are few, and those are in the Southern Balkans, namely Greece and North Macedonia (Tomić 1959; Feher *et al.* 2012). Findings from Lake Dojran, North Macedonia were only empty shells found in the sediment of *Dreissena* (Fischer *et al.* 2009), and the age of these shells has not been estimated. These non-Danubian occurrences together with numerous findings in Danube catchment indicate a much wider and more frequent occurrence of this species in the recent past (19th and 20th century).

Theodoxus transversalis typically inhabits flowing waters, but does occur in still waters, such along the shores of lakes. According to the available literature (see Marković 2014), *T. transversalis* prefers unpolluted, well-oxygenated water, so it can be used as an indicator for water quality assessment. Finally, according to molecular studies, it is one of the earliest members of *Theodoxus* and, therefore, very interesting from a phylogenetic point of view (Bunje & Lindberg 2007).

Ecoregions are a useful concept for the study and management of global, regional, and local faunas. Illies (1978) introduced the delineation of ecoregions (hereafter identified by "ER" followed by the ecoregion number) for the European freshwater fauna. According to him, the greatest number of the ecoregions converge in the Western Balkans and Serbia. Fine tuning of Illies' ecoregions has taken place in the years after his work, but nothing significant has changed (Paunović *et al.* 2012). If we exclude ER 9, we can argue that the Western Balkans and Serbia harbour all ecoregions in which *T. transversalis* occurs. As in most other parts of its range, the species was more common in the past than it is today. Water pollution and the spread of invasive species have been cited as the main threats and reasons for this decline (Tittizer *et al.* 2000; Féher *et al.* 2012; Marković 2014). In the 19th and 20th centuries, *T. transversalis* was common in the northern and central parts of Serbia inhabiting medium-sized and large rivers such as the Tisa, Jadar, and Moravica rivers, while also being widespread in the Danube (Tomić 1959; Arambašić 1994; Marković 2014). Additionally, *T. transversalis* was reported from some atypical habitats such as a channelized muddy lowland stream Jelenački potok (Živić *et al.* 2000).

Considering that distribution and status of populations of this endangered species have not been assessed for more than a decade, we aim to provide up-to-date information based on the latest research. The current and older data are considered, and predictions for the future are briefly discussed.

Materials and Methods

An extensive field survey on the distribution of *Theodoxus transversalis* was carried out by the Faculty of Biology of the University of Belgrade in the summer of 2024. It included the main drainage basins in Serbia, with a more thorough investigations in the catchments of the Drina, Velika Morava, Južna Morava, Nišava, and the Danube, where the species had been previously reported. We have also included relevant results of regular monitoring throughout 2023 by the Serbian Environmental Protection Agency (SEPA) to include as much recent data as possible. Our sampling was carried out using standard benthological hand nets or by hand where possible. Due to the size and remarkably characteristic shell features of *T. transversalis*, the species was mostly identified in the field, especially where it was most abundant. Population density was estimated at each site by using metal square measuring frame (1 m^2) and expressed as low (<10 individuals per m^2), moderate (11–100 individuals per m^2), and high (<100 individuals per m^2) according to simplified adapted scale for density assessment (Marković 2014). In some sites where *T. transversalis* is rare, it was identified from composite macroinvertebrate samples taken with a benthological hand net and fixed in situ with 70% ethanol; these samples were processed in the laboratory. In some of those composite samples only empty shells were found.

Results

Living *Theodoxus transversalis* were found at 15 sites, while only empty shells were found at three localities (Table 1). Of these 15 sites, all but one (site 13, Prahovo) belong to ER 5 (Fig. 1). Most sites were in the Velika Morava-Južna Morava-Nišava catchment. Examples of collected live specimens from a few localities from this catchment are shown in Figure 2.

Theodoxus transversalis was estimated to be common (high population density) at five sites (four in the Velika Morava-Južna Morava-Nišava catchment). In contrast, the species was assessed as less common (low population density) at six localities, most noticeably in the Danube River.

We found seven new localities (Fig. 1). Six of these localities—two on the Drina River, two on the Zapadna Morava River, and two on the Nišava River—are within ER 5. The

Table 1. Findings of *Theodoxus transversalis* during the 2023–2024 field survey in Serbia. "Potentially present" (pp) refers to samples/sites where only empty shell/s were found in the area with known recent presence of the species.

Site no.	River catchment	Locality	Date	Latitude °N	Longitude °E	Estimated density
1	Velika Morava	Markovac	29.VII 2024	44.2250	021.1530	Low
2	Velika Morava	Krušar	10.VIII 2024	44.0053	021.3267	Low
3	Velika Morava	Ćuprija	29.VII 2024	43.9375	021.3679	pp
4	Velika Morava	Varvarin	29.VII 2024	43.7170	021.3839	High
5	Zapadna Morava	Maskare	11.VI 2024	43.6981	021.4013	High
6	Zapadna Morava	Miločaj	30. X 2023	43.7696	020.6473	Moderate
7	Južna Morava	Stalać	07.VIII 2023	43.6765	021.4108	Moderate
8	Južna Morava	Mojsinje	07.VIII 2023	43.6124	021.5243	Moderate
9	Južna Morava	Aleksinac	03.VIII 2024	43.5269	021.7122	Low
10	Nišava	Niš	03.VIII 2024	43.3252	021.9252	Low
11	Nišava	Brzi Brod	03.VIII 2024	43.3159	021.9657	High
12	Nišava	Prosek	03.VIII 2024	43.3124	022.0530	High
13	Nišava	Crvena Reka	05.VIII 2024	43.2702	022.2440	pp
14	Nišava	Bela Palanka	05.VIII 2024	43.2326	022.3180	Moderate
15	Danube	Prahovo	27.VII 2024	44.2972	022.5781	Low
16	Danube	Radujevac	27.VII 2024	44.2734	022.6769	pp
17	Drina	Gornja Koviljača	09.VIII 2024	44.4925	019.1340	High
18	Drina	Banja Koviljača	09.VIII 2024	44.5272	019.1756	Low

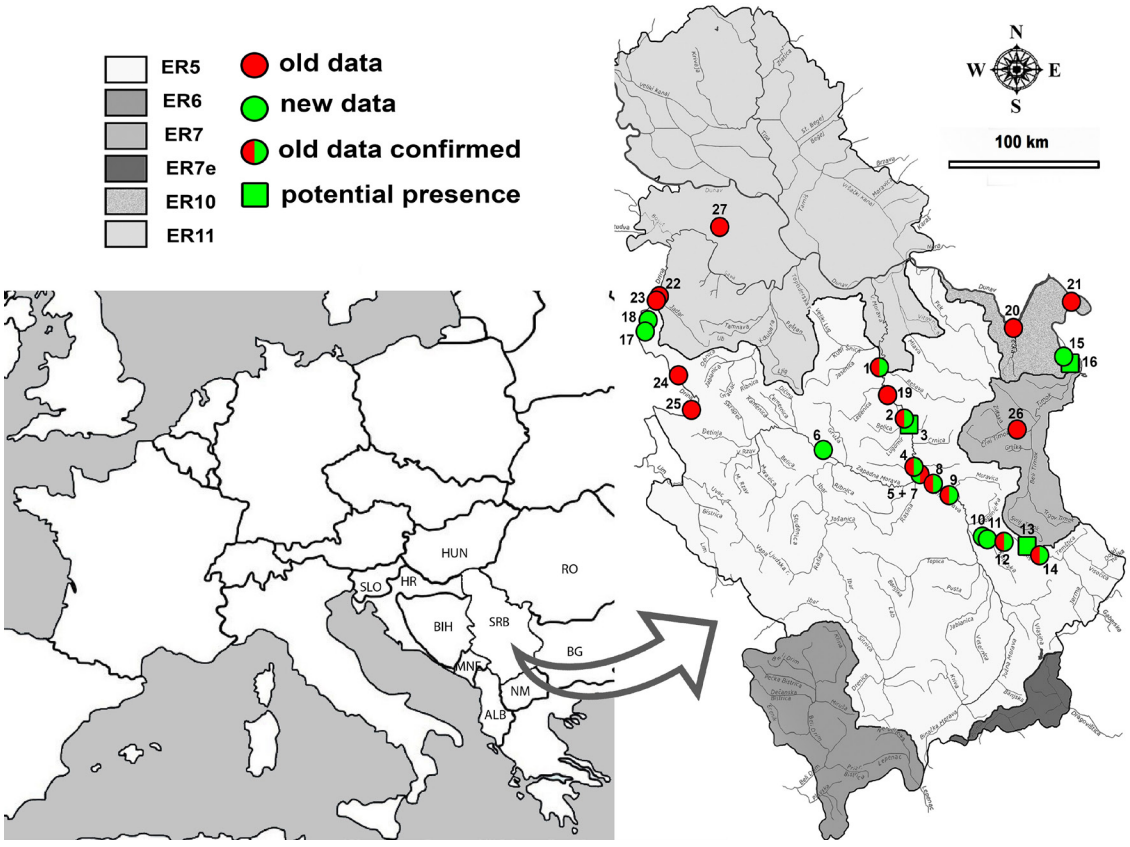

Figure 1. *Theodoxus transversalis* findings during the 2023–2024 survey (green circles) and findings from 1994–2013 surveys (red circles); mixed circles represent continuous presence/confirmed findings. Localities are numbered as in Tables 1 and 2. Ecoregion codes (ER) are as used by Paunović *et al.* (2012).

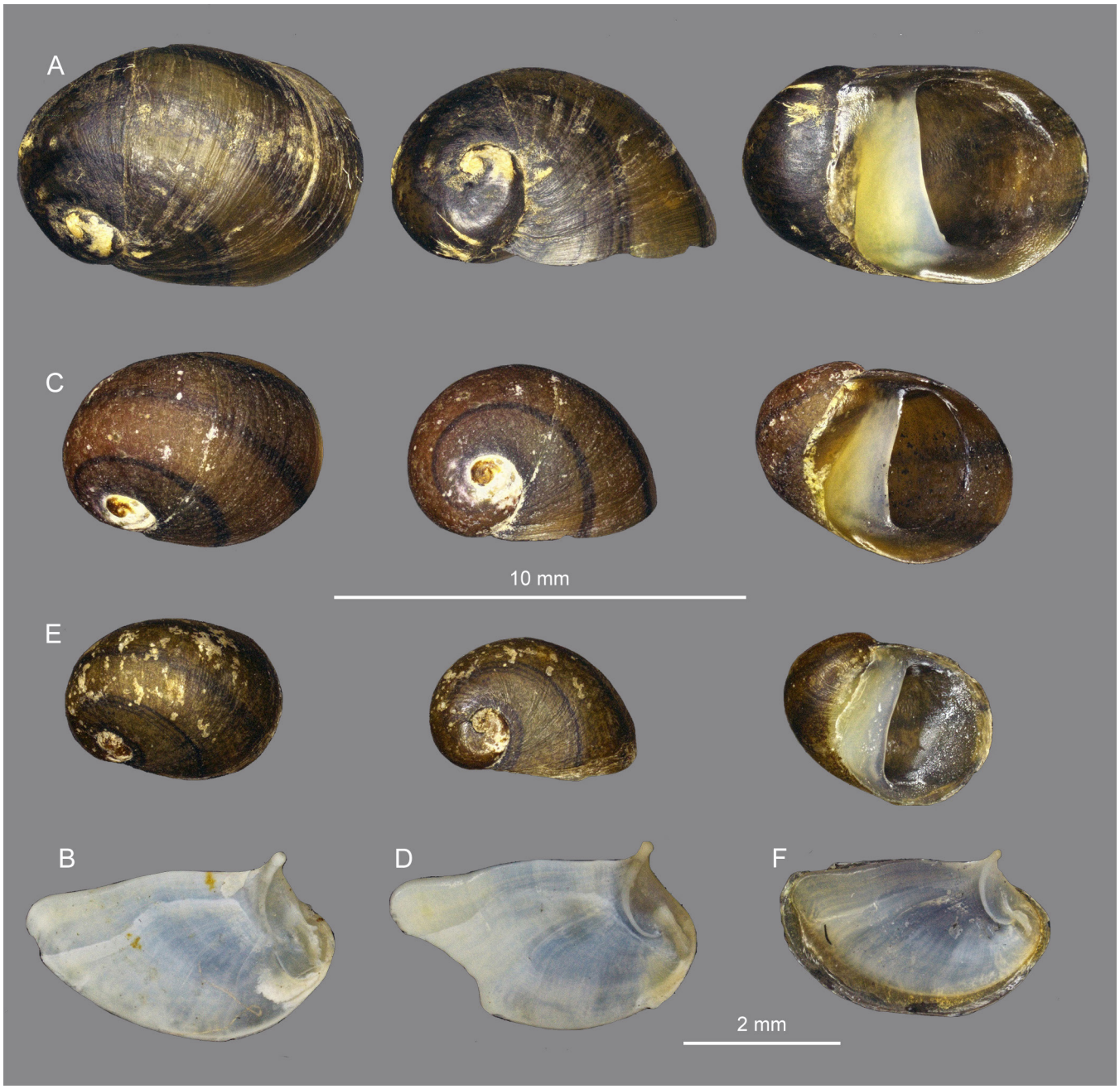

Figure 2. *Theodoxus transversalis* shells and opercula from different catchments in our survey. **A**, **B**, from Južna Morava River, Aleksinac. **C**, **D**, from Nišava River. **E**, **F**, from Velika Morava River, Varvarin; **B**, **D**, and **F** show inner side of opercula.

remaining new site comes from the Danube River. The sites on the Drina and Nišava rivers are 5–10 km apart, so these localities could be considered part of a single population.

We failed to find *T. transversalis* at nine of its historical localities (Table 2). Four of these historical localities are in the Drina River catchment (Fig. 1). Two historical sites came from the Danube at the Iron Gate and one each from the Velika Morava and Crni Timok rivers and Jelenački potok stream. Most of these historical sites were under heavy anthropogenic pressure, as our observations during the survey revealed.

Discussion

The Velika Morava-Južna Morava-Nišava catchment and ER 5 remains the most important refuge for *Theodoxus transversalis*, a rare snail in the Western Balkans. Comparing the current data with the data reported by Marković (2014), the

Table 2. Findings of *Theodoxus transversalis* during 1994–2013 field surveys in Serbia (localities not included in Table 1); SEPA (data from the Serbian Environmental Protection Agency).

Site no.	River catchment	Locality	Year	Latitude °N	Longitude °E	Reference
19	Velika Morava	Bagrdan	2010	44.0851	021.1897	Petrović 2014
20	Danube	Donji Milanovac	1994–1995	44.4645	022.1534	Simić & Simić 2004
21	Danube	Kladovo	1994–1995	44.6138	022.6134	Simić & Simić 2004
22	Drina	Jadar	2008–2011	44.6327	019.2734	SEPA
23	Drina	Jelav	2008–2010	44.6166	019.2427	SEPA
24	Drina	Ljubovija	2011	44.1731	019.4025	SEPA
25	Drina	Bajina Bašta	2011	43.9740	019.5411	SEPA
26	Timok	Crni Timok	2011	43.9242	022.1744	SEPA
27	Jelenački Stream	Ruma	2000	45.0081	019.8493	Živić *et al.* 2000

species in this refuge is quite stable. New localities (e.g. Brzi Brod) and some greater abundance at others (Prosek, Brzi Brod, Varvarin), suggest that *T. transversalis* could spread to other tributaries with potentially suitable habitats (e.g. the Resava, Crnica, or Zapadna Morava rivers). Its dispersal within the Zapadna Morava River catchment has probably already begun. We found *T. transversalis* in the Zapadna Morava River for the first time. One locality is near the confluence with the Južna Morava River (Stalać site), near the abundant Varvarin population. The second locality is more than 100 km upstream (Miločaj site), and we consider this site to have one the most isolated populations of *T. transversalis* in the investigated region. The only comparable record would be from Jelenački potok stream (Živić *et al.* 2000; Fig. 1), from 25 years ago. We speculate that the Zapadna Morava River population likely could be accidental, brought in from nearby road infrastructure works of the so-called Morava motorway. The main source for gravel needed in those works was the Velika Morava River, particularly at the Varvarin site, which has one of the most abundant recent populations. A major difference between the Jelenački potok and Miločaj sites (if we suppose that both might be "accidental") is that the population at the later site has a better chance of persisting due to the habitat being more like that in the Velika Morava, Južna Morava, and Nišava rivers. The Jelenački potok is a small Pannonian stream under heavy anthropogenic pressures caused by hydromorphological alterations, canalisation, communal and industrial waste, and agricultural lands wash offs. As such, Jelenački potok is much less likely to harbour favorable conditions for *T. transversalis* than the Zapadna Morava River, which is larger, more diverse, and more resilient in general to water pollution.

Based on the previously published data of Marković (2014), a secondary refuge for this snail in Serbia is the Drina-Lim drainage basin. Until our survey, all records of *T. transversalis* from this river system were more than 15 years old. Because those records were sparse and included only one or two specimens in each sample, and other *Theodoxus* species occur in the river, and the species was not reconfirmed by numerous subsequent investigations conducted by the first author and by the SEPA (unpublished data), there is the possibility that the species had been misidentified, at least in some cases (the Lim River, most notably). For this reason, our newly found abundant population at the Gornja Koviljača site (Drina River) is of great interest and importance. Such a discovery emphasizes the importance of surveying as many localities as possible. Another investigation of rare freshwater gastropod species in the region has also shown the importance of a similar approach (Gojšina *et al.* 2024).

Another noteworthy finding of our survey comes from the Prahovo site in the Danube River. Apart from a few possible misidentifications, *T. transversalis* has not been reported or confirmed from the Serbian stretch of the Danube stretch for over 30 years (Simić & Simić 2004). The presence of this species in the Bulgarian stretch of the Danube (Lower Danube; e.g. ICPDR 2020; Menabit *et al.* 2023) may indicate recovery of the Danube population and its upstream spread. However, the low population density and the lack of previous recent reports despite frequent surveying, including national and international monitoring of the Danube (ICPDR 2002, 2008, 2015, 2021), suggest the possibility that the newly reported occurrence of *T. transversalis* in the lower Serbian stretch of the Danube might be an unstable population.

Outside of ER 5 (its main refuge), *T. transversalis* was present at only one site in ER 10, in the immediate vicinity of ER7 (Fig. 1). However, the delineation of ecoregions (Paunović *et al.* 2012) should be viewed with caution in this area. Based on the typology of the Danube by Sommer-

häuser *et al.* (2003), which has been confirmed by several international studies (ICPDR 2008, 2015, 2021), this section of the Danube belongs to the western Pontic Danube and is part of the so-called "lower Danube". ER 12 (Pontic Province) includes parts of the Wallachian Plain surrounding the Lower Danube (Illies 1978). In view of this, this lowest Serbian section of the Danube could naturally be regarded as the westernmost part of ER 12. Bulgaria, the country with the most numerous recent populations of *T. transversalis* (Hubenov 2007; Georgiev & Hubenov 2013; Pavlova *et al.* 2013), includes only two ecoregions (ER 7 and 12; Illies 1978), unlike Serbia, with the western borders of these two ecoregions reaching Serbia (Timok catchment and lower Danube stretch). Although we have not confirmed the recent presence of this species in the western part of ER 7, its presence there is quite possible, given its past occurrence (Fig. 2, Table 2) and its presence in Bulgaria. In this area, there is a possibility that populations there could soon recover, similar to those in the lower, Serbian stretch of the Danube. Although there are no recent records of the species in ER 11 (Pannonian plain, or the "Hungarian lowlands" of Illies (1978), historical records and the occurrence of populations in the bordering Drina and Velika Morava Rivers (Fig. 1) suggest that it *T. transversalis* might be found in Serbian part of the ER 11 in the near future.

Although *T. transversalis* is recovering in some parts of its geographic range in Serbia, hydrological alterations present a major threat to its populations. A typical example is the Nišava River upstream of Crvena Reka (where only empty shells were found by us). Upstream of Crvena Reka is the Vrgudinac mini-hydropower plant. Immediately below the dam, we observed extremely low water with minimal flow during the summer. A large part of the riverbed was dry, and the flow was reduced to a narrow, muddy, still-water centre of riverbed. The water quality had severely been altered, particularly the increased organic matter and silt load. Stones, which are the microhabitat for the species, were covered with a thick layer of mud and an extremely dense algal growth. These conditions are hardly optimal for this species (Marković 2014). We found only empty shells of *T. transversalis* at this site (thus, we consider this as a site where the species is "potentially present"). The need to transition to renewable energy sources and the resultant expansion of mini-hydropower plants may become a major threat to the survival of *T. transversalis* in the region. Another potentially threat to this snail in Serbian rivers could be extensive mining in the vicinity of its habitats. This is particularly true for the Drina River, where in 2014 the flotation tailings pond collapsed at the Stolice mine and caused significant pollution downstream, which included toxic metals such as arsenic, cadmium, mercury, lead, antimony, and zinc (Belanović Simić *et al.* 2023). Mining has long been a threat to natural ecosystems of the Drina catchment area, and nowadays perhaps even more considering the planned Rio Tinto's Jadarite mine in the Jadar Valley, which has already led to pollution of the Jadar River by toxic metals during the exploration phase of the ore deposit (Đorđević *et al.* 2024).

In our study, we were able to find considerable progress in the restoration of the former geographic range of *T. transversalis* in Serbia, and even its possible spread into new areas, the Zapadna Morava River catchment. We assume that the populations of this species are recovering, but stable populations are still mainly localized. Our data suggest that the species might be more resilient to anthropogenic threats and might have a more pronounced adaptive capacity than reported in the available literature. A more detailed ecological and genetic study focusing on the Velika Morava (and its tributaries), Danube, and Drina rivers would provide greater insight on the presence and prospects of *T. transversalis* in the region.

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