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Research Article

Invasion on the doorstep: will the Carpathians remain free from the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817)?

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Abstract

The success of biological invasions relies, among other factors, on the abiotic environment. The presence or absence of an invasive alien species in its non-native range may therefore be helpful in understanding the factors facilitating or hampering its invasion. The aim of our study was to determine whether the Carpathians are free from the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817), a successful freshwater invader in Europe and locally in Africa. We hypothesised that local factors, mostly climate (i.e. water temperature), have an impact on this species, limiting its spread. However, atypical local habitats with suitable abiotic conditions—in particular artificial reservoirs—might be hubs for *F. limosus*. The study was conducted in 2018 in Carpathian waters. We found that despite being present in plain areas adjacent to the Carpathians for decades, *F. limosus* does not ingress deeper into this mountain range. The exceptions are two dam reservoirs and the lower reaches of some of their tributaries, close to their inflows. The Carpathians are climatically distinct from the surrounding areas, which is also reflected in mean water temperature – *ca.* 1.5 °C lower than in adjacent lowland areas. Thus, we suggest that relatively severe climate may be the main reason behind the limited range of *F. limosus* in mountains. However, other factors, like current velocity, substrate type, or slope, may contribute to the absence of the species in the studied area. Dam reservoirs providing warmer aquatic habitats and lentic environment may facilitate its invasion related to climate warming.

Key words: biological invasions, climate change, mountain ecosystem, Cambaridae

Introduction

The recent high volume of international transport leads to enormously fast species dislocation around the World. On a global scale, the number of dislocated species has reached approx. 45,000, and 17,000 of them have successfully colonised non-native ranges (Seebens et al. 2017). Becoming invasive species, they lead to major socio-economic and environmental losses (Gurevitch and Padilla 2004; Clavero and García-Berthou 2005; Pimentel et al. 2005), including in aquatic ecosystems (Keller et al. 2018). The success of the biological invasion depends on a complex set of factors which may be divided in two main categories: 1) species biology and

2) ecosystem susceptibility (Barney and Whitlow 2008). Understanding the factors driving the success of invasive alien species is crucial to both predicting and reducing the threats posed by them (Yonvitner et al. 2020). Furthermore, defining the features of areas free from invaders is important in the context of local biodiversity conservation.

Areas naturally resistant to given species invasion may become more susceptible to invasion when altered by human activity (Marvier et al. 2004). In riverine ecosystems, major alterations are dam reservoirs which turn lotic habitats into lentic ones. Dam reservoirs, as man-made habitats, are more susceptible to colonisation by alien species (Strayer and Dudgeon 2010; Wilk-Woźniak and Najberek 2013). Besides hydromorphological changes, dam reservoirs may provide optimal temperature conditions in relatively cold areas. This is especially important in mountains, where shallow streams and rivers may reach temperatures near 0 °C during the winter, whereas deep dam reservoirs still offer at least approx. 4 °C (Mihu-Pintilie et al. 2014).

Invasions are also related to invading species' colonisation potential. In freshwater ecosystems, some of the most successful invaders are crayfish species, which are among the largest aquatic invertebrates (Twardochleb et al. 2013). It is accepted that more than 30 species of crayfish have been translocated into new areas (Gherardi 2010) due to commercial enterprises as a food source or due to the pet trade (Padilla and Williams 2004; Chucholl and Wendler 2017; Patoka et al. 2018; Yonvitner et al. 2020). A relatively high resistance to dehydration improves their ability to disperse among waterbodies, for example in fishery equipment (Kouba et al. 2016). Thus, some of them are considered to be highly invasive organisms worldwide, and their negative impact on local diversity, including indigenous crayfish, is well documented (Twardochleb et al. 2013). Both in native ranges and the areas of their invasion, they often affect biomass and energy flow in food webs (Pacioglu et al. 2020). North American crayfish are also carriers of crayfish plague, *Aphanomyces astacii*, causing mass mortalities among native European crayfish (Mrugała et al. 2017; Putra et al. 2018).

One of the most successful species of crayfish invader in Europe is the spiny cheek crayfish *Faxonius limosus* (Rafinesque, 1817). This North American cambarid species is native to the Districts of Columbia, Pennsylvania, Maryland, New Jersey, New York, Virginia and West Virginia (Hamr 2002). The introduction into Europe started in 1890, with *ca.* 100 individuals released in experimental breeding ponds in Berneauchen, Germany (now Baranówko in north-western Poland; Śmietana 2011). Next, the species was transferred to other regions in Poland, Germany, Austria and France (Holdich 2002). Recent genetic analysis supports the hypothesis that the successful introduction in Europe happened only once, and thus this relatively small number of individuals became ancestors of the entire European (meta)population of this species (Filipová et al. 2011). It was noted that invasion success in this species may result from higher fecundity of females colonising new areas (Pârvulescu et al. 2015), but crayfish plague transmission and successful competition is also important (Lele and Pârvulescu 2017; Pârvulescu et al. 2012). Despite being widely distributed across Europe, there are some observations of uneven occurrence of *F. limosus*. It has been demonstrated that mountains are less invaded than lowlands and lower uplands by this species (Kouba et al. 2014). This is also true for the Carpathians, a region with a distinctly colder climate than the adjacent areas (Hess 1965; Kottek et al. 2006). Besides the climate, the montane or submontane character of the watercourses may also hamper the species' invasion (Petrusek et al. 2006). In this mountain range only records near the edge of the region have been known to date (Pârvulescu et al. 2012; Kouba et al. 2014; Lele and Pârvulescu 2017), with evidence for negative impact on native crayfish species. On the other hand, if global warming progresses further - as the predictions demonstrate (IPPC 2018) – we can also expect an increase in water temperature in mountain rivers. As a result, further invasion of *F. limosus* into mountain rivers by populations living at the edge of the region is possible. However, other factors, like current velocity, substrate type, etc. might negatively affect the invasion.

The purpose of our study was to determine whether rivers of the Carpathians are free from *F. limosus* (Hamr 2002). The second aim was to investigate whether the species is present in large Carpathian dam reservoirs, which feature lentic conditions and warmer water than the prevalent natural streams.

Materials and methods

Study area

We conducted studies at 41 sites located in nine rivers in the Western Carpathians within the Polish borders. All nine (including the Raba river) of the studied streams lie in the Vistula river drainage area and, with the exception of two of them (rivers Ropa and Jasiołka), all drain both the Carpathian and Subcarpathian areas. Additionally, as *F. limosus* was known only from dam reservoirs, we investigated five dam reservoirs in the Carpathians and one adjacent to the northern Carpathian border (see map, Figure 1). We defined the borders of the Carpathians according to Kondracki (2000). The reference site of the field inventory was the Dobczyce dam reservoir, where the presence of *F. limosus* was confirmed several times (A. Amirowicz 2018, *pers. comm.*). For the field inventory in rivers, we looked for localities similar in terms of distance from the source of the river, altitude and drainage area to the Raba river in the location where it has been altered into the Dobczyce reservoir (49.876671°N; 20.083284°E, Figure 1).

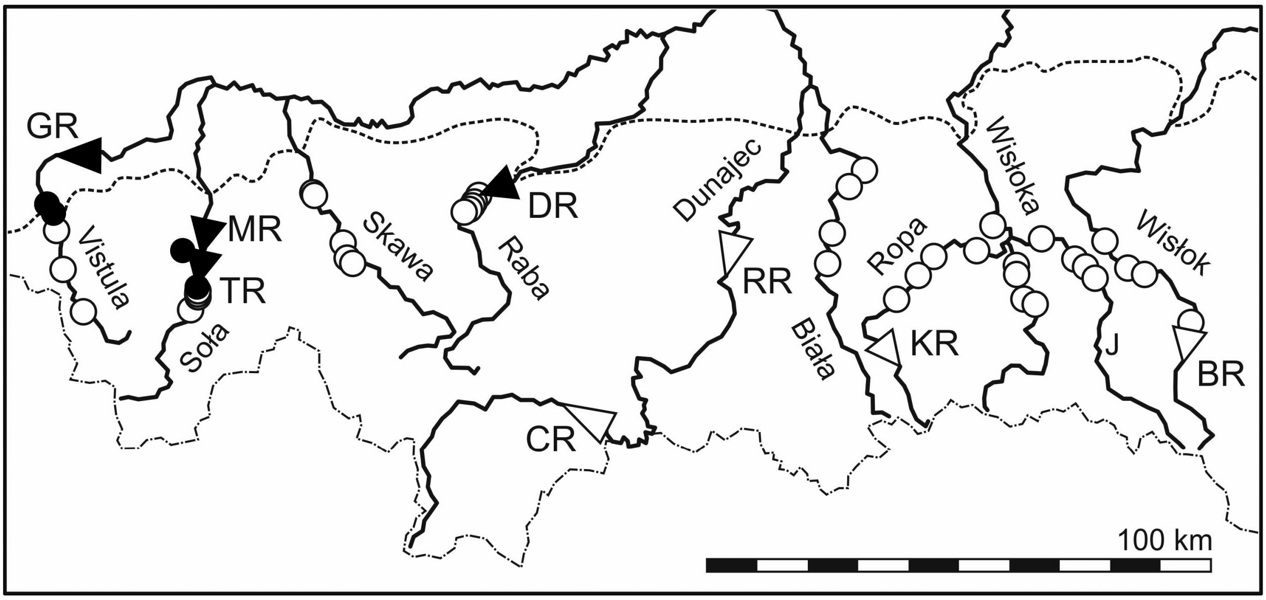

Figure 1. Results of the inventory of *Faxonius limosus* in the main rivers (circles) and reservoirs (triangles) in the Polish part of the Western Carpathians in 2018: J – Jasiołka river, BR – Besko reservoir, CR – Czorsztyn reservoir, DR – Dobczyce reservoir, GR – Goczałkowice reservoir, KR – Klimkówka reservoir, RR – Rożnów reservoir, TR – Tresna reservoir and MB – Międzybrodzkie reservoir. The dashed line shows the northern border of the Carpathians according to Kondracki (2000). Symbols filled with black indicate the presence of the species. *Faxonius limosus* was also detected in two tributaries of the Tresna reservoir, not shown in the map due to picture clarity (see Supplementary Table S1 for details).

Field inventory of crayfish

Within each of the selected river sections, we chose three to five 200–420-m long sampling sites for the crayfish inventory (Supplementary material Table S1). Moreover, we also surveyed the Raba river at five sites located up to about 3 km upstream from its inflow to the Dobczyce reservoir. During the summer of 2018 we searched for crayfish along parts of the rivers where the bottom was clearly visible (visual encounter survey), according to the method described by several authors (Reynolds et al. 2010; Marzec and Okrągła 2018; Bonk et al. 2019). In all the sites we conducted surveys at least several days after rainfall to avoid elevated water level and increased turbidity, and for safety requirements. Apart from the rivers, we also surveyed dam (artificial) reservoirs. In each dam reservoir we conducted at least one 30-minute night check in shallow shore habitats after sunset. The two largest, the Rożnów and the Czorsztyn reservoirs, were checked twice. Due to the already known presence of the species in the Dobczyce reservoir, we also checked eleven 200-m sites on all its six tributaries with the same method as the other river sections. In the Tresna reservoir, after confirmation of *F. limosus* presence, we additionally investigated three sites in two tributaries (Table S1). According to the other observations from stagnant waterbodies (Bonk et al. 2019), the visual encounter survey was assumed to be a satisfactory method for sampling mountain reservoirs.

Water temperature

To describe the water temperature in Carpathian watercourses and adjacent lowlands, we used data of mean temperatures of the Vistula and its tributaries in the Carpathians and the area adjacent to the Carpathians (Data of the Chief Inspectorate of Environmental Protection, referred hereafter as CIEP). In total, we collected temperature data from nine rivers and 59 measuring points. Data were collected from 2008 to 2017. Temperature data were also available for two dam-reservoirs from the period 2011 to 2016. We compared temperatures between lowlands and mountains using the GLM procedure performed in R 3.5.1 (R Core Team 2018) with gamma error distribution.

Results

Field inventory of crayfish

In the range of the Carpathian Mountains we detected *Faxionus limosus* only in one river resembling the Raba river (the Soła river); in this case we found crayfish near the inflow of the dam reservoir (Table S1, Figure 1). At the site in the Vistula river located close to the Carpathian borders, but outside their boundary, we found only one exuvium of a juvenile individual. We also confirmed the presence of *F. limosus* in three reservoirs: one adjacent to the Carpathians (the Goczałkowice reservoir), and two in the Carpathians (the Tresna reservoir and the Dobczyce reservoir, Table S1, Figure 1). Moreover, individuals of *F. limosus* were present in two small tributaries (the Żylica and Łękawka brooks) of a Carpathian reservoir (the Tresna reservoir), upstream from their inflows into the reservoir. In six tributaries of the Dobczyce reservoir (border of the range of the Carpathians), including the Raba river above the reservoir, we did not find any specimens of *F. limosus*. In other studied rivers the species was also not recorded.

Water temperature

Sites located within the Carpathians were on average colder than sites outside the mountain range. The difference between these two categories was on average 1.51 °C ($p < 0.05$, Table S2). The temperatures differed among the rivers, although the interaction between particular rivers and the location of measuring points was not significant, showing that the temperature differences are highly related to the region (Carpathians *vs.* Subcarpathians). For two dam reservoirs for which data were available and where the inventory for crayfish was conducted, the temperatures were higher by *ca.* 8 °C for the Sieniawa-Besko reservoir compared to the montane sections of Carpathian rivers, and by *ca.* 6 °C for the Goczałkowice reservoir compared to lowland sections of the studied rivers.

Discussion

Faxonius limosus is widespread in Europe (Kouba et al. 2014; Puky and Schád 2006). It is relatively evenly distributed in lowlands near the northern Carpathian border (Kouba et al. 2014; Śmietana 2011; M. Bonk and K. Kukuła 2019, *unpublished data*) and is also present in lowlands southward from the Carpathians (Pârvulescu et al. 2009, 2012, 2015; Lele and Pârvulescu 2017). Despite being found at the margins of the Carpathians, to our best knowledge it does not penetrate submontane/montane river courses within the region, except the Dobczyce reservoir, the Tresna reservoir environs, and in the Międzybrodzie Reservoir (Śmietana et al. 2018). Our findings are consistent with the available species distribution maps for Europe (Kouba et al. 2014) and for Poland (Śmietana 2011). In addition, other contributions concerning crayfish in the area do not confirm *F. limosus* presence therein (Bonk et al. 2014; Bylak and Kukuła 2015). Moreover, the species was also not detected in the Carpathians during the national monitoring of the noble crayfish *Astacus astacus* (Linnaeus, 1758) (GIOŚ 2014, 2018) based on baited traps and a visual encounter survey method (Bonk et al. 2019), and during citizens' crayfish data collection (the data from 20 observers collected from 2013 to 2019 showed only *A. astacus* presence within the Polish part of the Carpathians; M. Bonk 2019, *unpublished data*).

The species has been known from plain landscape adjacent to the Carpathians (the Kotlina Oświęcimska basin, Vistula drainage) for at least five decades (Śmietana 2011); in addition, in the lowlands of Romania near the Carpathians it has been known for at least several years (Pârvulescu et al. 2009). Notably, the maximum yearly spreading rate is estimated at up to 24 km per year (Hudina et al. 2009). Pârvulescu et al. (2012) recorded 14 km distances of spreading of the species. Distribution maps for Poland and Europe from the last decade (Śmietana 2011; Kouba et al. 2014; Śmietana et al. 2018) suggest *ca.* 11 km per year on average (according to the time of the introduction and Euclidean distance from the site of the first stocking to the westernmost European sites in France). Thus, the Carpathians should already have been colonised by *F. limosus,* whereas we detected the species only in three dam reservoirs on the edge of the Carpathians, and only exceptionally found it in montane or submontane watercourses feeding one of these reservoirs. This leads to the question: what are the factors affecting the invasion in this mountain range?

Faxonius limosus is considered to prefer a mild climate. Its breeding success is related to relatively warm temperatures (Dubé and Portelance 1992). Thus, one of the possible explanations of *F. limosus* absence in the studied area may lie in the water temperature. The Carpathians are climatically distinct from adjacent areas in Central Europe. The annual mean temperature decreases with increasing altitude by an average rate of

0.5 °C per every 100 m of elevation (Hess 1965). This results in vertical climatic zones in the mountain range. Climate conditions are also seen in water temperatures in rivers, which are typically lower in their Carpathian reaches of the studied rivers than in the lowland ones – as the monitoring data from the last decade in Poland show. One may argue that extreme temperatures may be more important, however, means reflect also the length of a cold season. In our study both in Subcarpathian and Carpathian reaches extremes reaching 0 °C have occurred during the last decade (CIEP). Additionally, in *F. limosus* individuals recovery after freezing down to −15 °C for 40 minutes was observed (J. Dołęga, M. Bonk *unpublished data*). Thus, an invasive species potentially moving upstream in a Carpathian water course needs to undergo generally more severe climatic conditions than in the surrounding areas, for instance "snow climate, fully humid with warm summer" (Dfb type; Kottek et al. 2006). Notably, the main area of the geographical distribution of *F. limosus* in Europe overlaps with milder "warm temperate climate, fully humid with warm summer" (Cfb type; Kottek et al. 2006), and the spreading was much more successful into the milder climate of Western Europe than the spreading into the more severe eastern part of the continent. According to the published data, the spreading speed of this crayfish is *ca.* 1.5 times higher westwards than eastwards (Kouba et al. 2014). *Faxonius limosus* does not exceed the lower parts of the temperate warm zone (defined by Hess 1965) in the Carpathians, and even there it occurs only occasionally. Thus, the distinctly lower average temperature, including water temperature, may be an important factor explaining the absence of the species in the considered part of the Carpathians.

In the studied area, *F. limosus* reaches an altitude of 358 m a.s.l. (in the Żylica brook; Table S1), which is much lower than records from some other localities from European mountain ranges. According to the map presenting data from the Swiss Alps, *F. limosus* inhabits sites there up to 889 m a.s.l. (Hefti and Stucki 2006). The highest occupied site is the Sihlsee reservoir, followed by two alpine lakes—Lake Brienz and Lake Thun—at 564 and 558 m a.s.l., respectively. This seems to be contrary to our findings. However, the temperatures of the main rivers therein (the Aare and the Rhine rivers) are closer to those obtained recently for the drainage of the upper course of the Vistula river and non-Carpathian parts of its tributaries (Uehlinger et al. 2009, CIEP data), thus resembling the water temperatures in the Subcarpathian lowlands rather than in the Carpathians, even at lower altitudes. Also, the temperate warm zone (as defined by Hess 1965), which is hardly colonised by *F. limosus* in the Carpathians (only within or nearby dam reservoirs), in the Alps starts at higher altitudes (Hess 1965), suggesting the optimal thermal condition for this species in highly located sites. Moreover, the Aare river seems to be incomparable with the studied Carpathian rivers as it is several times larger in terms of distance from the source and the catchment area. The Aare river downstream from Lake Biel at 429 m a.s.l is the only riverine area for the common occurrence of *F. limosus* in Switzerland (Hefti and Stucki 2006), whereas the majority of records from that area (the Swiss Plateau) originate from lakes at considerably lower altitudes, below 500 m a.s.l. Also, Beran and Petrusek (2006) found this species in the Lipno Reservoir (726 m a.s.l.), far from the next downstream lowland site in the Vltava River at České Budějovice (*ca.* 380 m a.s.l.). The climate hypothesis is also consistent with the presence of *F. limosus* only within dam reservoirs in the area of our study. According to data from Carpathian rivers and reservoirs, the mean annual temperature for reservoirs may exceed the temperatures in rivers by about 8 °C (CIEP). Studies from the Ropa river and Klimkówka reservoir showed that the reservoir cools the water in the river downstream in summer but increases its temperatures in winter (Wiejaczka 2011). It is also worth noting that the edge of the *F. limosus* range in north-eastern Central Europe, with a relatively severe climate (Dfb type; Kottek et al. 2006), overlaps spatially with glacial lakelands (Kouba et al. 2014; Śmietana 2011; Aklehnovich and Razlutskij 2013). Also, within the native range of the species, ingression into the relatively severe Dfb climate type (Kottek et al. 2006) overlaps with the lakelands of New York State (Hamr 2002). Dam reservoirs, as stagnant waterbodies, may thus support the occurrence of the species in mountains by providing suitable temperature conditions, supporting the idea that climate is a major factor limiting *F. limosus* dispersion in the mountains.

The recent climate of the Carpathians may hamper *F. limosus* invasion. However, compared to the preindustrial level, global temperature has increased by 1.5 °C, and an increase of 1.4 to 4.9 °C is predicted within the next 100 years (Karl and Trenberth 2003; Easterling and Wehner 2009; IPPC 2018). Also, the temperature of water ecosystems is rising, as observed in the Dobczyce reservoir, where an increase rate of 0.75 °C has been observed for a decade (Amirowicz 2013). If climate is a major obstacle for *F. limosus* to colonise the Carpathians, we cannot exclude further colonisation there independently of dam reservoirs, given that montane areas are considered to be highly prone to climate warming (Pepin et al. 2015). This global process will cause shifts in the vertical pattern of the organisms' distribution, which has also been noted in the Carpathians (Kaczka et al. 2015). As predicted, some warm water invasive crayfish may increase their range in Europe (Capinha et al. 2012) northwards as the climate increasingly warms. Also, most probably, *F. limosus,* avoiding cooler upland streams, may eventually colonise higher elevated regions.

Despite the fact that climate seems to be a one of the factors limiting the colonisation abilities of *F. limosus* in Europe, other factors should also negatively affect the species therein. The Carpathian river systems are dominated by small headwater streams with steep channels and a cobble bottom substrate, often dislocated during flood events. To the contrary, lowland watercourses near the Carpathians colonised by the species have mostly sandy bottoms (authors' own observations). This may be an additional factor hampering colonisation, as streams with the occurrence of bottom substrate dislocation events are considered to be a suboptimal habitat for *F. limosus* (Hamr 2002 and Peay and Füreder 2011). In our study area, only Carpathians watercourses colonised by this species were, besides the small distances to reservoir, located within a relatively plane region of the Żywiec Basin. A similar explanation was also suggested for another North American crayfish, the signal crayfish *Pacifastacus leniusculus* (Dana, 1852), which is less common in high gradient streams in the upland landscape of California (Light 2003). Notably, the abundance of *P. leniusculus* in that area was also positively related with decreasing distance to artificial reservoirs. Subcarpathian watercourses colonised by *F. limosus* are located in plane or low upland landscapes providing less step slopes. Again, both climate and landscape-connected factors are mitigated by the stagnant water of dam reservoirs, and thus these man-made habitats may act as hubs for survival and potential upward spreading into Carpathians rivers.

Further studies on more variables, like current velocity, hydromorphology, water chemistry, biotic elements, and variables other than climatic variables, are needed for a better understanding of the absence of *F. limosus* in the Carpathians. This requires sampling from a wider range, including the presence sites near this mountain range. The 41 sites investigated in our study can be used in future for the monitoring of potential colonisation of Carpathian rivers by other invasive crayfish. Assuming the limited spreading of *F. limosus* in the Carpathians (whatever the limiting factors are), due to the potential difficulties in the colonisation of such mountainous regions, such areas create opportunities for preserving indigenous crayfish species. In the Western Carpathians this mostly concerns *A. astacus*, which was the only crayfish species observed during our survey in the main Carpathian rivers (M. Bonk *unpublished data*), as also supported by citizens' data and national monitoring. Other parts of the Carpathians may also be refuge for native stone crayfish *Austropotamobius torrentium* (von Paula Schrank, 1803), and the recently described *Austropotamobius biharensis* Pârvulescu, 2019 (Pârvulescu 2019). On the other hand, reservoirs probably create more optimal conditions for *F. limosus* and facilitate the spreading of the crayfish itself or their diseases, according to the stepping stones population model (Havel et al. 2005). Therefore, preserving the natural conditions of montane rivers should be considered as one of the ways of reducing *F. limosus'* impact on *A. astacus* in the Carpathians. The Carpathian rivers and streams may provide "ark sites" (cf. Peay and Füreder 2011) for the conservation of native and endangered European crayfish. Unfortunately, other invading Europe crayfish species may not be susceptible to the severe Carpathian conditions. This may be especially true for *P. leniusculus,* with closer to indigenous crayfish species ecology (Chucholl 2016). Nonetheless, stopping the invasion of at least one important invader makes this mountain range of special conservation value in contrast to the lowlands nearby.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Sites controlled in Carpathian rivers and dam-reservoirs with *Faxonius limosus* occurrence (1) and absence (0) data.

Table S2. Water temperatures in Carpathian and Subcarpathian rivers in relation to localisation (Carpathians *vs*. lowlands).

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