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Nature-based fish habitat enrichment of non-damming beaver structures positively affects fish species richness and density

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ABSTRACT

The return of beavers to the strongly structurally altered Central European stream systems results in a variety of conflicts, potentials and opportunities. Among monetary compensation issues for landowners, target species conflicts with fish conservation remain unresolved. This work investigated the impact of beaver structures of the Eurasian beaver (*Castor fiber* L.) on the fish community of a Bavarian stream system to quantify potential ecosystem services provided by the ecosystem engineering activities of beaver. In addition to beaver structures, artificial structures, constructed from bank clearcuttings, were introduced for comparison. Electrofishing and abiotic measurements were carried out to quantify the effects of the morphological and functional beaver structures on the fish community. In addition, structural characteristics, such as building material and volume, were characterized. Individual fish densities and species diversity were significantly higher in the beaver structures compared to both the reference reaches and the artificial structures. Species such as European chub (*Squalius cephalus* L.), common dace (*Leuciscus leuciscus* L.), European spirlin (*Alburnoides bipunctatus* Bloch 1782), and common nase (*Chondrostoma nasus* L.) benefited most from the beaver structures, particularly smaller size classes <15 cm. Artificial structures had a lower number of species and individuals. They not only differed from the beaver structures in their general fish communities, but particularly in the presence of target species of conservation and fish sizes. In addition to the already well-documented effects of beaver dams, our findings contribute important knowledge to the ecosystem engineering capabilities of the Eurasian beaver. Since the beneficial fish habitat effects of the beaver structures was mostly related to construction material, positioning, total and pore volume as well as flow velocity, these identified properties can also be used to guide future efforts of nature-based structural enrichment of stream habitats.

1. Introduction

Beavers act as ecosystem engineers and are a natural component of streams and floodplains in the Northern Hemisphere (Johnston, 2017). Their activities of introducing dead wood into streams and rivers create diverse aquatic habitats and trigger successional processes in these environments (Whitfield et al., 2015). This co-existence of these large rodents and other organisms such as fishes has likely resulted in co-evolutionary processes (as shown for salmonids, Johnson-Bice et al., 2018; Collen and Gibson, 2000).

After beginning to be overexploited in the 17th and 18th centuries, beaver populations in Europe collapsed completely in the 19th century as a result of overhunting (Halley et al., 2021). In the 20th century some European countries set up protection goals for this species. For example, the beaver has been protected in Germany since 1910, and first individuals were reintroduced to Bavaria, southern Germany, in 1966 (Schwab and Schmidbauer, 2003). The population has now spread and increased in numbers which are already close to the historical status (Halley et al., 2021). It is assumed that the populations will continue to grow throughout Europe, and latest estimates are at about 1.5 million individuals in Eurasia (Halley et al., 2021).

Increasing beaver populations throughout Europe result in an increasing number of conflicts, but they also provide ecological potential (Bylak and Kukuła, 2018). Since the original coexistence of beavers and other aquatic and semi-aquatic life in the pre-industrial age in Europe, major landscape and biological changes have occurred in most European streams (Kemp et al., 2012). Anthropogenic influence has resulted in the degradation of many watersheds (Needham et al., 2021) and dense settlements in Europe, most of them being at least partly irreversible (Auerswald et al., 2019). This situation has further

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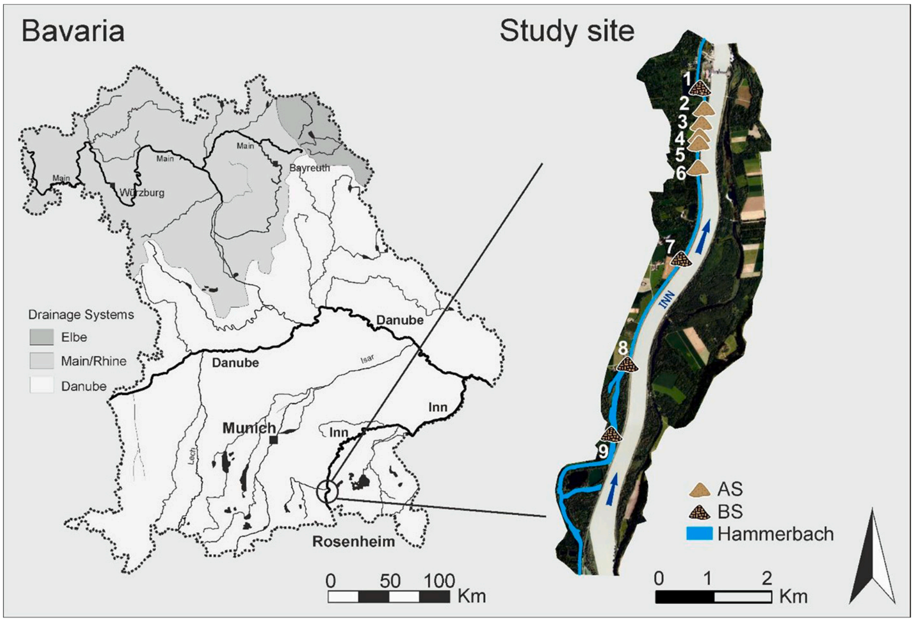

Fig. 1. Overview of the study area with indication of the Hammerbach and the assessed beaver structures (BS) and artificial structures (AS). BS were classified according to Collen and Gibson (2000) as non-damming small structures made by Eurasian beaver (*Castor fiber* L.) such as food storages or beaver lodges. Note that the respective references cannot be displayed in this scale since they were in close spatial proximity 30 m to 50 m upstream to BS and AS, respectively. Numbers next to BS and AS correspond to the labelling of sites in Fig. 5.

exacerbated the conflicts between humans and beavers (Thompson et al., 2021).

Besides the conflicts that beaver activity can cause, beavers are ecosystem engineers with a suite of construction abilities, and they typically create several structures out of chopped trees or dead wood to improve their living conditions in the aquatic environment. These beaver structures typically include dams to optimize living conditions by regulating the water level, beaver lodges where the animals breed and hide, and smaller non-damming structures that are created by the animals as food storages (as defined in Collen and Gibson, 2000). According to many authors, (e.g. Brazier et al., 2021; Larsen et al., 2021; Grudzinski et al., 2022), beaver dams can potentially have positive and negative impacts on fish populations. Kemp et al.'s (2012) literature review found that, depending on the region and the range of fish species present, the most common detriments were restriction of fish migration by beaver dams, colmation of spawning sites, and decreasing oxygen concentrations in beaver-generated ponds, which are impounded former stream reaches. In addition, such structures are thought to favor river warming and high stream temperatures (Weber et al., 2017) that can be critical for cold stenothermic aquatic organisms such as salmonids (Smialek et al., 2021). However, based on expert opinion, generally more positive effects on fish populations can be assumed (Kemp et al., 2012). These include (1) increased fish productivity or abundance, (2) increased fish habitat and habitat complexity, (3) emergence of overwintering habitats and additional juvenile habitats, and (4) increased fish growth rates. In addition, it is known that not only fish populations benefit from beaver structures, but also other groups of organisms such as aquatic invertebrates, amphibians, birds, and bats (Rosell et al., 2005; Stringer and Gaywood, 2016). In this context it is important to highlight the positive role of beaver engineering activity in the restoration of sandy lowland streams (Bylak et al., 2024) and positive effects of beaver related restoration on mountain stream macroinvertebrate communities. (Bylak and Kukuła, 2022). These examples indicate that beaver structures can fulfill important morphological and biological deadwood functions, because the wood structures created increase habitat diversity in lentic and lotic areas (Law et al., 2016; Larsen et al., 2021). This is especially true in degraded, structurally poor and monotonous water bodies of Europe (often classified as heavily modified water bodies (HMWB) in the European water framework directive, European Parliament, 2000), such as the Inn River in Bavaria (Pander et al., 2021).

Since habitat loss and homogenization of waterbodies in particular leads to declining fish populations in the alpine regions of Bavaria (Mueller et al., 2018), a better understanding of potential effects of beaver structures and man-made surrogate structural dead wood enrichments (Pander and Geist, 2010; Pander and Geist, 2016,) on riverine target species of conservation is needed (Pander and Geist, 2018). Whilst ecological effects of beaver dams are well described (reviewed in Kemp et al., 2012; Larsen et al., 2021), effects of the smaller beaver structures (e.g. beaver loges or food storages) on the fish community are largely unknown. Consequently, the overall aim of this research was to determine the impact of small and non-damming beaver structures such as lodges or food storages of the Eurasian beaver (*Castor fiber* L.) on the fish community, in particular concerning their habitat functions for target fish species of conservation and for their vulnerable (early) life stages. We also tested if self-constructed artificial structures (made from felled trees) mimicking those built by beavers would have equal ecological effects.

Specifically, we hypothesize that

(i) Beaver structures and artificial structures made of the same building material result in similar effects on the fish community composition
(ii) Both structures have a positive effect on the local fish fauna as evidenced by increased species abundance, diversity and presence of protected species compared to reference sites without such structures.
(iii) We further expect that structure-dependent and smaller fish benefit most strongly from beaver structures.

2. Material and methods

2.1. Study design and site description

The Hammerbach (HB, district of Rosenheim, Germany) was selected as a representative midsize river north of the Alps to investigate the ecological effects of beaver structures on the fish community. No large

Fig. 2. Photographs and schematic drawings of beaver structure (BS, left) versus artificial structure (AS, right). MWL = mean water level. BS were classified according to Collen and Gibson (2000) as non-damming small structures made by Eurasian beaver (*Castor fiber* L.) such as food storages or beaver lodges.

beaver dams exist in this river and the assessed beaver introduced structures were classified as non-damming beaver structures such as beaver lodges or food storages of the Eurasian beaver (*Castor fiber* L.), as defined in Collen and Gibson (2000). The Hammerbach was considered an ideal study stream due to its high beaver activity and generally rich fish community (Pander et al., 2017; Pander et al., 2022). It flows as a right tributary into the River Rott near Lengdorf, municipality of Rott am Inn, and runs as a left accompanying channel of the Inn River. In addition to the beaver structures (BS), artificial structures (AS), self-built from riparian wood cuttings, were introduced into the Hammerbach to test how effectively natural structures created by the beaver can be replicated artificially. The fish community assessment was carried out in autumn and winter 2021. The HB is a heavily modified stream ecosystem within the upper Inn catchment in the city of Rosenheim in Bavaria, Germany (47°57′43.00"N, 12°09′22.13″E, Fig. 1). The gauge zero elevation of the measuring point in the city of Rosenheim corresponds to 445.34 m NN. The catchment area covers 9.20 km^2 and the mean discharge (MQ) is 9.29 m^3/s (www.hnd.bayern.de/pegel/inn/rosenheim-18312009/stammdaten?, last accessed 23 Feb 2024). The structures investigated were located upstream from the Feldkirchen barrage along a flow section of about 5 km (see Fig. 1).

2.2. Selection of beaver structures and construction of man-made structures

In the described section of 5 km length, beaver structures were mapped and marked for later assessment. In order to test whether beaver structures can be easily reproduced, five artificial structures consisting of riparian wood cuttings were introduced into the Hammerbach at the end of September 2021 (Fig. 2). For this purpose, mainly willows (*Salix fragilis* L., *Salix alba* L., *Salix viminalis* L.) and alders (*Alnus glutinosa* L., *Alnus incana* L.) of the predominant riparian vegetation were used for the construction. Three to five approximately 10 cm thick branches (about 1.8–2.2 m long) per structure were sharpened with a chainsaw and driven into the sediment with a sledgehammer. Thicker and longer branches (up to 3 m long and 15 cm thick) were first placed between these posts. Further weaker and defoliated material was then braided between the existing branches to mimic the close interlocking of woody material in a beaver structure. In addition to the beaver structures (BS) and artificial structures (AS), reference reaches in close proximity (< 30–50 m distance) were also sampled and are referred to as RA and RB, depending on their closer proximity to AS or BS, respectively. These reaches had otherwise similar hydromorphological characteristics (e.g., width, depth and current speed) to allow a fair determination of the effects of AS and BS against reaches without such structures. A 26-day waiting period was maintained between construction and assessment of the structures.

2.3. Characterization of beaver and artificial structures

The length, width, and depth of all nine structures, as well as the ratio of above- and below-water surface areas, were determined using a graduated measuring rod. The length and thickness of 22 to 30 branches were measured per structure. The branches were either carefully pulled out of the structure or measured on the surface of the structure. The measurement accuracy of the length, determined with a measuring tape, was 1 cm. The thickness was determined with a caliper gauge in the middle of each branch to an accuracy of 1 mm. To determine the overall volume of the structures (VS), a half rotational ellipsoid was assumed, and the volume was calculated from the measured length, width and depth of the structure. The volume was calculated assuming a measurement inaccuracy of +/− 10 cm when the data was recorded. To measure the branch volume, a plastic bin (60 L) was used. For each beaver structure, an area of 30 × 50 × 20 cm (approximately 30 L) was removed with hedge shears and transferred to a plastic bin. To prevent the branches from floating, they were weighted down. The bin was filled with a 5 L measuring cup with a millimeter scalar until reaching the previously marked 50 L mark. The amount of water that still fit into the bin, including branches, was noted to the nearest liter. The difference between the 50 L when empty and the water that fits in the bin until the 50 L mark is reached while the bin is filled with branches was taken as branch volume. The method is based on the principle of water displacement (Archimedes' principle) and it is widely used in agriculture for analogous volume measurements (Keightley and Bawden, 2010). To determine the pore volume of the structure (PV), the total volume of the structure and the branches volume of the building material were calculated first. The pore volume corresponds to the subtraction of the branch volume from the total volume.

2.4. Abiotic habitat variables

Ecologically relevant physico-chemical variables were measured in three replicates in the free-flowing drain of the HB along each BS, AS, RB and RA. Temperature (T, [°C]), dissolved oxygen (O_2, [mgL^{-1}]), electrical conductivity (EC, [μScm^{-1}], corrected to 20 °C), and pH-value (pH) were measured with a hand-held WTW® Multimeter 340i (WTW GmbH, Weilheim, Germany). In addition, turbidity (TURB, [NTU]) was assessed using a WTW® Turb 355 IR measuring set. Water depth (D, [cm]), current velocity [$m\ s^{-1}$] 10 cm above ground (vb) as well as 10 cm below surface (vs) were measured at each study segment (Ott MFpro, Ott Hydromet GmbH, Kempten, Germany) according to Pander et al. (2015), at 3 measurement points distributed along the study segment in 0.5 m from the shoreline considering BS and AS as bank extensions. The first measurement of the chemical-physiological parameters took place on 21 October 2021 and the second measurement took place on 13 December 2021. During both measurements, the weather conditions were constantly cloudy and windy with no precipitation. Since macrophytes are known to be important structural enrichments in fish habitats, macrophyte coverage of the river bed at the respective sampling site (M, [%]) was estimated in each BS, AS, RB and RA as described in Pander et al. (2015).

2.5. Fish community assessment

To assess the fish community, a total of 18 segments were fished seasonally in autumn and winter 2021 (4 BS and RB, 5 AS and RA). Each of the fished segments were 10 m long, with BS and AS located in the middle of the stretch. For each segment, a reference stretch at the same river bank of the same length was fished upstream. Fish community assessment in the beaver structures, artificially created structures and the adjacent bank habitats (references) was carried out following the approach described in Pander and Geist (2010). All BS, AS, RB and RA were sampled with a boat-based 8 kW electrofishing generator (EFKO FEG 8000, EFKO-Elektrofischfanggeräte GmbH, Leutkirch, Germany). The study segments were consecutively sampled working from downstream to upstream direction with the same electrofishing crew within a 4-h period between 11:00 h and 15:00 h. For the electrofishing a single anode was used, and all stunned fish were collected by a second person using a dipnet with a mesh size of 0.5 cm. All fish of each study segment were collected in a separate plastic bin (80 L) with oxygen supply and determined to the species level and their total length (TL, to the nearest 0.5 cm) was determined with a graduated measuring rod. All fish were released immediately after the procedure in good condition at the study segment they were caught from. The electrofishing activities were carried out under the license number 31–7562 issued by the district office of Freising, Bavaria, Germany.

2.6. Data analysis

The number of species and number of individuals are given as total numbers detected in BS, AS, RB and RA. Since all study segments had the same bank length of 10 m, no further standardization was applied to the catch data. To express a measure of fish diversity in the assessed BS, AS, RB and RA Shannon diversity (Shannon and Weaver, 1949) and Evenness (Pielou, 1966) were computed. For univariate multiple-group comparisons of abiotic habitat variables, each dataset was tested for normal distribution (Shapiro-Wilk test) and homoscedasticity (Levene test). Since data did not fulfill the criteria for parametric testing, the non-parametric Kruskal Wallis test was applied to test for significant differences. A subsequent post-hoc Wilcoxon test with Bonferroni correction for multiple comparisons was used to determine whether values differed significantly between BS and AS. Univariate statistics were carried out using statistical and graphical open-source software R (version 4.0.3R, www.R-project.org/, last accessed on 27 July 2024).

To analyze fish community composition in BS, AS, RB and RA respectively, Bray-Curtis-similarities from fish abundance data were computed in PRIMERv7. To account for zero values, dummy variables were computed as recommended by Clarke et al. (2014) as a standard procedure in PRIMER v7. Based on the calculated Bray-Curtis resemblance matrix, an analysis of similarities (ANOSIM) was applied to test for significant differences in the fish community composition between BS-AS, BS-RB, AS-RA and between different seasons fall and winter. Seasonal differences in the fish community composition of BS, AS, RB and RA were visualized by metric multidimensional scaling (nMDS, Clarke et al., 2014) based on the same Bray-Curtis-similarities. Significance was accepted at $p \leq 0.05$ (= 95 % probability). Similarity Percentages (SIMPER, Clarke et al., 2014) analysis was used to identify the fish species contributing most to the similarity between BS, AS, RB and RA. To examine relations between environmental data and fish community data, BEST linear modeling was used. Following variables were included in the BEST: T, O_2, EC, pH, TURB, D, vb, vs, M, VS and PV. In addition, the standard deviation (SD) of vb and vs was integrated in the analysis. The main rationale for the BEST procedure in PRIMER v7 is to find the best match between the multivariate among-sample patterns of an assemblage and that from environmental variables associated with those samples. The extent to which these two patterns match reflects the degree to which the chosen environmental data 'explain' the biotic pattern (Clarke et al., 2014). All environmental variables were displayed in the nMDS plot using the "overlay function" in Primer v7. To visualize which size of fish preferentially used BS, AS, RB, and RA structures, all fish regardless their species affiliation, were grouped into three size classes and displayed in the nMDS plot using the "Bubble function" (in Primer v7) that gives an indication of the number of fish per size class using the respective structure. In addition, all fish species were classified according to their structure affiliation to dead wood or boulders following Zauner and Eberstaller (1999), where European freshwater fish were classified into three classes of structure-affiliated species, "high", "less" and "no". These three classes of structure-affiliated species were also visualized in the nMDS plot using the "Bubble function" (in Primer v7).

3. Results

3.1. Assessment of building material from beaver structures and artificial structures

Beavers engineered the assessed beaver structures using the trees in spatial proximity of the site, mostly willows and elders. BS were made out of branches with no side branches and with no leaves on. Maximum branch length used by beavers was 400 cm and maximum branch thickness was 12 cm. BS varied in size between 0.6 m^3 and 6.5 m^3 with a mean PV of 77 %.

The VS of the beaver structures was on average 3.5 m^3 and almost

Table 1
Abiotic characteristics of the study segments. T = temperature, O_2 = dissolved oxygen, EC = electrical conductivity (corrected to 20 °C), pH = pH-value, TURB = turbidity, D = water depth, vb = current speed measured 10 cm above ground, vs = current speed measured 10 cm below surface, M = macrophytes coverage, VS = volume of the beaver structures and artificial structures, PV = pore volume of the beaver structures and artificial structures, BT = branch thickness and BL = branch lengths. BS = beaver structures, AS artificial structures, RB = reference structures in spatial proximity to beaver structures, RA = reference structures in spatial proximity to artificial structures.

	T [°C]	O_2 [mgL^{-1}]	EC [uScm-1]	pH	TURB [NTU]	D [m]	vb [ms^{-1}]	vs [ms^{-1}]	M [%]	VS [m^3]	PV [m^3]	BT[cm]	BL[cm]
BS	8.8	10.4	560	8.2	2.11	0.64	0.19	0.30	39.4	3.5	2.7	2.8	116
	5.8–11.7	9.0–11.7	527–598	8.1–8.2	1.40–3.72	0.29–1.18	0.00–0.88	0.00–1.22	10–70	0.6–6.5	0.4–3.7	0.4–12.0	10–400
AS	8.7	10.3	554	8.2	2.37	0.66	0.17	0.39	43.0	2.0	1.4	1.8	97
	5.9–11.5	9.1–11.5	533–576	8.1–8.2	1.65–3.20	0.20–1.11	0.00–0.51	0.00–0.89	0–70	0.8–3.4	0.6–1.5	0.4–11.0	18–294
RB	8.9	10.4	557	8.2	2.39	0.61	0.18	0.27	41.3				
	5.9–11.5	9.1–11.5	533–574	8.1–8.2	2.20–5.31	0.33–0.80	0.06–0.83	0.07–0.84	0–60				
RA	8.7	10.3	554	8.2	3.70	0.50	0.28	0.46	30.0				
	6.0–11.7	8.6–11.6	511–598	8.1–8.2	1.43–6.19	0.35–0.88	0.00–0.48	0.02–0.81	15–75				

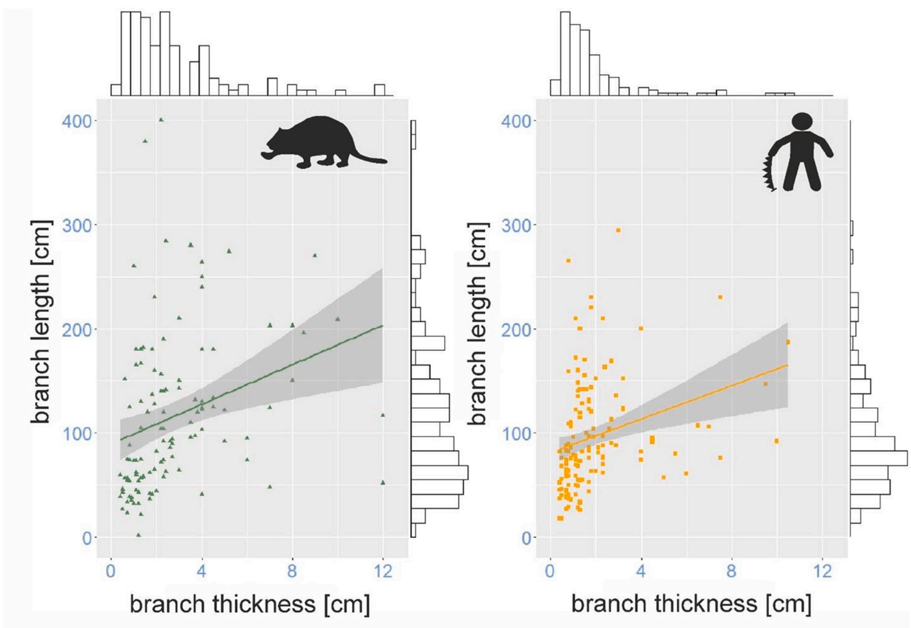

Fig. 3. Relation of branch length to branch thickness for beaver structures (BS, left) and artificial structures (AS, right). The marginal indicate the slope of the predicted probability plot at the mean branch thickness of the respective structure.

1.8-fold the size of the artificial created structures (2.0 m^3). They also comprised an almost two-fold higher PV (Table 1). The mean ratio of the VS and the PV was 1.3 for beaver structures and 1.4 for artificial structures. However, due to the low number of replicates this difference was not significant (Kruskal-Wallis test, $p < 0.05$). The ratio of branch length and thickness varied more in the beaver structures than in the artificial structures (Fig. 3). Many thin branches were used in the artificial structures, while beavers also used very thick branches (max = 12 cm). Branches in the beaver structures were on average 19 cm longer and 1 cm thicker than branches in the AS. However, branch lengths did not differ significantly between beaver structures and artificial structures. In contrast to the branch length, thickness of branches in the beaver structures was significantly higher than those in the artificial structures (Kruskal-Wallis, $p \leq 0.001$, df = 1). The building material of the artificial structures was more homogeneous than that of the beaver structures with respect to branch thicknesses and branch lengths used (Fig. 3).

3.2. Fish community characterization

Fish community composition in BS, AS, RB and RA was significantly different (Fig. 4, ANOSIM global $R = 0.421$, $p < 0.001$, Table 2). Strongest differences as indicated by the R-value were detected for the comparisons of beaver structures BS and the references RB (ANOSIM global $R = 0.619$, $p < 0.001$) and RA (ANOSIM global $R = 0.758$, $p < 0.001$). The differentiation between beaver structures BS and artificial structures AS was much smaller (ANOSIM global $R = 0.365$, $p < 0.01$) and weakest for the comparison of both references RB and RA (ANOSIM global $R = 0.219$, $p < 0.05$). There were no significant differences in fish community composition between fall and winter sampling within BS, AS and within both reference structures RA and RB (Table 2). As indicated by bubbles in the nMDS plot in Fig. 5, most small fish <15 cm TL occurred in beaver structures BS and artificial structures AS compared to their references. In addition, BS and AS kept the highest concentration of structure-affiliated fish species, however, individuals with no affinity to structures were also detected in highest numbers in these habitats (Fig. 5).

The SIMPER-based characterization of fish community composition in the different habitat types of BS, AS, RB, and RA revealed a different set of species contributing in sum with more than 75 % to the similarity within the replicates of a respective habitat type. In both BS and AS *Squalius cephalus* (average abundance BS = 15.1 and AS = 7.0) and *Perca fluviatilis* L. (average abundance BS = 8.6 and AS = 1.3) were detected as steadily occurring species. In addition, the replicates of beaver structures BS were characterized by *Alburnus bipunctatus* (average abundance 60.1) and *Leuciscus leuciscus* (average abundance 24.1) whilst artificial

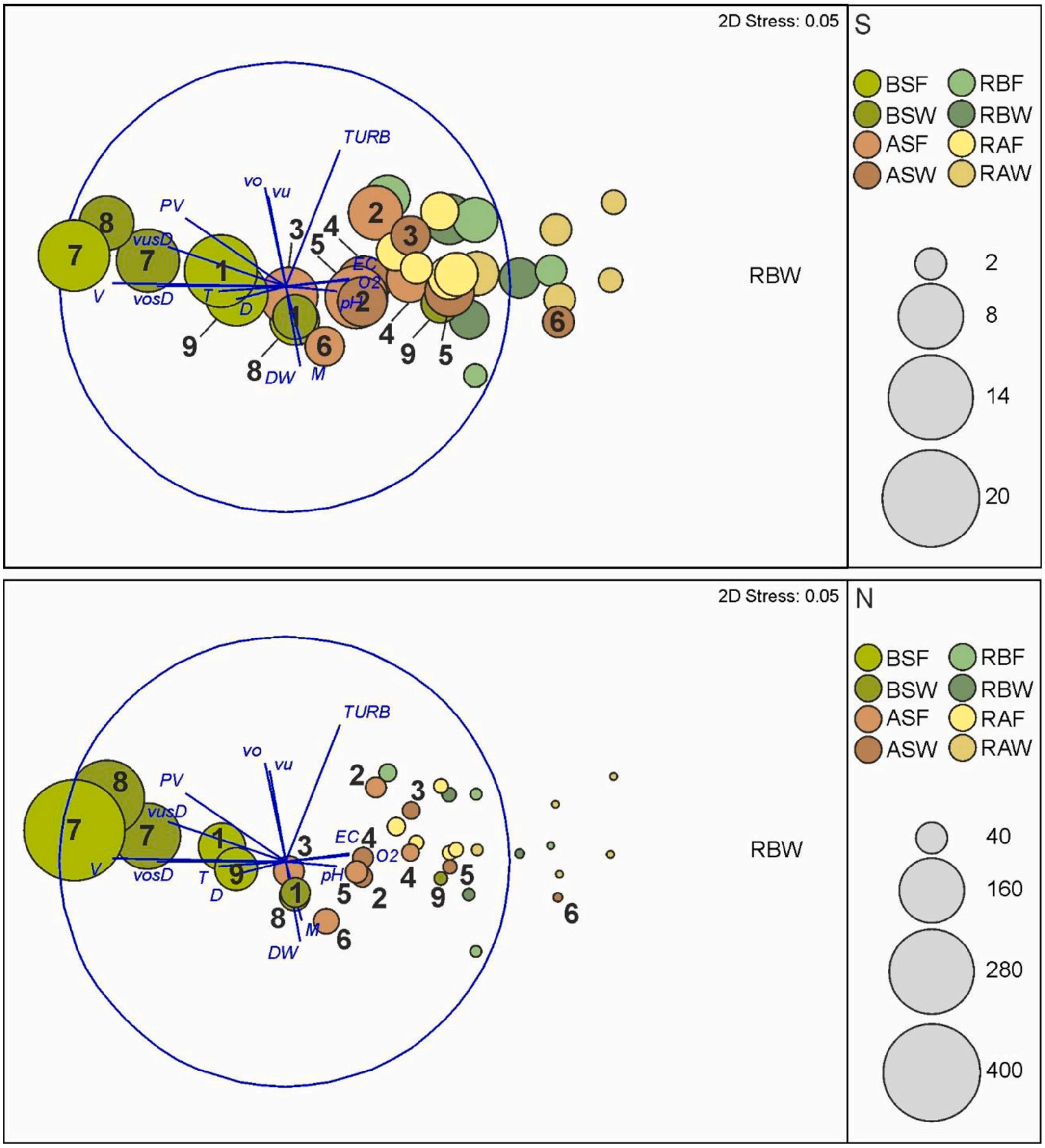

Fig. 4. Non-metric multi-dimensional scaling (nMDS) of the fish community composition in beaver structures (BS), artificial structures (AS), reference sites of the beaver structures (RB) and the reference sites of the artificial structures (RA) in fall (F) and winter (W). S = number of species, N = number of individuals, T = temperature [°C], O_2 = dissolved oxygen [%], EC = electrical conductivity ([uScm^{-1}] corrected to 20 °C), pH = pH-value, TURB = turbidity [NTU], D = water depth [cm], vb = current speed measured 10 cm above ground [ms^{-1}], vs = current speed measured 10 cm below surface [ms^{-1}], SD = standard deviation, M = macrophytes coverage [%], VS = volume of the beaver structures and artificial structures [m^3], PV = pore volume of the beaver structures and artificial structures [m^3]. Black numbers at BS and AS correspond to those given in Fig. 1 and indicate the spatial arrangement of structures in the Hammerbach.

structures AS were characterized by *Barbatula barbatula* L. (average abundance 1.8) and *Cottus gobio* L. (average abundance 1.2). In the two rip-rap dominated reference types RB and RA fish such as *Cottus gobio* (both types, average abundance RB = 1.6 and RA = 2.1) and *Leuciscus leuciscus* (average abundance only RB = 0.6) and *Squalius cephalus* (average abundance only RB = 1.0) as well as *Barbatula barbatula* (average abundance only RA = 1.2) were most common across replicates.

BEST revealed a set of 5 variables (D, O_2, vs, vb SD and PV) fitting the ordination in the nMDS plot ($R = 0.843$) The direction of vectors of the BEST-selected variables vb SD and PV indicate that beaver structures BS provide a higher standard deviation of current velocity on the bottom and a higher pore volume. In contrast to these both variables, the correlation of O_2 and D was much weaker as indicated by the smaller dimension of the vector (Figs. 4, 5). The vector of the variable vs indicates stronger differences among replicates of habitats than between habitat types. An alternative set of variables with the $R = 0.837$ selected by BEST, suggests the variables D, O_2, vb, vs SD and VS, indicating that according to the length of the vector, the volume VS of the structure also plays a major role for fish community composition.

3.3. Species and individual numbers, diversity, protected species and fish length

Overall, 17 species out of 9 families with 1305 individuals were detected in this study. Most prominent families were Leuciscidae (6 species) and Salmonidae (3 species). All other families were represented by only one species. Most frequently caught species were spirlin, *Alburnus bipunctatus* Bloch 1782 (484 individuals), dace, *Leuciscus leuciscus* L. (222 individuals), and chub, *Squalius cephalus* L. (200 individuals).

In beaver structures BS, significantly more species (mean 6.9) were caught than in the references RB (mean 2.8) and RA (mean 2.6, Fig. 6)

Table 2
Comparison of the fish community composition by ANOSIM between BS = beaver structure, AS = artificial structure, RB = reference beaver structure, RA = reference artificial structure, F = fall, W = winter.

		R	*p*-value
Global Test		0.357	< 0.001
Habitat comparison	BS - AS	0.377	< 0.01
	BS - RB	0.619	< 0.001
	AS - RA	0.252	< 0.01
	RB - RA	0.033	> 0.05
Seasonal comparison	BSF - BSW	−0.083	> 0.05
	BSF - RBF	0.875	< 0.05
	BSW - RBW	0.375	> 0.05
	BSF - ASF	0.338	< 0.05
	BSW - ASW	0.225	> 0.05
	ASF - ASW	−0.01	> 0.05
	ASF - RAF	0.362	< 0.05
	ASW - RAW	0.474	< 0.05
	RBF - RBW	−0.188	> 0.05
	RAF - RAW	0.668	< 0.01

with no significant differences between fall and winter sampling. However, the average number of species in the beaver structures BS was higher in fall (9 species) compared to winter (5 species). The decline during the winter sampling in the number of species in beaver structures BS was not evenly spread across the replicates. Individual beaver structures still had very high species numbers of 8 species during the winter sampling. In the artificial structures AS, the number of species fell on average from 6 to 4 species in winter and in the references RB and RA an average of 3 or 2 species, respectively, were caught in this season.

Most fish individuals were caught in beaver structures BS ($N = 1042$; 80 %), followed by artificial structures AS ($N = 165$; 13 %) and least fish were caught in the references RA ($N = 56$; 4 %) and RB ($N = 42$; 3 %) (Fig. 6). During the sampling in fall, significantly more fish (+20 %) were caught compared to the sampling in winter. Shannon diversity was highest in beaver structures followed by artificial structures, and was lowest in the reference stretches RB and RA. In contrast, Evenness was highest in the reference stretches RB and RA and lowest in beaver structures and artificial structures (Table 3).

Most protected species according to international, national or

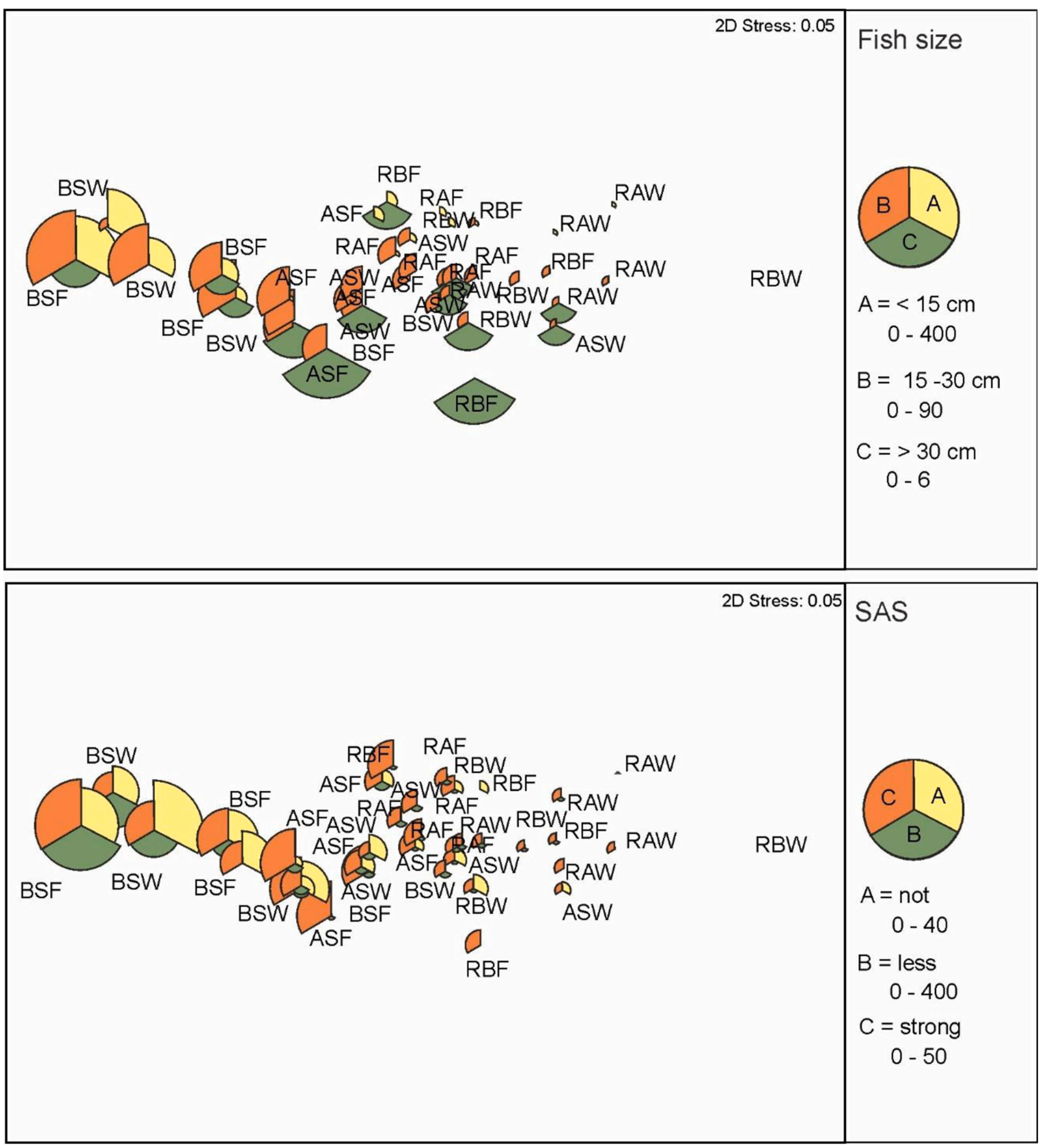

Fig. 5. Non-metric multi-dimensional scaling (nMDS) of the fish community composition with fish size and structure-affiliated species (SAS) displayed as bubbles in beaver structures (BS), artificial structures (AS), reference sites of the beaver structures (RB) and the reference sites of the artificial structures (RA) in fall (F) and winter (W).

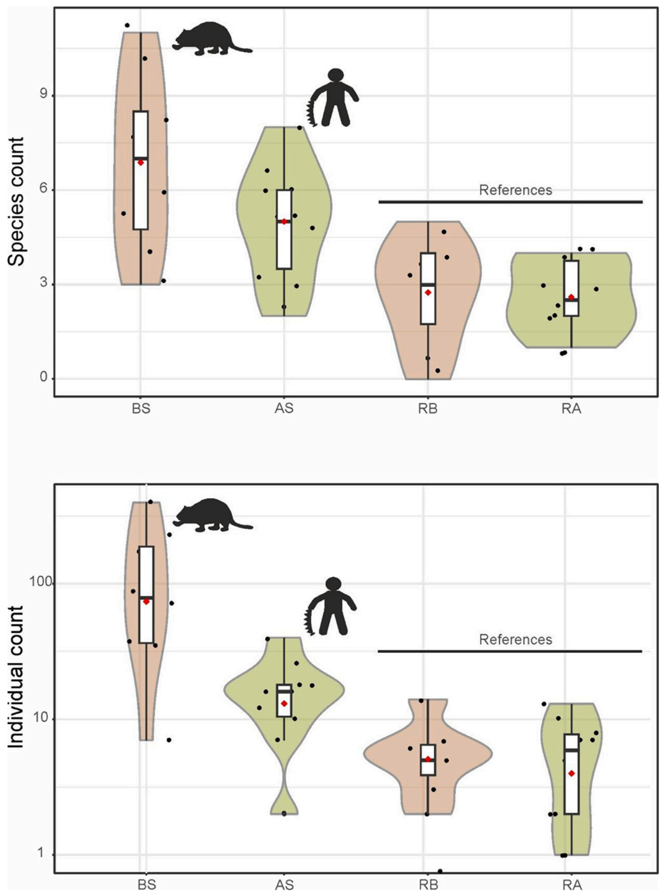

Fig. 6. Violin plot of species and individuals count for BS = beaver structures, AS = artificial structures, RB = reference sites beaver structures and RA = reference sites artificial structures. Median is given as black line, mean values as red triangles. White box corresponds to the 25 % and 75 % quantile, coloured area indicates the kernel density estimation of data distribution.

Table 3
Species richness, individual numbers, Shannon diversity and Evenness, BS = beaver structure, AS = artificial structure, RB = reference beaver structure, RA = reference artificial structure, S = number of species, N = number of individuals, SH = Shannon diversity, E = Evenness, TL = fish total length.

		S	N	SH	E	TL
BS	mean	6.9	130.3	1.31	0.72	10.0
	min-max	3–11	7–398	0.88–1.94	0.49–0.87	1–47
AS	mean	5	16.5	1.25	0.81	13.9
	min-max	2–8	2–40	0.43–1.77	0.39–1.00	2–47
RB	mean	2.8	5.3	0.83	0.92	15.1
	min-max	0–5	0–14	0.00–1.48	0.71–1.00	2–49
RA	mean	2.6	5.6	0.77	0.91	9.7
	min-max	1–4	1–13	0.00–1.28	0.72–1.00	4–78

regional red lists were caught in beaver structures (5 listed species), followed by artificial structures (4 listed species). The references RB and RA both held 3 listed species. In beaver structures, 15 from the overall 17 species could be caught and one species (*Chondrostoma nasus* L.) was exclusively caught there (Table 2). In artificial structures, 13 species, and in references RB 9 species and in RA 8 species were found. *Salmo trutta* L. and *Hucho hucho* L. were exclusively found in the references RB and RA respectively; however, these two salmonid species were only caught in low numbers (6 *Salmo trutta*, 2 *Oncorhynchus mykiss* Walbaum 1792 and 1 *Hucho hucho,* Table 4).

Fish length between beaver structures, artificial structures and the references RB and RA differed significantly (Kruskal-Wallis, $p \leq 0.001$, df = 3, for all pairs Mann-Whitney-U, $p \leq 0.001$). In beaver structures, mean total fish length was 10 cm and almost 4 cm smaller than in artificial structures and more than 5 cm smaller than in the reference RB. Smallest mean fish length was detected in the reference RA, however, in this habitat also the largest size range of fishes was detected (Table 3).

4. Discussion

The results of this study indicate that fish community composition in small to medium-sized streams can strongly benefit from non-damming structures engineered by the Eurasian beaver (*Castor fiber*), which is in line with hypothesis (i) herein and observations from larger structures such as beaver-dams elsewhere (Collen and Gibson, 2000; Kemp et al., 2012; Bouwes et al., 2016; Law et al., 2016). Our findings also reveal that artificially made structures from bank clearcuttings did not fully mimic the same functions for the fish community like the ones created by beavers as indicated by differences in fish community composition. This is likely due to differences in building material and engineering. Beavers seem to provide more interwoven structures with less ramification and a slightly larger branch diameter (mean = 2.8 cm, max = 12 cm) and longer branches (mean 116 cm, max = 400 cm) compared to artificial structures (branch diameter mean = 1.8 cm, max = 11.0 cm and branch length mean = 97 cm, max = 294 cm). To ensure highest similarity of artificial structures to beaver structures, these dimensions and the engineering method of the beaver should be considered during construction.

In general, the observation that dead wood can have positive effects on fishes is well-documented for a variety of aquatic habitats such as natural streams (e.g. Naiman et al., 2002; Verdonschot and Verdonschot, 2023) and heavily modified streams (e.g. Pander and Geist, 2010; Pander and Geist, 2016), albeit it may be less important in situations where other structural hiding places such as large bed-rock prevail (Bretzel et al., 2024). Natural and artificial deadwood can be an important trigger of riverine processes such as sediment relocation (Wohl and Scott, 2017). It is known to provide habitat (Collen and Gibson, 2000), nutrient input in rivers (Elosegi et al., 2007; Entrekin et al., 2008) and is steering productivity (Naiman et al., 2002). Dead wood is also known to create structural diversity (Gurnell et al., 2005; Antón et al., 2011), similar to the functions of macrophytes which also affect interstitial processes (e.g., Braun et al., 2012). This, in turn, can lead to a high diversity of aquatic organisms (Bisson and Wondzell, 2003). This is particularly true for fishes (Pander and Geist, 2010) and is in addition reflected in the results of this study, where beaver structures aggregated highest species and individual numbers as well as highest fish diversity, which is in line with hypothesis (ii). In most European rivers, dead wood, natural as well as artificial, is highly managed and scarce due to the many competing interests such as flood protection, securing energy production in hydropower plants, shipping or the avoidance of bridge clogging (Pander and Geist, 2013). This is particularly true for larger dead wood such as trees or beaver dams (if considered as one contiguous structure) which have often been removed from river systems, despite their valuable functions for the ecosystem. In this context, the presence of beavers in HMWBs creating large dams or fallen trees can pose many conflicts with anthropogenic uses. However, as evident from the data of this study, the assessed small beaver structures also contribute valuable functions for the ecosystem and provide habitat for a high fish diversity, similar to artificially inserted deadwood fascines (Pander and Geist, 2010). In contrast to larger dead trees or beaver dams, the beaver structures assessed herein are rather small and consist of mostly small branches without ramifications of maximum 4 m length and 12 cm diameter. They likely do not threat any anthropogenic infrastructure due to clogging and they also do not block free fish migration, but instead provide valuable habitats that are favored by many fish species as evident from the aggregation of a large number of individuals in fall and winter. In addition, most hydropower plants can handle such size woody debris easily and clogging on

Table 4
Species list and classification. Overall = number of individuals, BS = beaver structure, AS = artificial structure, RB = reference beaver structure, RA = reference artificial structure, FFH = European Fauna Flora Habitat Directive, RLG = Red List Germany, RLB = Red List Bavaria, NL = not listed, V = early warning list, * = not threatened, 2 = highly endangered, 3 = endangered, n = not listed. SAS = Structure-affiliated species according to Zauner and Eberstaller, 1999.

		Overall	BS	AS	RB	RA	FFH	RLG	RLB	SAS
Alburnoides bipunctatus	Spirlin	484	481	1	2		NL	V	*	weak
Alburnus alburnus	Bleak	63	58	1	4		NL	*	*	no
Barbatulus barbatulus	Stone loach	48	14	18	4	12	NL	*	*	weak
Barbus barbus	Barbel	4	1	3			Annex V	*	*	weak
Chondrostoma nasus	Common nase	17	17				NL	V	3	weak
Cottus gobio	Bullhead	50	4	12	13	21	Annex II	*	*	high
Esox lucius	Northern pike	15	6	8		1	NL	*	*	high
Gasterosteus aculeatus	Three-spined stickleback	8		7	1		NL	*	*	no
Gobio gobio	Gudgeon	36	18	4		14	NL	*	*	weak
Hucho hucho	Danube salmon	1				1	Annex II	2	2	weak
Leuciscus leuciscus	Dace	222	193	20	5	4	NL	*	*	weak
Oncorhynchus mykiss	Rainbow trout	2	2				NL	n	n	weak
Perca fluviatilis	European perch	83	69	13	1		NL	*	*	no
Phoxinus phoxinus	European minnow	2	1	1			NL	*	V	weak
Rutilus rutilus	Roach	64	57	7			NL	*	*	no
Salmo trutta	Brown trout	6			4	2	NL	*	V	high
Squalius cephalus	Chub	200	121	70	8	1	NL	*	*	high

infrastructure such as bridges is not an issue due to its small size. The valuable habitat function and the small impact on anthropogenic HMWBs use (heavily modified waterbodies according to the European Water Framework Directive, European Parliament, 2000), lead to the recommendation to support and not to remove such small beaver structures.

To enhance the availability of such structures, it can be beneficial to create them artificially in addition to the beaver-made ones. In this study, it turned out that there is a difference in functionality for the fish community likely being explained by the measured slight differences in structure, despite the great similarity of both structures on first glance. More fish species and more fish individuals preferred the beaver structures in comparison to the artificial ones and the adjacent reference sites. However, it should be noted that not all beaver structures performed in the same way and that some beaver structures required a longer period to be colonized. Some structures seem to be more attractive for fish than other ones. This can be explained by differences in incident flow, construction material and pore volume. In addition, the successional stage and the intensity of the beaver maintenance may also lead to differences in fish habitat use. In this context, a restructuring of the artificial structures was observed in the post experimental phase of the study. Creating artificial dead wood structures that ideally mimic beaver structures can be very time consuming as experienced during the construction work on the artificial structures herein (construction time was 1.5 h per structure). Suitable trees must be provided, all leaves must be removed and the branches for engineering must be cut in a way that less to no ramifications exist. Subsequently, they have to be packed very dense, requiring a great amount of building material and time to engineer. This gives beaver structures a double value that is additional to their positive effect for the fish community, particularly attributed to their cost effectiveness and maintenance since beaver overwork and expand such structures regularly, and in the case of this study, using branches of the artificial structures as well. However, it has to be considered that the assessed artificial structures still held more fish than the adjacent reference sites and can therefore be a good alternative in rivers where no beaver activity is possible due to conflicts with other needs or where dead wood content is generally too low.

Fish species can be classified according to their preference or dependence on structures, mainly dead wood or boulders (e.g. Zauner and Eberstaller, 1999). According to hypothesis (iii), it was expected that preferably structure-affiliated species and small fish use beaver structures as well as artificial structures. The results of this study only partially support this hypothesis for the use of these structures by small fish. In general, structure-affiliated species such as pike and chub used the dead wood intensively. However, species with no structure-affiliation like perch, dace or roach also used the dead wood very intensively, indicating that a wider range of species than expected use these habitats. It is likely that the low water temperatures, typical in this temperate region and observed herein, reduced fish activity and led to fish aggregations in the dead wood structures where fish tried to hide. Since the interstices inside the structures were rather small, typically small fish or small growing species used them intensively, with those structures performing best that provided the largest pore volume. Since the size of fish in dead wood structures was rather small, it likely indicates that fish presence to an increasing degree was more attributed to their small size than to their structure-affiliated classification or the belonging to a certain species, except for the three salmonids detected in this study. The three salmonid species brown trout, rainbow trout and Danube salmon did not use these structures intensively. This is in line with observations from Norway, where salmonids did not strongly respond to dead wood introductions (Bretzel et al., 2024) or beaver dams (Malison and Halley, 2020) if other hiding places and structures were present. However, since the catch numbers of salmonids herein were rather low, this result must be interpreted with caution. It is possible that salmonid species in other size classes or other seasons potentially would have used the dead wood habitats more intensively as detected by other authors for natural dead wood accumulations (Fausch and Northcote, 1992; Antón et al., 2011; Hafs et al., 2014).

5. Conclusions

This study provides additional evidence that beavers are important ecosystem engineers creating and maintaining valuable small deadwood structures that are highly attractive for fish in fall and winter. In contrast to large beaver dams that can cause conflicts, these structures can more easily be tolerated in HMWBs because they are not conflicting with other restrictions. Ideally, beaver activities in rivers that lead to such small deadwood structures should be supported since their anthropogenic engineering is rather time-consuming, costly and does not fully mimic the ecological functionality for fish. Since some of the structures performed better than others due to differences in incident flow, construction material and pore volume, particular attention should be given to these parameters during construction. In some countries, the capabilities of the beaver are already being used as a cost-effective and nature-based method for stream restoration. In the U.S., the United States Fish and Wildlife Service's Beaver Restoration Guidebook offers suggestions for restoring streams, wetlands, and floodplains using beavers (Pollock et al., 2023). However, it must be noted that wider restoration measures are needed in HMWBs, particular addressing the restoration of critical life stage habitats, to reach long-term sustainable fish populations.

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CRediT authorship contribution statement

Joachim Pander: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Janette Otterbein:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Christoffer Nagel:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Juergen Geist:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Juergen Geist reports financial support was provided by Verbund Innkraftwerke GmbH. Juergen Geist reports a relationship with Verbund Innkraftwerke GmbH that includes: funding grants. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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