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Distribution of the species of *Theodoxus* Montfort, 1810 (Gastropoda: Neritidae) in Serbia: an Overview

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Abstract: The distribution of freshwater snails of the genus *Theodoxus* in Serbia is examined. The study comprises literature data and field surveys carried out at 84 watercourses and 5 reservoirs during 2010-2013. The occurrence of three species is confirmed: *Theodoxus fluviatilis*, *T. danubialis* and *T. transversalis*. The most widespread species is *T. fluviatilis* (river nerite). The previously dominant nerite *T. danubialis* (Danube nerite) currently persists mainly in hilly and mountain parts of central Serbia and remains in few localities only in large rivers such as the Danube and the Sava. The endangered species *T. transversalis* (striped nerite) shows patchy distribution; the Drina River – Lim River and the Velika Morava River – Južna Morava River – Nišava River systems are revealed as important refugia for this species. Moreover, at some localities at the Nišava River and the Velika Morava River, the striped nerite is found to be the dominant in the present gastropod communities. Regular studies are crucial for the timely prediction of population health and for conservation of freshwater nerite species in Europe.

Keywords: Field survey, literature data, *Theodoxus fluviatilis*, *T. danubialis*, *T. transversalis*

Introduction

The gastropod family Neritidae (nerites) is one of the oldest lineages of snails. It includes marine, brackish and freshwater taxa restricted to the tropical regions and the Southern Hemisphere. The exception is the genus *Theodoxus* Montfort, 1810, a freshwater and brackish group native to Europe and the Mediterranean region. No other freshwater nerites are distributed sympatrically with *Theodoxus* spp. (Bandel 2001, Bunje, Lindberg 2007). The members of this genus are dioecious and semelparous snails with biennial or triennial life cycle; they lay capsules with numerous eggs that hatch a single juvenile per capsule and the remaining eggs serve as nourishment for it (Fretter, Graham 1962, Bandel 2001). The species are herbivores and detritivores, and usually dwell on hard substrates (preferably rocks) in well-oxygenated, calcium-rich rivers (Fretter, Graham 1962, Glöer 2002).

There are at least 34 described species of the genus *Theodoxus* (see Bunje 2004), although some authors consider that the real diversity is much lower and recognise only few valid species (Bunje, Lindberg 2007). The species are characterised by a pronounced phenotypic plasticity resulting into substantial morphological variability (Zhalay *et al*. 2008, Fehér *et al*. 2009), which makes the morphological identification difficult. In this regard, misidentifications may occur, as in the case of *Theodoxus danubialis* (C. Pfeiffer, 1828) in Italy (details in Bunje 2007) or *T. prevostianus* (C. Pfeiffer, 1828) in Romania (Sîrbu, Benedek 2005).

On the territory of the central Balkans and Serbia, three species are present: *Theodoxus fluviatilis* (L., 1758), *T. danubialis* and *T. transversalis* (C. Pfeiffer, 1828).

The Balkan region is recognised as one of the European centres of biodiversity (Savić 2008). Serbia is part of this remarkable region, the central Balkans, including the silicate west part of the Dinarides and the carbonate east parts of the Carpathians and Stara Planina (Balkan) Mountains. Through the northern part, which belongs to the Pannonian Basin, some of the largest European rivers (Danube, Sava and Tisa) flow. The central part is occupied by the Velika and Južna Morava river basins, which serve as a sort of connection with the Vardar River and the Mediterranean basins. According to Illies (1978), four ecoregions are present on the territory of Serbia. A recent delineation of these ecoregions is given by Paunović (2007).

Despite the numerous investigations, there are still not sufficient data regarding the diversity and distribution of the freshwater gastropods in this region. The first data about the freshwater snails in Serbia were provided by Pfeiffer (1857) and Möllendorf (1873), with recognition of two *Theodoxus* species. Many authors have given their contribution to the better knowledge of the freshwater snails in Serbia (see details in Karaman, Karaman 2007), either by studying specific groups (e.g. Hydrobiidae, see Radoman 1977) or in frames of more or less extensive malacological studies (e.g. Hesse 1929, Jaeckel *et al*. 1958, Frank *et al*. 1990). The most detailed overview is provided by Karaman, Karaman (2007).

The main aim in this work is to give a comprehensive and up-to-date review of the past and recent distribution of *Theodoxus* spp. in the central part of the Balkans (Serbia). We also try to draw more attention to the IUCN endangered taxon *T. transversalis* in this part of its range. Finally, providing the list of records is necessary for some more detailed studies such as assessment of the intraspecies and interspecies variability.

Material and Methods

The study is based on an extensive data-set, which includes the available literature and databases obtained by long-term investigations (internal data of Department of Hydroecology and Water Protection, Institute for Biological Research 'Siniša Stanković'), regular monitoring (Annual Water Quality Reports 1999-2010, 2011-2012) or from mixed sources (BAES; Simić *et al*. 2006). In addition, recent field investigations in 2010-2013 provided new data. Our four-year field campaign covered 84 rivers, streams or canals as well as 5 lakes. We collected 638 samples from 159 localities. The investigations involved the whole territory of Serbia, including the catchment areas the rivers Danube, Tisa, Sava, Kolubara, Velika Morava, Južna Morava, Zapadna Morava, Ibar, Lim, Nišava, Mlava, Pek and Timok. The benthic samples were taken by a standard hand-net (semi-quantitative technique), preserved in 70% ethanol solution or 4% formaldehyde solution and further processed in the laboratory. The identification of the gastropods was performed by using appropriate keys (Pfleger 1999, Glöer 2002). All collected materials were deposited in the collection of the Benthological Section of the Institute for Biological Research 'Siniša Stanković' in Belgrade.

The relative abundance of species was evaluated according to the scale given in Table 1.

Table 1. Scale for estimation of the relative abundance of *Theodoxus* spp. in Serbian waters.

Relative abundance	Description	Number of individuals per sample
1	present	1
2	low abundance	2-5
3	moderate abundance	6-30
5	high abundance	31-60
7	very high abundance	61-100
9	mass present	>100

Results and Discussion

Three species belonging to the genus *Theodoxus* were reported from Serbian waters. Typical habitats of these species in Serbia are large rivers in the case of *T. fluviatilis* (Fig. 1a), and smaller rivers for *T. danubialis* and *T. transversalis* (Fig. 1b).

***Theodoxus fluviatilis* (Linnaeus, 1758) – river nerite**

The distribution range of the most widespread species of *Theodoxus* covers the area of Europe from Scandinavia (Skoog 1971) to Greece and Crete Island (Schutt 1986, Bunje 2005), and from Ireland and the Iberian Peninsula (Lucey *et al*. 1992, Zettler *et al*. 2004) to the Sea of Azov Sea and the Baltic States (Anistratenko *et al*. 1999). This species is also recorded in Asia, i.e. Anatolia (Yildirim 1999) and Iran (Glöer, Pešić 2012) while its reports from Africa are doubtful (Brown 2002). According to IUCN database, it is currently regarded as invasive in the Danube River basin (Kebapçı, Van Damme 2012). The tolerance of *T. fluviatilis* to organic pollu-

Fig. 1a. Locality Golubac (Iron Gate; the Danube River): an example of typical locality of *Theodoxus fluviatilis* in Serbia

Fig. 1b. Prosek (the Nišava River): a locality with abundant populations of *Theodoxus transversalis* and *Theodoxus danubialis*

tion (Mouthon, Charvet 1999), which is recognised as one of major treats to the Danube River, facilitates its spreading. Due to the patchy distribution and phenotypic plasticity of the river nerite, a vast number of various morphs is present. Among them, the best known are probably the freshwater (*f. fluviatilis*) and brackish (*f. littoralis*) forms, which differ morphologically, ecologically, reproductively and behaviourally (Glöer 2002, Glöer, Meier-Brook 2003). Bunje (2005) showed on the basis of genetic studies that the taxonomic distinctions of these forms are insignificant, though some of them have been described as separate species. Therefore, even the common freshwater and brackish forms are most likely to be only ecomorphs of this highly plastic species (Zettler *et al.* 2004, Zettler 2008).

In general, the shell has an elongate ovoid form, with only a slightly prominent spire and usually up to 2½ whorls (protoconch 1 whorl, and teleoconch up to 1½) (Pfleger 1999, Bandel 2001). The colouring of periostracum is very variable and ranges from almost black to various brighter with darker zigzag stripes, often with triangular whitish spots (Fig. 2a). The operculum is reddish, usually with red edges. The opercular hinge has a broad (lamellar) ridge. (Fig. 2b)

The freshwater form (*T. fluviatilis*) prefers central and lower parts of larger rivers. It feeds dominantly on periphyton, forages mostly at night and requires a hard substrate (preferably rock or wood) (Bandel 2001, Glöer 2002). *T. fluviatilis* tolerates moderate organic pollution and very low oxygen contents (even below 2 mg/l) but does not endure too long periods of drought or ice (Carlsson 2000, Glöer 2002). Similarly to the majority of the European nerites, *T. fluviatilis* has biennial life cycle. Sexual maturity is reached at the age of av. 18 months. Up to 150 eggs are laid in a yellowish spherical capsule about 1 mm in diameter, which is attached to any hard substrates, including on other snails. The egg laying occurs in the warmer period (usually from mid-April to October). Normally, only one embryo develops to a miniature adult, depending on temperature (20°C – 65 days, 25°C – 30 days) (Orton, Sibly 1990).

Theodoxus danubialis (C. Pfeiffer, 1828) – Danube nerite

Theodoxus danubialis is native to the Danube River basin. Besides, there are some documented populations in northern Italy (Bodon, Giovannelli 1995). Although the species is not on the IUCN Red List, the Danube nerite is critically endangered in Germany (Jungbluth, von Knorre 2009), Austria (Reischütz, Reischütz 2007) and Czech Republic (http://mollusca.sav.sk/malacology/redlist.htm).

The shell has a short semi-ellipsoid form (more globular than in *T. fluviatilis*) and the slightly prominent spire accounts for about one third of its length (Bodon, Giovannelli 1995, Pfleger 1999). The colour pattern of the shell is predominantly with brownish or purplish zigzag stripes on a yellowish or whitish background (Fig. 3a) but in some cases brown or almost black specimens were found (Fehér *et al.* 2009). The operculum is usually paler than in *T. fluviatilis* and without a broad lamellar ridge (Fig. 3b). Two main forms, *stragulatus* and *danubialis*, are distinguished on the basis of the shell morphology, i.e. more or less conspicuous keel on body whorl is present in *stragulatus* (Glöer 2002). Some authors consider the populations with more sharp and pronounced ridges, which are found in the Sava River drainage (mainly in Croatia), as another valid form, and argue that the *stragulatus* form is a transitional between the sharp-keeled *carinatus* and non-keeled *danubialis* forms (Schutt 1988). The closer relations between these forms and their taxonomic differenti-

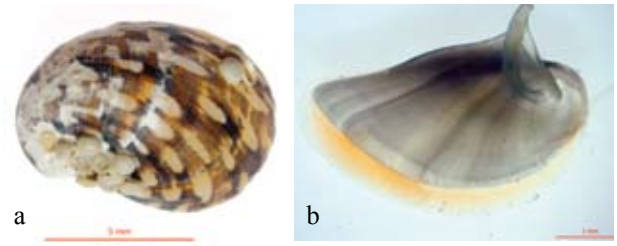

Fig. 2. *Theodoxus fluviatilis* (Golubac, the Danube River): a) shell; b) operculum

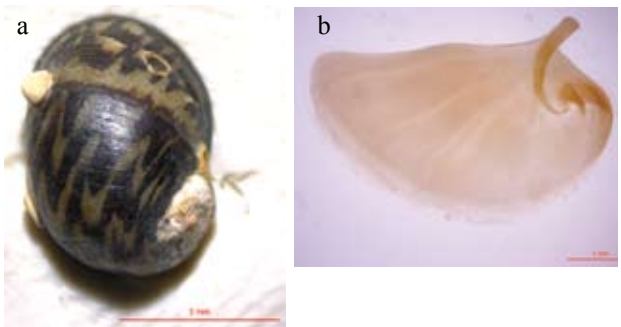

Fig. 3. *Theodoxus danubialis* (Prosek, the Nišava River): a) shell; b) operculum

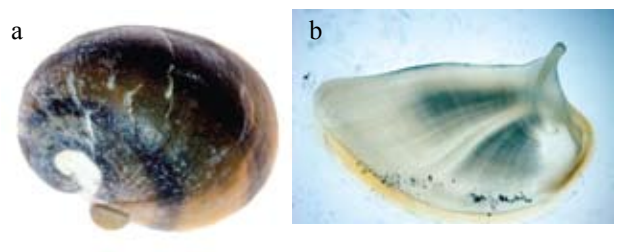

Fig. 4. *Theodoxus transversalis* (Prosek, the Nišava River); a) shell; b) operculum

ation as subspecies is questionable (Nesemann *et al*. 1997, Glöer 2002, Fehér *et al*. 2009).

It should be noted that *T. danubialis* is closely related to the extremely rare black nerite (*T. prevostianus*). The latter species is listed as critically endangered by IUCN and forms a clade native to the Pannonian basin (Bunje 2007, Fehér *et al.* 2009).

Theodoxus transversalis (C. Pfeiffer 1828) – striped nerite

The striped nerite is endemic for the Danube River basin. Once common, it is currently an endangered species according to IUCN (Sólymos, Fehér 2011), with most of the remnant populations existing in some smaller tributaries, where the water quality is still suitable.

The periostracum is grey or yellowish-grey, with three dark longitudinal or transverse bands (Fig. 4a). Rarely, the entire shell may be dark brown, black or yellowish-brown without bands. The operculum is usually reddish, with red margins, resembling the colouration of *T. fluviatilis* but the difference is the lack, similarly to *T. danubialis*, of a broad lamella on the big apophyse ridge (Fig. 4b).

T. transversalis, according to a recent phylogenetic analysis (Bunje, Lindberg 2007), forms a monotype clade that is located at the very base of the *Theodoxus* genealogy (approximately 30 million years old). Therefore, this relict has great significance in attempts to reveal the phylogeny of the whole genus.

Historical data

The first documented reports of *Theodoxus* in Serbia were published by Pfeiffer (1857) and Möllendorff (1873). *Theodoxus transversalis* was present in both reports (as *Neritina transversalis* in the Danube River near Golubac) while Möllendorff (1873) reported for the first time the presence of *T. danubialis* (*T. danubialis stragulatus* as *Neritina stragulata* from the Danube).

The presence of the most common European *Theodoxus* species (*T. fluviatilis*) was not reported in the Serbian waters until the late 20th and the beginning of the 21st centuries. The first documented findings of the river nerite in Serbia were in 1992 in the Danube River at Karataš, near Kladovo (Karaman 2001) and in 1993 in the Svrljiški Timok River (Simić 1993). Since then, it has rapidly become the dominant nerite species and, along with *Lithoglyphus naticoides* (C. Pfeiffer, 1828), the dominant gastropod species in the Danube River and some of its main tributaries (Tisa). This status was confirmed by three large international investigations of the Danube River in the period from 2001 to 2007: First Joint Danube Survey (JDS1), Aquaterra Danube Survey (ADS) and JDS2. Simić, Simić (2004) did not found *T. fluviatilis* in the investigations at the Iron Gate (conducted during 1994, 1995 and 2000) while it was present and common already in 2001 (JDS1). Therefore, basing on these data, it could be assumed that the beginning of the 21st century marked the beginning of a rapid spread of the river nerite in the Serbian Danube. Besides its tolerance to organic pollution, the species is also well adapted to the conditions of increased sedimentation, such as those present at the Iron Gate in the late 20th and the beginning of the 21st century. Another possibility is that *T. fluviatilis* has been overlooked and misidentified as *T. danubialis*, at least in some cases. The morphological similarity of these two species (*T. fluviatilis* and *T. danubialis*) could be a reason for taxonomical confusion as it was speculated in the case of the nerites in northern

Italy. Bodon, Giovannelli (1995) hypothesised that the Italian populations of *T. danubialis* represent a recent (historical) invasion of populations from the eastern tributaries of the Adriatic Sea. However, it is also possible that much older samples of *T. danubialis* in Italy had simply been overlooked or misidentified as *T. fluviatilis* (Bunje 2007).

The literature data reveal that *T. danubialis* was the most common nerite in Serbia in the past. Some of these old records are quite interesting, as is the case with Krupačko Vrelo, a karst well near the Nišava River in east Serbia. Two specimens of the Danube nerite were collected by L. Dokić in the late 19th century (deposited in the Museum of Natural History in Belgrade, see Karaman, Karaman 2007), and after that, this population was vanished. *T. danubialis*, in contrast to the results of recent investigations, was present in the Ibar River, the Svrljiški Timok River and the Crnica River. The species was also found in the Karaš canal and in the Vrujci well.

The past distribution of the rare striped nerite, similarly to that of the mentioned Danube nerite in the Danube River, is much wider. It was found at several sites along the Danube River, from Novi Sad, through the Iron Gate to the Timok River confluence. The striped nerite was also reported for some other rivers such as the Sava River and the Moravica River. The more recent reports were from the Iron Gate, where the species was assessed as common (Simić, Simić 2004). With regard to this species we should point to the specimen found in the Jelenački stream, Fruška Gora Mountain (Živić *et al*. 2000). This finding could indicate the potential presence of an isolated population of that rare snail. Furthermore, such streams could be considered as possible refugia for some rare taxa in the polluted environment of the Pannonian Plane.

Recent investigation

The recent field investigations (2010-2013) confirmed the presence of all three *Theodoxus* spp. and showed their wide distribution. The snails were found in 112 samples at 51 localities in 17 rivers and one lake, which were in the expected range of distribution of this genus in Serbia (Paunović 2007). The localities of those recent records are provided in Fig. 5. The majority of sites were located in the Danube River (16). The river nerite (*T. fluviatilis*) was present at 33 localities, the Danube nerite (*T. danubialis*) was registered at 25, and the striped nerite (*T. transversalis*) at 15 localities. At 9 localities, mixed occurrence of different *Theodoxus* spp. were found. The juvenile specimens at those sites were identified as *Theodoxus* sp. At 17 sites only one *Theodoxus* species was found; that was most often *T. fluviatilis*. The rare striped nerite species, *T. transversalis,* was found as the only *Theodoxus* species at Markovac Bridge (the Velika Morava River). On the other hand, at only five sampling sites, all three species were found: Bagrdan (the Velika Morava River), Niš (the Nišava River), Lešnica (the Jadar River), and Priboj and Prijepolje (the Lim River). However, all three species were not found together in any of the samples.

The distribution of *T. fluviatilis* covers the north part, *i.e.* the large Pannonian Rivers (the Danube River, the Tisa River and the Sava River) but it is also spreading to the south, through the larger watercourses (the Velika Morava River – Nišava River system as the main corridor). On excluding the reports from sampling sites on the tributaries (the Kolubara and the Nera Rivers) situated in proximity to the above-mentioned large rivers, some isolated findings at the rivers Jadar and Lim are noteworthy. As these were a single sample and specimen findings at localities with relatively stable populations of *T. danubialis*, they may well be accidental. The frequency of occurrence and the relative abundance of *T. fluviatilis* in *Theodoxus* samples varied during the investigated period (Figs. 6 and 7).

The Danube nerite, on the other hand, is barely present in the Danube River, absent in the Tisa River, while in the Sava River coexists with the

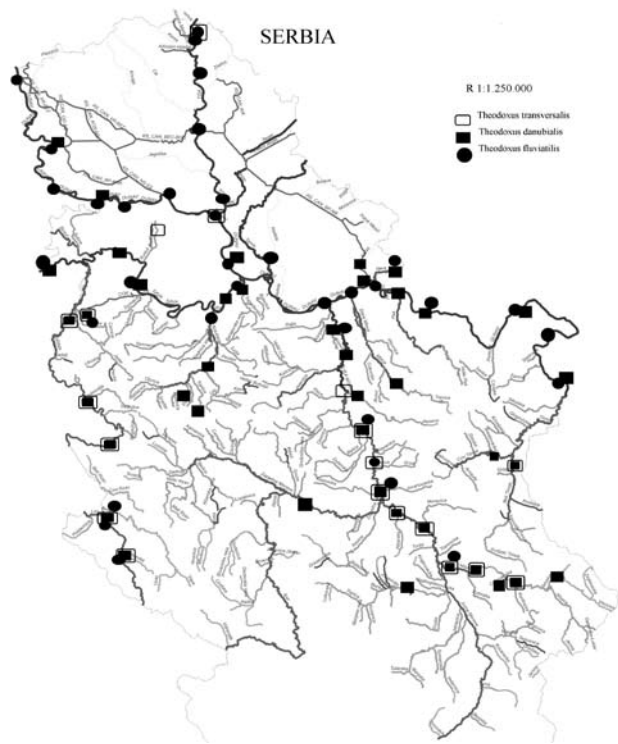

Fig. 5. Distribution of *Theodoxus* species in Serbia (the last decade)

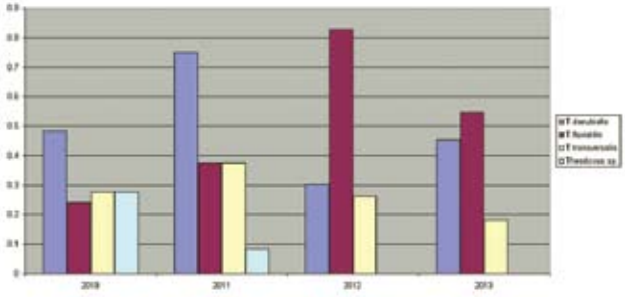

Fig. 6 .Average frequencies of *Theodoxus* taxa in positive samples (period 2010-2013)

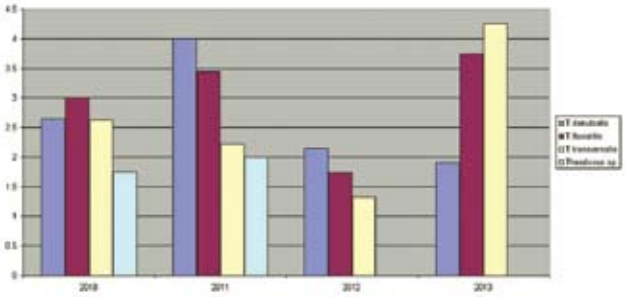

Fig. 7. Average relative abundances of *Theodoxus* taxa in positive samples (period 2010-2013)

river nerite and according to our findings, the latter species has become dominant. However, due to its relatively wide distribution in the southern, hilly and mountainous part of Serbia (Fig. 5), the Danube nerite is not considered as endangered on the national level; yet, continuous monitoring is needed. The most abundant populations were found at the rivers Drina, Lim, Velika Morava, Južna Morava, Nišava and Beli Timok. Populations with lower abundances were registered at the rivers Kolubara, Mlava, Zapadna Morava, Toplica and some other smaller watercourses. The Nera River and Ram – Banatska Palanka (Danube sites) could be singled out because of the presence of moderately abundant co-occurrence of *T. danubialis* and *T. fluviatilis*. The Ram – Banatska Palanka site is characterised by diversity of habitats, unusual for this part of the Danube River (Paunović *et al.* 2005) and by a rich gastropod community. The Nera River is a mountainous river with gravel substrate and relatively unpolluted water. The case of the Ibar River, a relatively large river flowing across hilly region of central Serbia, could also be mentioned. With regard to the structure of the habitats in comparison with some similar watercourses in the region (e.g., the Zapadna Morava and Nišava Rivers), the Ibar River fulfills the primary conditions for maintaining communities of grazing prosobranch snails. The riverbed includes a lot of hard substrates and plenty periphyton, and the water is well oxygenated. Yet, according to our field investigations, the gastropod community there is composed only of *Ancylus fluviatilis* Müller, 1774 and *Amphimelania holandrii* (C. Pfeiffer, 1828) (unpublished data). The absence of *Theodoxus* species in the Ibar River is intriguing and could be related to the intense anthropogenic pressures in the near past, mostly related to the intensive mining and resulting heavy metal pollution (details in Miladinović *et al*. 2012).

The striped nerite, *T. transversalis,* was found in the Danube River in only one sample (Stari Slankamen, 2012) and was assessed as low abundant. This finding is of special interest considering that this species was reported as extinct in the upper part of the Danube River (Frank 1984, Frank *et al*. 1990), and extremely rare in the middle and lower parts (Cioboiu 2010). In addition, it was not recorded during the large international investigations of the entire Danube River course (JDS1, ADS and JDS2). Pavlova *et al.* (2013) reported recently the presence of this taxon on two islands in the lower Danube River and supposed that such unpolluted river islands might be its preferred habitat. As this particular site (Stari Slankamen) is located just upstream of the Tisa mouth and is relatively well preserved, with a few river islands nearby, it could be considered as one of the few remaining refugia for *T. transversalis* in this part of the Danube River. There were some rare findings in the Tisa River (site Martonoš) and Crni Timok River (site Zaječar). Therefore, the main refugia for the striped nerite were found to be the Drina River – Lim River and Velika Morava River – Južna Morava River – Nišava River systems, especially the last one. The most representative locality is Prosek, at the Nišava River (downstream of the Sićevo gorge), in which mass abundance of the striped nerite population was assessed (sample taken during 2013). While at the mentioned locality two *Theodoxus* species (*T. transversalis* and *T. danubialis*) coexist, only the species *Theodoxus transversalis* was found at the Markovac Bridge site in the Velika Morava River. The species was assessed as moderately abundant during the investigated period.

In conclusion, the data about the distribution and ecological preferences of the species are dynamic variables that require regular monitoring. The increased pollution and degradation of habitats results in the overall freshwater diversity loss. The most resistant and tolerable species (*T. fluviatilis*), expands its range from the large rivers of the Pannonian plain to mountainous watercourses, suppressing and replacing the natives. As this mountainous part of Serbia acts as the main refugia for the other two spe-

cies, among which is *T. transversalis* listed as endangered by IUCN, the range expansion of *T. fluviatilis* surely raises some concerns. However, our investigation also revealed the possibility of an increased adaptability of the native species. In support of this it may be noted that the most abundant populations of *T. transversalis* were found at the Velika Morava River –Južna Morava River – Nišava River system, which is under an intense anthropogenic influence. According to the recent ecological status assessments (Marković *et al*. 2011, Kolarević *et al.* 2012), the Velika Morava River was a moderately polluted river (with increased organic pollution). However, unless the ecological state of these rivers improves, a possibility of extinction of these *Theodoxus* populations may arise. Therefore, as mentioned above, regular monitoring of these rivers, as well as of the entire Serbian surface-water network, is crucial for timely prediction of the population health and for conservation of rare species.

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