

Beaver slides provide reproduction habitat for the endangered thick-shelled river mussel (*Unio crassus*) in modified streams

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Abstract – Freshwater mussels are among the most threatened animal groups globally, with many species declining due to habitat degradation and lack of recruitment. The *Unio crassus* complex, like other unionids, depends on host fish for larval development, but requires access to shallow riverbanks where females release their glochidia larvae. This study describes beaver slides, which are sloped riverbank paths created by *Castor fiber*, as a spawning habitat for *U. crassus* in structurally modified stream systems. Mussel densities were surveyed across 159 quadrats placed directly at and near beaver slides in four streams in Bavaria, Germany. During the period of larval release, most mussels (80%) were found within 0.5 meters of the river bank, with peak densities occurring in direct vicinity to the beaver slides. These findings suggest that beaver slides can locally provide key habitats at least for *U. crassus* reproduction in the form of shallow near-bank areas at beaver slides, especially in highly structurally degraded systems such as regulated or channelized streams. While the ecological impact of beavers on mussels seems to be controversial and species-specific, our study supports that beaver activity can also create beneficial microhabitats for certain mussel species.

Keywords: Freshwater mussels / *Castor fiber* / spurting behavior / microhabitat / reproduction

1 Introduction

Freshwater mussels are among the most threatened animal groups globally, with dramatic declines in both species richness and population sizes documented across continents (Bogan, 1993; Strayer *et al.*, 2004; Lopes-Lima *et al.*, 2018; Aldridge *et al.*, 2023b; Lopes-Lima *et al.*, 2023). In Europe, nearly half of all assessed native freshwater mussel species are threatened, and similarly alarming trends are seen elsewhere, *e.g.*, with over 42% imperiled or extinct species in North America, underscoring a global conservation crisis for this group (Lopes-Lima *et al.*, 2017; Lopes-Lima *et al.*, 2018; Aldridge *et al.*, 2023b). The primary drivers of these declines include habitat degradation (especially from damming and channelization), pollution, increasing functional interactions with invasive alien species, altered hydrology, and the loss of suitable host fish populations essential for their reproduction (Lydeard *et al.*, 2004; Stoeckl *et al.*, 2015; Lopes-Lima *et al.*, 2017; Geist *et al.*, 2025), often in the context of climate change (Cushway *et al.*, 2025).

Unionid mussels, including the *Unio crassus* complex, have a particularly complex life cycle. After internal fertilization, females release larvae (glochidia) that must

attach to specific host fish to complete their development, making mussel recruitment highly dependent on the presence and density of suitable fish hosts. Many unionids have evolved specialized behaviors and morphological adaptations to increase the likelihood of their larvae encountering host fish such as lures, mimicry, or active behaviors to attract or interact with potential hosts (*e.g.*, Zanatta and Murphy, 2006; Barnhart *et al.*, 2008; Aldridge *et al.*, 2023a). The *U. crassus* complex, *e.g.*, exhibits a unique reproductive strategy: during the spring breeding season, females move towards riverbanks and actively “spurt” water jets containing glochidia into the stream, sometimes even anchoring themselves at the water’s edge and raising their posterior above the waterline (Vicentini, 2005; Aldridge *et al.*, 2023a). This spurting behavior is thought to attract host fish by disturbing the water surface, thereby increasing the chances of successful larval attachment (Aldridge *et al.*, 2023a). Such specialized reproductive habits may also render the species particularly vulnerable to changes in river margin structure and bank stability. Mussels of the *U. crassus* complex are typically found in streams with moderate to higher flow velocities and coarser substrates, but juveniles often occur in areas with low shear stress, as high currents can be detrimental (Zajac and Zajac, 2011; Stoeckl and Geist, 2016; Zajac *et al.*, 2018). These mussels also tend to inhabit sites with higher amounts of organic matter and fine sediments (Denic *et al.*, 2014).

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Despite its high conservation status in the European Union, many suitable habitats of *U. crassus* remain severely degraded (e.g., Stoeckl *et al.*, 2020; Dobler *et al.*, 2024), partly due to the fact that a significant portion of these habitats are either not protected at all or only fall under low protection categories (Dobler *et al.*, 2019). The legal protection of the thick-shelled river mussel currently only refers to one single species, *U. crassus*, even though recent work proposes the existence of several distinct genetic units within an *U. crassus* complex from which the “nanus” form occurs throughout the study region (Egg *et al.*, 2025; Lopes-Lima *et al.*, 2024).

The European Beaver (*Castor fiber*) was once widespread across Europe but became extinct in most European waters by the 19th century due to overhunting and habitat destruction (Halley *et al.*, 2021). However, extensive reintroduction and conservation programs initiated from the 1920s onward have enabled the species to recover and rapidly expand its range, with beavers now re-established in most of the European countries and continuing to expand their range (Nolet and Rosell, 1998). *C. fiber* is well-recognized as ecosystem engineer, profoundly altering freshwater habitats and aquatic fauna through dam-building and riverbanks modification (Majerova *et al.*, 2015; Neumayer *et al.*, 2020; Bylak and Kukula, 2022; Bylak *et al.*, 2024). Beaver dams may serve as beneficial habitats for *U. crassus* by providing flow refugia during periods of high near-bed shear stress, creating more suitable substrates composed of gravel and fine sediments, increasing seston availability, and facilitating the colonization of new areas by host fish (Bylak *et al.*, 2020). Moreover, even non-damming beaver structures have been shown to increase fish species richness and densities (Pander *et al.*, 2025), which could directly benefit mussels dependent on host fish. Despite these potential advantages, beaver reintroductions remain controversial in species conservation (e.g., Kemp *et al.*, 2012; Grudzinski *et al.*, 2022). While many positive ecological effects have been documented, beaver activities may also negatively affect certain sensitive species under specific local conditions (Rudzite, 2005; Schwarzer *et al.*, 2025). However, such concerns are often based on single populations or particular habitat types (Kemp *et al.*, 2012).

In addition to dam construction, beavers frequently create “beaver slides”, sloped paths used to access the water, which can significantly modify riverbank morphology, especially in degraded or channelized streams. These structures can increase both riparian and in-stream habitat heterogeneity, promote the deposition of fine sediments, and form microhabitats along river margins. Given the *U. crassus* complex's reliance on near-bank habitats, not only during reproduction but also throughout the year due to excessive shear stress in mid-channel areas, it is plausible that beaver slides may potentially provide suitable microhabitats such as shallow, low-flow zones with fine sediments along river margins for mussel spawning and persistence, particularly in channelized streams where natural bank structures have been lost or degraded. The intersection between beaver ecosystem engineering and mussel reproductive ecology thus represents a potentially important, but yet understudied opportunity for advancing freshwater mussel conservation in human-impacted landscapes.

In this study, we examined whether the *U. crassus* complex utilizes beaver slides as spawning habitat during its

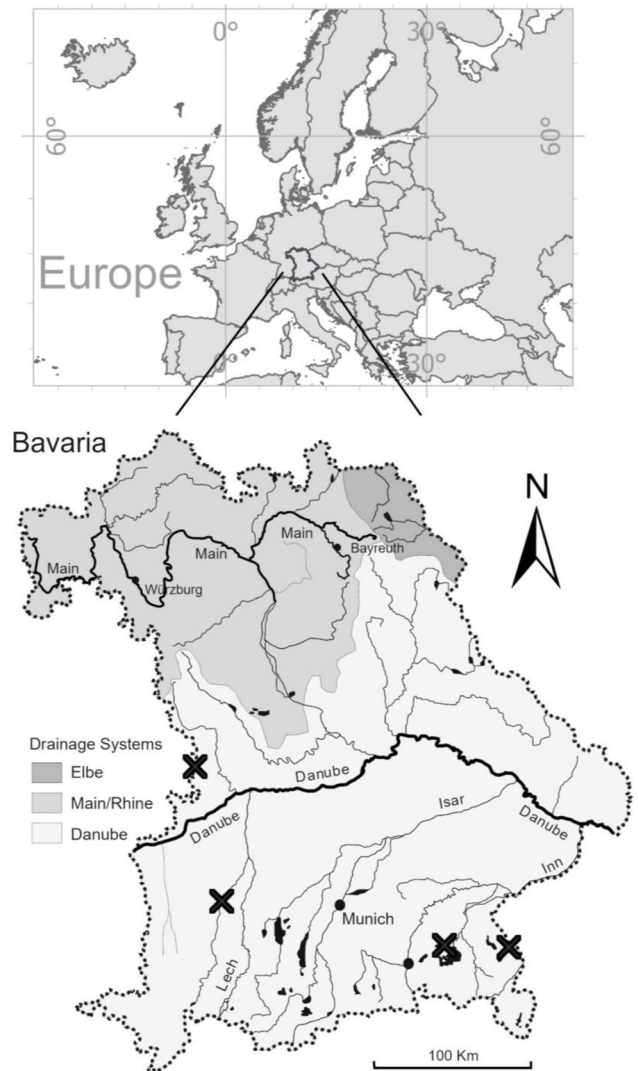


Fig. 1. Location of the study area including the four sampled streams (black crosses) in the state of Bavaria, Germany.

reproductive season. Specifically, we compared mussel densities directly at beaver slides and at set distances upstream and downstream of these features across different streams.

We hypothesized that mussel density would be higher at beaver slides than in surrounding areas, indicating that the sloped paths may provide more suitable conditions for the *U. crassus* complex to crawl onto the riverbanks for reproduction.

2 Materials and methods

2.1 Study location and design

In spring 2025, during the reproductive season, we surveyed the abundance of the *U. crassus* complex in and around beaver slides across four streams known to support populations of both beavers and *U. crassus* (Fig. 1). In each stream, we selected two to three beaver slides for sampling and compared mussel densities at the slide itself with areas located two and four meters upstream (us) and downstream (ds). At each of these five positions, we arranged three 50 × 50 cm

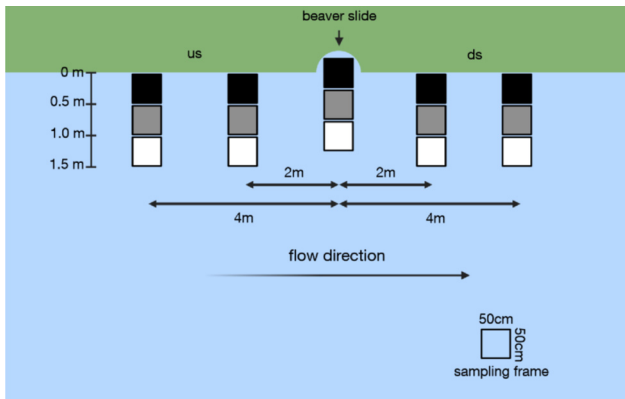


Fig. 2. Schematic illustration of the design of the beaver slide sampling. Squares represent the quadratic sampling frames (50×50 cm), which were placed at the beaver slide and at two and four meters upstream (us) and downstream (ds) of the slide. Shading of frames represents lateral distance from the stream bank (black = directly at the bank, grey = 50 cm into the stream, white = 1 m into the stream).

quadrat frames in a lateral row along the streambed, starting from the riverbank (Fig. 2).

We counted all mussels within each sampling frame and identified the species.

2.2 Data analysis

Statistical analyses were conducted in R (version 4.3.3, R Foundation for Statistical Computing, Vienna, Austria) using the RStudio interface (version 2023.12.1.402, PBC, Boston, MA). Mean values and standard deviations were calculated for *U. crassus* density and the proportion of individuals, and statistical significance was accepted at $p < 0.05$. The proportion of individuals found in each frame relative to the total mussels sampled per beaver slide was calculated. Data were tested for normality and homogeneity of variances using the Shapiro-Wilk test and Levene's test, respectively. Due to non-normality and heteroscedasticity in the data, non-parametric tests were used where appropriate. A significantly higher number of individuals was found in frames closest to the river bank (Kruskal–Wallis test, $p < 0.001$). Therefore, subsequent analyses of mussel density between locations were restricted to these near-bank frames. This restriction enhanced both ecological relevance and statistical robustness by minimizing noise from sparsely populated areas. Differences between the two groups, across locations and distance from the bank, were analyzed using the Kruskal–Wallis test, followed by pairwise Wilcoxon rank-sum tests with Bonferroni correction.

3 Results

In a total of 159 frames, we found 142 individuals of *U. crassus*, corresponding to a mean density of 3.6 ± 8.6 individuals m^{-2} (Tab. 1), six *Anodonta anatina* (two in Ischler Achen and four in Schinderbach), and one *U. pictorum*

(in Schinderbach). Most *U. crassus* (113 individuals; 80%) were located directly at the river bank (0–0.5 m), with the highest density of 18.3 ± 20.4 individuals m^{-2} observed at the beaver slides (Fig. 3). Significantly fewer *U. crassus* were found at 0.5–1 m (22 individuals; 15%) and 1–1.5 m (7 individuals; <0.1%) from the river bank (Kruskal–Wallis test, $\chi^2 = 37.5$, $df = 2$, $p < 0.001$), respectively.

On average, $17 \pm 29\%$ of the *U. crassus* found in the vicinity of beaver slides were located directly at the slides (Fig. 4). Lower proportions were found at downstream locations, with $4 \pm 7\%$ at 2 m and $3 \pm 7\%$ at 4 m, while the lowest values occurred at upstream locations of the beaver slides ($3 \pm 6\%$ at 2 m and $3 \pm 7\%$ at 4 m). *U. crassus* densities in the near river bank frames (0–0.5 m) differed significantly between locations (Kruskal–Wallis test, $\chi^2 = 11.6$, $df = 4$, $p < 0.05$), with pairwise tests indicating a marginally significant difference between the beaver slide and the upstream 2 m location ($p < 0.05$). All other pairwise comparisons were not statistically significant ($p > 0.05$).

4 Discussion

Our results clearly show that during the reproduction season greatest mussel densities occurred directly at beaver slides which are obviously used as reproduction habitat by the *U. crassus* complex. Most of the mussels were found at or near the river bank, and a clear trend toward accumulation at beaver slides, followed by the sites directly downstream of these structures, was observed. It has already been described that individuals of certain species of the *U. crassus* complex crawl to the stream banks during reproductive period and release their larvae into the stream via water jets to attract host fish, thereby enhancing their reproduction success (Vicentini, 2005; Aldridge *et al.*, 2023a), and that mussels require shallow banks to facilitate their migration. However, the role that beaver slides can play in this context, particularly in structurally modified stream systems where shallow bank areas are otherwise scarce, has to the best of our knowledge not been previously described. In natural streams with a higher diversity of bank habitat structures than in the structurally modified streams investigated in our study, the effects of beaver slides may be less important, analogously to the effects of dead wood structures on salmonids which only occur when shelter structures are limiting (Bretzel *et al.*, 2024).

Freshwater mussels such as *U. crassus* continue to struggle with the consequences of anthropogenic changes in streams, including structural habitat alterations (Geist, 2011; Lopes-Lima *et al.*, 2017), which are often irreversible (Auerswald *et al.*, 2019). Although highly protected and with more positive population development compared to the freshwater pearl mussel (*Margarifera margaritifera*), there are still many pressing challenges in *U. crassus* habitats (Dobler *et al.*, 2024). Many of the *U. crassus* streams in the study region are deepened and have steep banks, which hampers the movement of mussels during reproduction and can negatively affect reproduction success.

As observed in our study, beaver slides locally change the structure of the stream bank (Figs. 5a–5b). Through their movement, frequently sliding into and out of the stream, beavers progressively abrade the stream banks, translocating

Table 1. Summary of sampling effort, mussel density, and beaver slide dimensions across the surveyed streams, including the number of sampled beaver slides, number of sampled frames, mean total mussel density (individuals m⁻²), mean *U. crassus* density (individuals m⁻²), and mean beaver slide width (cm) per stream and in total.

	Sampled streams				Total
	Goldbach	Schinderbach	Scharlach	Ischler achen	
Number of sampled beaver slides	3	2	3	3	11
Number of sampled frames	33	27	45	54	159
Mean total mussel density (Ind. m ⁻²)	1.6 ± 3.6	7.3 ± 12.1	3.5 ± 11.3	3.5 ± 5.7	3.7 ± 8.7
Mean <i>U. crassus</i> density (Ind m ⁻²)	1.6 ± 3.6	6.7 ± 11.8	3.5 ± 11.3	3.3 ± 5.6	3.6 ± 8.6
Mean beaver slide width (cm)	52.3 ± 11.7	67.0 ± 2.8	54.3 ± 17.9	88.3 ± 12.6	65.4 ± 19.2

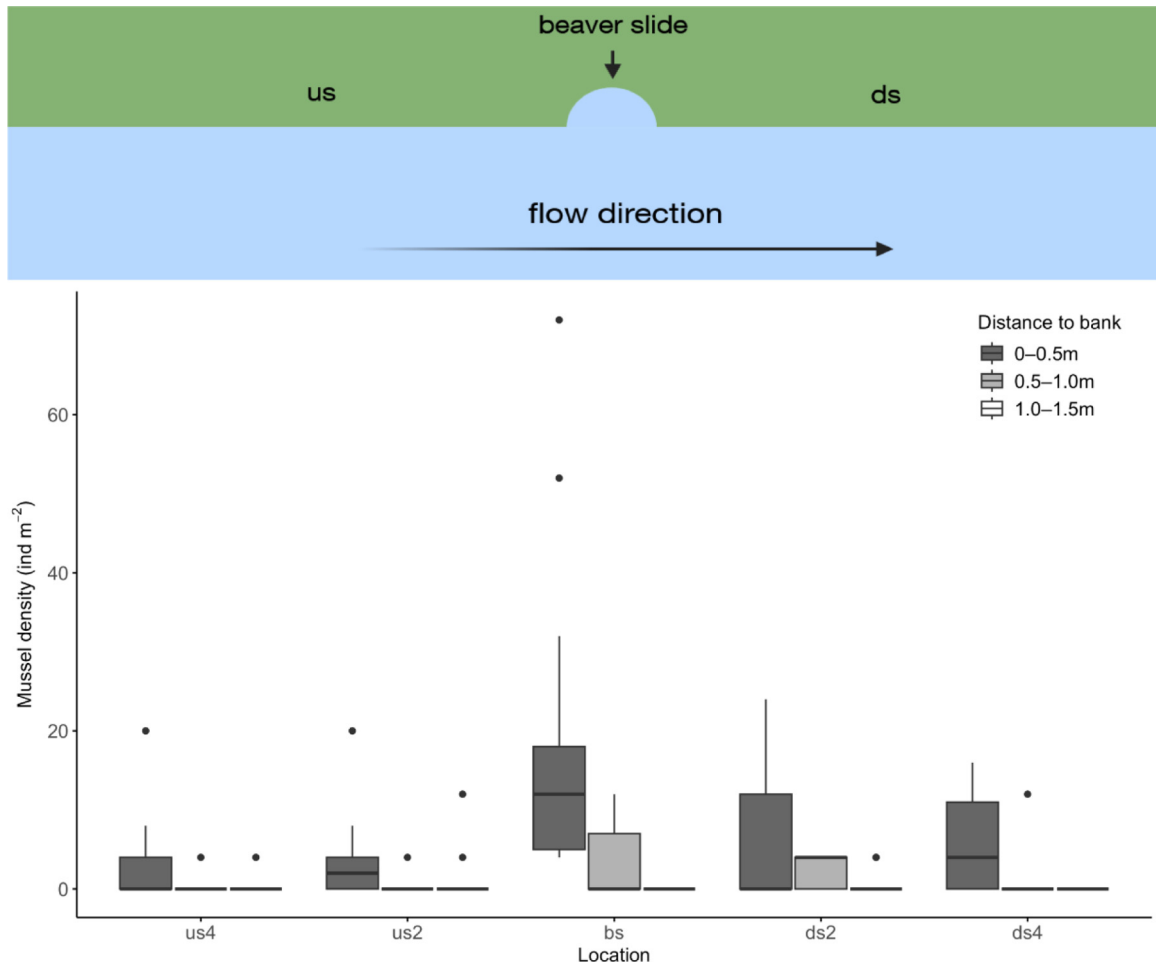


Fig. 3. Boxplot of the mussel density at each sampling location (two and four meter upstream (us) and downstream (ds) and at the beaver slide) in three distances 0–0.5 m, 0.5–1.0 m and 1.0–1.5 m to the bank. Boxes represent the 25 and 75 percentiles with the median marked by a horizontal line. Dots represent outliers defined as values outside 1.5 times the interquartile range.

substrate into the water. This creates local areas with a shallower structure, which may be particularly suitable for *U. crassus* individuals to crawl onto. In contrast to *M. margaritifera*, which is highly sensitive to fine sediment (Geist and Auerswald, 2007), the thick-shelled river mussel is

much more tolerant to fine sediments (Stoeckl and Geist, 2016; Inoue *et al.*, 2017). Since it needs shallow and soft bank areas for its reproduction movement, the introduction of fine sediment through the beaver slides facilitating its movement even seems to be beneficial in this context.

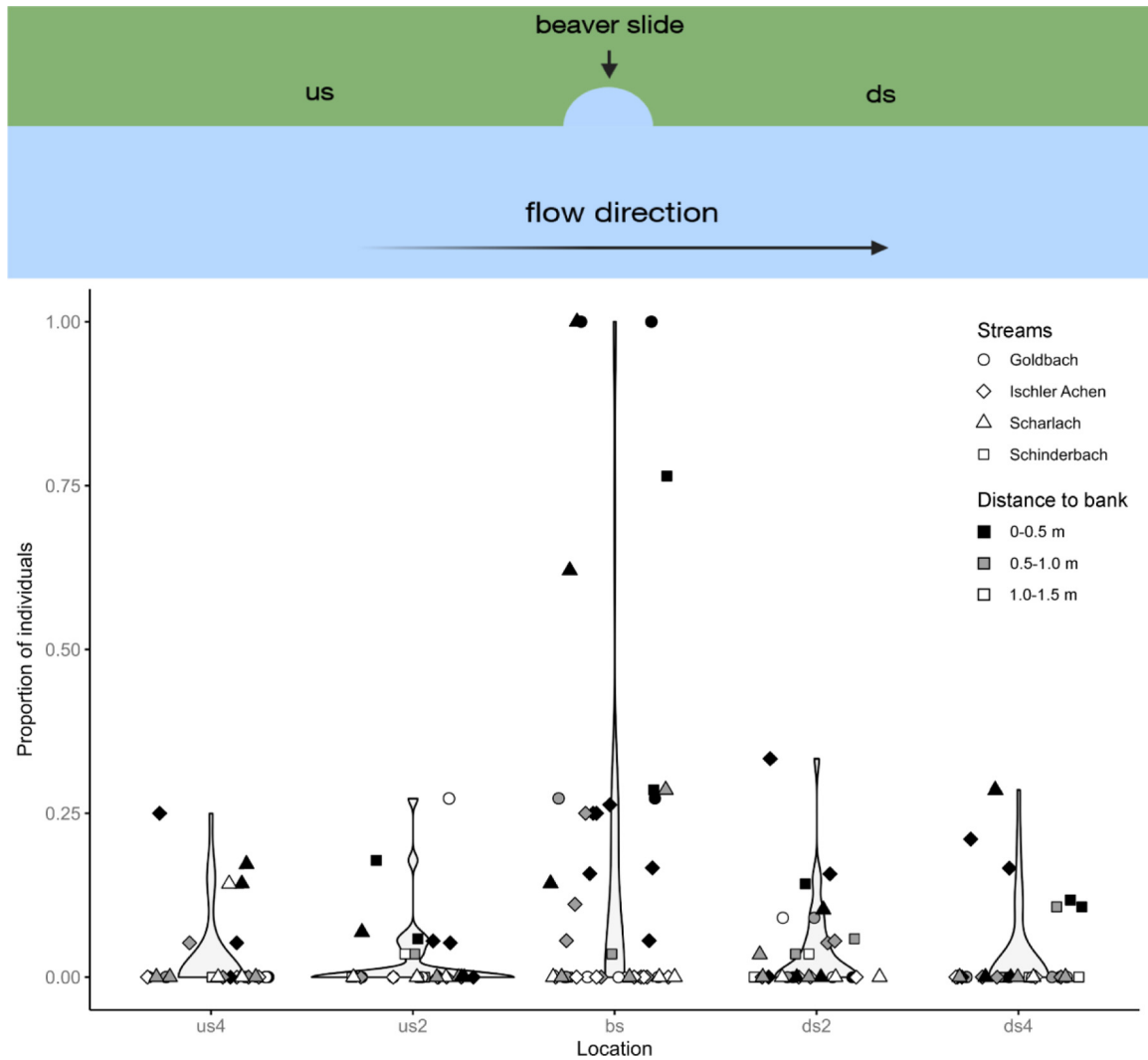


Fig. 4. Proportion of individuals found at each location (two and four meter upstream (us) and downstream (ds) and at the beaver slide) relative to the total mussels sampled per beaver slide. Different shapes indicate the stream (circle = Goldbach, square = Schinderbach, diamond = Ischler Achen, triangle = Scharlach), while the shading represents lateral distance from the stream bank (black = directly at the bank, grey = 50 cm into the stream, white = 1 m into the stream; see Fig. 2). Points are jittered slightly for clarity.

While our results indicate higher densities of *U. crassus* at beaver slides compared to other near-bank areas, it is important to note that detailed environmental variables such as substrate composition, water depth, current velocity, slope, or shading were not measured. Factors such as sediment type, microtopography, and vegetation cover may contribute to mussel distribution and density, and the observed patterns at beaver slides may result from a combination of these habitat characteristics. Furthermore, although *U. crassus* is known to migrate to near-bank areas during reproduction, it remains unclear whether the mussels use these habitats exclusively during breeding season or also occupy them throughout the year. Therefore, our study describes associations rather than direct causal mechanisms. Future studies incorporating quantitative habitat and sediment analyses will be necessary to determine the specific environmental factors driving mussel aggregation near beaver-engineered structures and to better

understand how these microhabitats influence reproductive success and overall population dynamics.

With the reintroduction of *C. fiber* into European water systems, a new ecosystem engineer has become established in habitats that are often highly degraded, which has at the same time exacerbated conflicts between humans and beavers (Thompson *et al.*, 2020). However, its arrival may also introduce new forms of disturbance that can also negatively affect mussel populations, and some conservationists consider the beaver being a key problem for functional mussel populations (Schwarzer *et al.*, 2025). An evidence-based discussion on the positive and negative effects of beavers will benefit from a better understanding of biotic interactions and their effects on specific mussel species which are still poorly understood. Nonetheless, growing evidence, including our findings and recent reports of *U. crassus* complex colonizing beaver dam and pond complexes (Bylak *et al.*, 2020), suggest

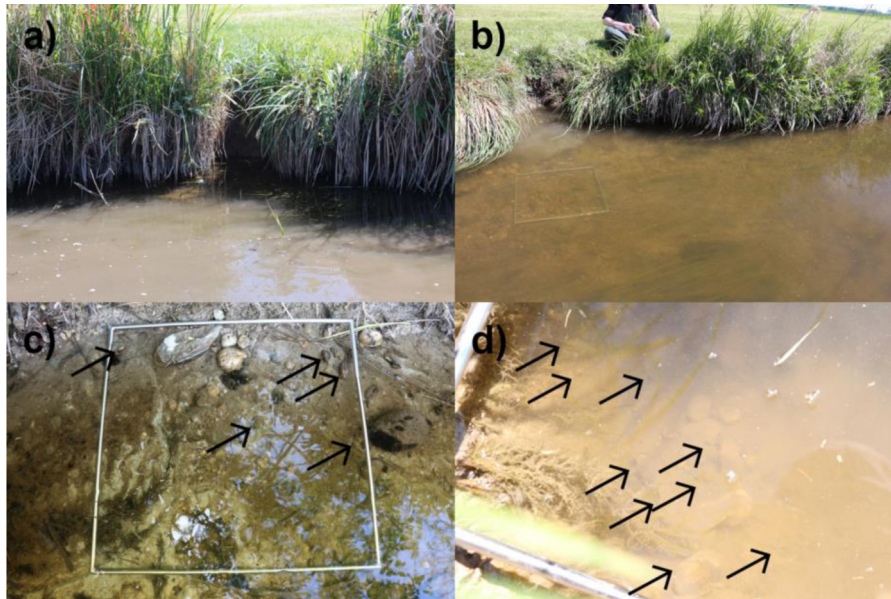


Fig. 5. Photographs of two beaver slides (a+b), depicting the structural differences of the beaver slide areas from the surrounding bank areas, and thick-shelled river mussels located within the first 50 cm of the beaver slides (c+d). Black arrows point at individual mussels.

that beaver activity can also create novel microhabitats that benefit certain mussel and fish species (Pander *et al.*, 2025). However, our results are limited to only one species of mussel, the thick-shelled river mussel, and the differences in its life history and habitat preferences to other species suggest that the observed impacts of beaver activity may be species-specific.

5 Conclusion

Our study provides evidence that beaver slides are associated with locally higher densities of *U. crassus* in structurally modified stream systems. These findings suggest that beaver activity may create or maintain shallow near-bank habitats that facilitate mussel movement and potentially support reproduction. While causative habitat mechanisms remain to be clarified, recognizing the role of ecosystem engineers like beavers can inform conservation strategies for *U. crassus* in human-impacted rivers. Future studies incorporating year-round observations and detailed habitat characterization will be essential to determine whether the accumulation of *U. crassus* at beaver slides persists outside the reproductive season and to identify the specific environmental factors driving these patterns.

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Conflicts of interest

The authors declare no conflicts of interest.

Data availability statement

Data are available from the authors upon reasonable request.

Author contribution statement

Andreas H. Dobler: Conceptualization, Project administration, Methodology, Investigation, Data Curation, Validation, Formal analysis, Visualization, Writing – Original Draft. Michaela Tille: Investigation, Writing – Review & Editing. Juergen Geist: Conceptualization, Supervision, Writing – Review & Editing.

Ethics approval

No ethics approval was required since experiments only involved freshwater invertebrates (unionids).

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