

**European beaver (*Castor fiber*) engineered habitats
and their invertebrate community in mountain streams**

Vom Europäischen Biber (*Castor fiber*) gestaltete Lebensräume
und ihre Wirbellosengemeinschaft in Bächen des Mittelgebirges

Dissertation
for
the doctoral degree of
Dr. rer. nat.

From the Faculty of Biology
University of Duisburg-Essen
Germany

Submitted by
Sara Schloemer
Born in Düren

Date of Submission
February 2024

Information on the Examination

The experiments and analysis on which the present work is based were conducted at the Faculty of Biology, Aquatic Ecology at the University of Duisburg-Essen.

1. Examiner: Prof. Dr. Daniel Hering
2. Examiner: Prof. Dr. Frauke Ecke

Chair of the Board of Examiners: Prof. Dr. Sonja Rückert

Date of the oral examination: 27.05.2024

DuEPublico

Duisburg-Essen Publications online

UNIVERSITÄT
DUISBURG
ESSEN

Offen im Denken

ub

universitäts
bibliothek

Diese Dissertation wird via DuEPublico, dem Dokumenten- und Publikationsserver der Universität Duisburg-Essen, zur Verfügung gestellt und liegt auch als Print-Version vor.

DOI: 10.17185/duepublico/82092
URN: urn:nbn:de:hbz:465-20240705-070759-0

Alle Rechte vorbehalten.

Table of Contents

| | |
|--|-----|
| 1. Summary | 4 |
| 1.1 English summary | 4 |
| 1.2 German summary | 5 |
| 2. General introduction..... | 7 |
| 2.1 The return of the beaver..... | 7 |
| 2.2 State of research..... | 8 |
| 2.3 Background of the study | 9 |
| 3 Main chapters | 11 |
| 3.1 A quantification of changes in hydromorphology and habitat complexity induced by beaver activities | 11 |
| 3.2 Species richness and abundance of macrozoobenthos are multiplied by beaver (<i>Castor sp.</i>) activities in small floodplains | 29 |
| 3.3 The macroinvertebrate fauna of maintained and abandoned beaver dams..... | 69 |
| 4 General discussion..... | 120 |
| 4.1 Summary..... | 120 |
| 4.2 Implications of the results..... | 120 |
| 4.3 Outlook | 122 |
| Acknowledgements | 124 |
| References | 125 |
| Curriculum vitae..... | 141 |
| Declarations..... | 142 |

1. Summary

1.1 English summary

Beavers (*Castor* spp.) shape and change their habitat more than almost any other animal species. Beaver dams, beaver ponds and their marginal bogs, stream splits, side channels, beaver meadows and large amounts of deadwood used to be common structures in small streams. The reintroduction and distribution of beavers in the northern hemisphere is accompanied by a continuous “restoration” of the small watercourses and their floodplains, the consequences of which has scarcely been explored to date.

To investigate the influence of beaver activities, I studied aquatic habitats created by beavers and compared them with aquatic habitats in comparable stream sections without beavers. I used the abundance, species richness and functional groups of the macrozoobenthos community, as well as the size, diversity and complexity of the habitats as indicators.

In the first chapter, I explored the impact of beaver activities on stream and floodplain morphology and habitat complexity, using aerial photography, transect mapping and a geographic information system. I focused on changes in wetted surface, macro- and micro-habitats, as well as the connectivity of the stream-floodplain complex. The results revealed that beaver activities drastically increased the wetted surface area and created a diverse complex of lentic, lotic and semi-aquatic habitats. Furthermore, beaver activities improved the connectivity of the stream-floodplain complex by lengthening the shoreline, reducing stream incision and thus enhancing the hydrological connection between the aquatic and the riparian area. Additionally, the number, diversity and heterogeneity of micro-habitats increased due to beaver activities. Especially, the amount of deadwood increased extremely, and - together with the presence of emergent macrophytes – contributed to a higher habitat complexity and diversity in comparison with stream sections without beavers.

In the second chapter, I studied the macrozoobenthos community in the beaver created habitats, such as ponds and side channels and compared them to habitats stream sections without beavers, e.g. riffles and pools. For this, I collected 188 habitat-specific macrozoobenthos samples that yielded more than 82,000 individuals. The differences between stream section types were analysed in terms of the abundance and species richness, as well as the flow preferences of the macrozoobenthos community. Beaver activities had a profound positive impact on macrozoobenthos diversity, significantly enhancing both species richness and abundance. In beaver territories, the flow preferences are more heterogeneous than in stream sections without beavers which are dominated by lotic taxa. Community composition was most similar between habitat types with comparable flow patterns, such as beaver ponds and pool-habitats in non-

beaver territories. In both stream sections types, rheophilous taxa accounted for the largest percentage (> 50 %) of the community. Furthermore, the results show that beaver activity increased the functional and taxonomical diversity of macrozoobenthos.

In the third and final chapter, the macrozoobenthos fauna of beaver dams was investigated in detail. Beaver dams are special habitats in the aquatic-terrestrial interface, but their macrozoobenthos community is hardly known. This study aimed to quantify and characterize this community, taking into account the maintenance state of the dams. Nine different areas of a dam were systematically sampled, from the top to the middle and bottom areas using a suction device specially developed for this purpose. The macrozoobenthos community of beaver dams proved to be diverse and predominantly rheophile. Differences in the colonizing structure were directly dependent on the degree of maintenance and the area of a dam. The species distribution indicated an increase of flow velocity from the top to the bottom of the dams. Thereby, the flow gradient was higher in maintained dams than in abandoned ones. In terms of feeding types, shredders were most strongly represented. However, these were less common in middle and bottom areas, especially in maintained dams, where passive filter feeders predominated. In addition, next to the typical running water fauna, semi-aquatic taxa also colonized beaver dams, preferably in middle and bottom areas of abandoned dams. The results show that beaver dams offer an impressively wide range of environmental conditions and habitat types that promote a high biodiversity in streams and floodplains.

Due to the sample size and the methods used, this study is one of the most detailed on this subject conducted to date. Therefore, this thesis provides new insights into the complexity of beaver engineering of aquatic ecosystems. In the context of the ongoing devastation of aquatic environments, the expansion of the beaver represents an outstanding potential for species and habitat conservation, restoration, maintenance and protection. In addition, the results may update the classic concept of the hydromorphology and invertebrate colonization of mountain streams, in which beaver activities have not yet been taken into account.

1.2 German summary

Biber (*Castor* spp.) formen und verändern ihren Lebensraum mehr als fast jede andere Tierart. Biberdämme, Biberteiche und ihre Randvermoorungen, Bachaufspaltungen, Nebengerinne, Biberwiesen und ein großer Totholzfall waren einst häufige Strukturen in kleinen Bächen. Die Wiederansiedlung und Verbreitung von Bibern auf der Nordhalbkugel, geht mit einer kontinuierlichen Wiederherstellung der kleinen Wasserläufe und ihrer Auen einher, deren Folgen bis heute kaum vollständig erforscht wurden. Um den Einfluss der Biberaktivitäten zu

untersuchen, habe ich aquatische Lebensräume, die von Bibern geschaffen wurden, genauer untersucht und sie mit aquatischen Lebensräumen in Bachabschnitten ohne Biber mit vergleichbaren Strömungsmustern verglichen. Ich habe die Häufigkeit, Artenvielfalt und funktionelle Gruppen der Makrozoobenthos-Gemeinschaft sowie die Größe, Vielfalt und Komplexität der Lebensräume als Indikatoren verwendet.

Im ersten Kapitel habe ich die Auswirkungen von Biberaktivitäten auf die Morphologie und die Habitatkomplexität erforscht, unter Verwendung von Luftbildern, Transektkartierungen und Geoinformationssystemsoftware. Ich habe mich auf Veränderungen der Gewässerfläche, der Makro- und Mikrolebensräume, sowie der Konnektivität des Bach-Auen-Komplexes konzentriert. Die Ergebnisse zeigten, dass Biberaktivitäten die Gewässerfläche erheblich vergrößerten und einen vielfältigen Komplex aus lenitischen, lotischen und semiaquatischen Lebensräumen schufen. Darüber hinaus verbesserten Biberaktivitäten die Konnektivität des Bach-Auen-Komplexes, durch Verlängerung der Uferlinie und die Verringerung der Bacheintiefung, womit die hydrologische Verbindung zwischen dem aquatischen und terrestrischen Lebensraum erhöht wurde. Zusätzlich nahm die Anzahl, Vielfalt und Heterogenität von Mikrolebensräumen in den Biberrevieren zu. Insbesondere das erhöhte Totholzvorkommen und die Entwicklung emerser Makrophyten in Biberrevieren trug zu einer höheren Komplexität und Vielfalt der Lebensräume bei.

Im zweiten Kapitel untersuchte ich die Artengemeinschaft des Makrozoobenthos in den durch Biberaktivitäten entstandenen Lebensräumen, wie z.B. Teiche und Seitengerinne und verglich sie mit den Lebensräumen in Gewässerabschnitten ohne Biber (z.B., Schnellen und Stillen). Hierfür habe ich 188 habitatspezifische Makrozoobenthosproben, mit über 82.000 Individuen gesammelt und analysiert. Die Unterschiede zwischen Gewässerabschnitten mit und ohne Biber wurden hinsichtlich der Abundanz, der Artenvielfalt sowie der Strömungspräferenzen des Makrozoobenthos analysiert. Die Biberaktivitäten hatten einen äußerst positiven Einfluss auf die benthische Wirbellosengemeinschaft, indem sie sowohl die Artenvielfalt als auch die Abundanz deutlich erhöhten. In Biberrevieren waren die Strömungspräferenzen heterogener als in Gewässerabschnitten ohne Biber, die von lotischen Taxa dominiert werden. Am ähnlichsten war die Zusammensetzung der Arten in Habitaten mit vergleichbaren Strömungsmustern, wie z.B. Biberteiche und strömungsberuhigte Zonen (Stillen) in Gewässerabschnitten ohne Biber. In Gewässerabschnitten mit und ohne Biber machten rheophile Taxa den größten Anteil (> 50 %) an der Artengemeinschaft aus. Darüber hinaus zeigen die Ergebnisse, dass Biberaktivitäten die funktionelle und taxonomische Vielfalt des Makrozoobenthos erhöht hat.

Im dritten und letzten Kapitel wurde die Makrozoobenthosbesiedlung von Biberdämmen im Detail untersucht. Biberdämme sind besondere Lebensräume an der aquatisch-terrestrischen Grenzfläche, bisher ist ihre Makrozoobenthosgemeinschaft aber kaum bekannt. Ziel dieser Studie war es, die Wirbellosenfauna von Biberdämmen zu charakterisieren und zu quantifizieren, wobei der Erhaltungszustand der Dämme berücksichtigt wurde. Neun verschiedene Bereiche eines Damms wurden systematisch, vom oberen über mittleren und unteren Bereich, mit einem speziell für diesen Zweck entwickelten Sauggerät beprobt. Die Makrozoobenthosgemeinschaft von Biberdämmen erwies sich als vielfältig und überwiegend rheophil. Unterschiede in der Besiedlungsstruktur waren direkt vom Erhaltungszustand und der Größe eines Damms abhängig. Die Artenverteilung deutete auf eine Zunahme der Fließgeschwindigkeit innerhalb der Dämme, von Dammkrone zum Dammfuß, hin. Dabei war das Fließgefälle in gewarteten Dämmen höher als in aufgegebenen. In Bezug auf die Ernährungstypen waren Zerkleinerer am häufigsten vertreten. Diese waren jedoch seltener in mittleren und unteren Dammbereichen, insbesondere von gewarteten Dämmen, wo passive Filtrierer dominierten. Zusätzlich zur typischen Fließwasserfauna besiedelten auch semiaquatische Taxa Biberdämme, vorzugsweise in mittleren und unteren Bereichen aufgebener Dämme. Die Ergebnisse zeigen, dass Biberdämme eine große Vielfalt an Umweltbedingungen und Lebensraumtypen bieten, die die biologische Vielfalt in Bächen und ihrer Auen fördern.

Aufgrund der Stichprobengröße und der angewandten Methoden ist diese Studie eine der detailliertesten zu diesem Thema, die bisher durchgeführt wurde. Daher bietet diese Arbeit neue Einblicke in die Komplexität von biberinduzierten Habitaten in aquatischen Ökosystemen. Im Zusammenhang mit der anhaltenden Zerstörung aquatischer Lebensräume stellt die Ausbreitung des Bibers ein herausragendes Potenzial für den Arten- und Lebensraumschutz, sowie für die Renaturierung und Erhaltung dar. Darüber hinaus können die Ergebnisse dazu beitragen, das klassische Konzept der Hydromorphologie und der Besiedlung durch Wirbellose in Gebirgsbächen zu aktualisieren, in dem der Biber bisher noch nicht berücksichtigt wurde.

2. General introduction

2.1 The return of the beaver

Since the Miocene, beavers (*Castor canadensis*, *C. fiber*) inhabited the entire northern hemisphere (Hood 2020), colonizing nearly all aquatic habitats and bodies of water (Naiman et al. 1988). However, overhunting and intensified land use led to the near extinction of beavers within their historical range by the 19th century (Nolet and Rosell 1998). By the early 20th

century, approximately 1200 beavers remained in this vast area (Müller-Schwarze 2011; Halley et al. 2021). The loss of beavers resulted in the depletion of habitats and ecosystem services (Scamardo et al. 2022), due to their crucial role as ecosystem engineers and keystone species, which significantly influences ecology, geomorphology, and hydrology (Rosell et al. 2005; Brazier et al. 2021). Conservation measures and multiple reintroduction projects are helping beavers to spread again and their population to recover (Müller-Schwarze 2011; Hartman 1994). The return of beavers is driving ongoing habitat restoration, especially in the upper reaches of streams, where beaver dams as vital structural components were absent (Burchsted and Daniels 2014; Scamardo et al. 2022). Gradually it is recognized that the concept of natural streams and the established baseline conditions are heavily influenced by our cultural landscape, which has lost structural elements such as accumulations of deadwood and beaver dams (Harthun 1999; Hering et al. 2001; Burchsted et al. 2010; Törnblom et al. 2011).

2.2 State of research

First studies on the effects of beaver activities on the wetted surface area, stream morphology, and in-stream habitats have been published since the 1980s (Naiman et al. 1984; Naiman et al. 1986; Naiman et al. 1988). In this context, macro-habitats, and almost exclusively beaver ponds, have been the primary focus (Burchsted and Daniels 2014). Subsequently, studies about changes of the morphology of watercourses caused by dam building beaver activities are quite common (Curran and Cannatelli 2014; Gurnell 1998). Several authors described the transition from one-channel streams into multi-braided stream networks, with an increased structural heterogeneity, floodplain connection and patch dynamics through beaver dams (Green and Westbrook 2009; Polvi and Wohl 2012; Pollock et al. 2007). Thereby, the pond sediments, as fine scaled substrates, (Butler and Malanson 2005; Green and Westbrook 2009; John and Klein 2003; Polvi and Wohl 2012; Rurek 2021) and sedimentation rates (Butler and Malanson 1995; Visscher et al. 2012; Kroes and Bason 2015) were of main interest. In terms of micro-habitats, other substrate types next to fine scaled sediments are rather neglected and research of other micro-habitats such as deadwood (Law et al. 2016) and vegetation (Wright et al. 2002) are rare. As a result, the assumption has solidified that the construction of beaver dams leads to the replacement of a rheophilic species community by a lentic one (McDowell and Naiman 1986). Research on macrozoobenthos support the observed transition from rheophile to limnophile species as result of beaver influence, which is based on investigating solely beaver ponds (Arndt and Domdei 2011; Bush and Wissinger 2016; Bylak and Kukuła 2022; Naiman et al. 1988). This also involves a change in the composition of functional feeding groups; gatherers and predators increase in beaver ponds, while shredders and grazers decrease (Naiman et al. 1988).

Research on the abundance of macrozoobenthos indicates an increase in beaver ponds compared to stream sections without beavers (Ford and Naiman 1988; Rolauffs et al. 2001). Most other studies compared watercourse sections up- or downstream of beaver territories (Smith et al. 1991; Fuller and Peckarsky 2011a, 2011b; Redin and Sjöberg 2013; Johansson 2014). Differences in the number of species and abundance were rarely or never observed. The focus mainly on beaver ponds and solely the fine-grained sediments they contain led to misinterpretations of the entire habitat complex that beaver create through their activities.

2.3 Background of the study

Only in recent years have beaver activities and the resulting habitats been examined in more detail and their specific biocoenoses studied. Bush et al. (2019) investigated invertebrate dynamics in beaver created habitats, revealing distinct taxonomic compositions at each successional stage, leading to approximately doubled Beta-diversity in the entire study-system. Harthun (1998) studied several beaver created habitats, such as side channels which turned out to provide permanent or temporary habitats for specific species. There were only two previous studies on the invertebrate fauna of beaver dams (Clifford et al. 1993; Rolauffs et al. 2001), both of which found an invertebrate fauna typical of fast-flowing streams. In addition, Rolauffs et al. (2001) demonstrated a significantly higher abundance and biomass of the species composition. Hood and Larson (2014) examined beaver channels created by digging activities, which led to an expansion of unique aquatic habitats with hotspots for predatory aquatic invertebrates. The influence of beaver engineering on terrestrial biodiversity have been quantified in detail by Orazi et al. (2022), which demonstrated increasing heterogeneity of habitats and species biodiversity. A quantification of aquatic biodiversity for all habitats created by beavers for larger floodplain sections has not yet been carried out. Furthermore, previous studies have mostly dealt with case studies with little or no replication or have only looked at single beaver created habitats (Ford and Naiman 1988; Smith et al. 1991; Margolis et al. 2001; Fuller and Peckarsky 2011a, 2011b; Johansson 2014; Wojton and Kukuła 2021). In addition, the limited exploration of beaver created habitats, particularly those of beaver dams, can be traced back to the difficulties in accessing their internal structures. It is therefore not possible to quantify the effects caused by beaver activities. The studies mentioned conclude that the scale level to be investigated in beaver-influenced streams must be smaller in order to be able to quantify the corresponding effects on the entire stream ecosystem.

The aim of this dissertation is to investigate a wide range of beaver-induced habitats in order to comprehensively analyze the changes caused by beaver activities. To achieve this, I employed

various methods that have not been applied before. These included conducting transect surveys in combination with aerial drone images to examine micro- and macro-habitats within entire stream sections with and without beaver influence on a small spatial scale. Additionally, I studied the macrozoobenthos in the different habitats to analyze the influence of beaver activities on their functional and taxonomic diversity. In order to ensure a high number of replicates, several streams and watercourse sections were investigated. Furthermore, I designed a special suction device to sample the macrozoobenthos within the inner structures of beaver dams. For the first time, the macrozoobenthos was systematically investigated, distinguishing the succession stage and different dam areas. I focused on small waterbodies where beavers need to build dams to colonize, so their impact is greatest in these areas. In addition, all the waterbodies studied were in near-natural condition, so that additional anthropogenic factors could be excluded. In total, I investigated three streams in the northern Eifel, located in the reintroduction area of the European beaver in North Rhine-Westphalia. The beaver created habitats were characterized in terms of area, substrate types and flow velocity and the macroinvertebrate community in beaver created habitats explored with the following scope:

- (1) Quantification and characterization of the aquatic habitats in beaver and non-beaver territories
- (2) Quantification and characterization of the macrozoobenthos in beaver and non-beaver territories
- (3) Beaver dams as habitat structure of macrozoobenthos

In the context of this doctoral work, the article "The macroinvertebrate fauna of maintained and abandoned beaver dams" was published in *Hydrobiologia*. 850 (8), 1763 – 1778. Furthermore, the article "Species richness and abundance of macrozoobenthos are multiplied by beaver (*Castor* sp.) activities in small floodplains" was submitted to *Freshwater Biology* on September 19th, 2023 and is still under review.

3 Main chapters

3.1 A quantification of changes in hydromorphology and habitat complexity induced by beaver activities

Abstract

Hydromorphology and habitat complexity of three beaver territories were investigated in comparison to three nearby stream and floodplain sections unaltered by beavers. We quantified macro-habitats, such as beaver ponds, dams, riffles and pools by field measurement and aerial photographs. Furthermore, we measured water width and incision depth along cross-sectional transects and the length of the shoreline to quantify water-floodplain connectivity. For micro-habitat heterogeneity and diversity, we measured the variation of water depth and quantity and quality of substrate types at 600 locations via transect mapping. Due to beaver engineering, wetted surface increased by factor of 6, and the ratio of lotic to lentic area reversed (beaver-territory: 1:6; non-beaver territory: 5:1). The length of the shoreline increased by 280 % on average and the incision depth decreased from a median of 50 cm in non-beaver territories to a median of 10 cm in beaver territories. The variance of water depth is high, in both beaver ($cv = 0.83$) and non-beaver territories ($cv = 0.77$), while there is clearly more variance in width of the water bodies in beaver territories ($cv = 0.97$) than in non-beaver territories ($cv = 0.32$). We detected two more substrate types in beaver territories (macrophytes and argyllal/loam), and the availability of many substrates increased drastically (e.g., dead wood: 2890 %, living parts of terrestrial plants: 11,550 %). The share of bottom area covered by larger stony substrates (≥ 6 cm) decreased, whereas the area of smaller stones (≤ 6 cm) increased. Beaver activities enhanced substrate diversity, as indicated by a higher Shannon-Diversity-Index of substrate types (beaver territories 1.9; non-beaver territories 1.6). Substrate heterogeneity, the sequences of substrate types per transect, increased in beaver territories as well ($cv = 0.36$; non-beaver-territories $cv = 0.29$). Our study highlights the diversifying effects of beaver activities on instream habitats through macro-habitat creation, improvement of connectivity, and increase of micro-habitat availability. We conclude that “beaver engineering” could be a cost-effective and impactful component of future restoration strategies.

Introduction

Watercourses in forested low mountain ranges are naturally dynamic ecosystems with a wide range of different substrate types such as silt and gravel, but also allochthonous organic matter such as leaf litter and dead wood (Reice 1974). The different substrate types in combination with the current lead to “patch-specific components” associated with specific benthic

communities that are characteristic of the local environment (Reice 1974; Pringle et al. 1988). Overall structural diversity is associated with abundance and species richness of benthic communities (Mocq et al. 2021). Therefore, structural diversity encompasses habitat heterogeneity (diversity of structural elements) and habitat complexity, which includes spatial scale, diversity, size, density, and arrangement of structural elements (Kovalenko et al. 2012). In stream ecosystems, benthic invertebrate diversity is assumed to be highly connected to size distribution and heterogeneity of substrate particles, as well as surface complexity (Kovalenko et al. 2012). Additionally, the proportion of insects that emerge, rather than drift downstream or end up in aquatic predators, is heavily influenced by habitat structure that retains and acts as a refuge for aquatic insects (Power and Rainey 2000).

Structures such as woody debris and depth variation increase transient storage and complexity by increasing retention of nutrients and particulates in streams. Furthermore, biodiversity in river corridors is also increased by the morphological diversity of the surrounding floodplains (Johnston and Naiman 1987; Pringle et al. 1988; Garcia et al. 2012). Stream channels with complex morphology and well-developed riparian vegetation maintain high transient storage even during high flows in comparison to simple channels (Kaufmann and Faustini 2012), making them more resilient to changing environmental conditions.

It has long been known, but rarely quantified, that beaver activities could greatly enhance structural diversity of streams (Burchsted et al. 2010; Burchsted and Daniels 2014; Dauwalter and Walrath 2018). “Ecosystem engineering” by beavers includes dam-building in small streams, which leads to deadwood accumulation and pond formation, thus fundamentally changing the environmental conditions (e.g., flow regime, substrate heterogeneity). Therefore, beaver activities create patches in streams and act as biotic vectors that affect fluxes of energy and materials across patch boundaries (Pringle et al. 1988). Flooding associated with beaver dams not only affects the stream channel but also surrounding terrestrial habitats, thus linking them more effectively to the aquatic system (Billings et al. 1987). Thus, beaver activities result in a significant increase in habitat heterogeneity and connectivity at the landscape scale (Billings et al. 1987; Hood and Larson 2015). However, quantifying changes in hydromorphology and habitat composition caused by beaver engineering has rarely been studied, as the focus so far has been almost exclusively on beaver ponds (Burchsted and Daniels 2014). In particular, changes at the micro-habitat level that are most relevant for benthic assemblages have been neglected. In this respect, pond sediments, such as fine-grained substrates (Butler and Malanson 2005; Green and Westbrook 2009; John and Klein 2003; Polvi

and Wohl 2012), and sedimentation rates (Butler and Malanson 1995; Visscher et al. 2012; Kroes and Bason 2015) have so far been the main subject of research.

Here, we quantified the hydromorphological changes associated with “beaver engineering” in small mountain streams by comparing floodplain sections modified by beavers with nearby sections without beaver activities. To capture changes at different spatial and functional scales, we considered various aspects of habitat complexity, such as water area, aquatic-terrestrial connectivity, water depth variability, habitat availability, as well as substrate heterogeneity and diversity. We addressed the following questions:

1. How is stream morphology, i.e. wetted surface area and quantity and composition of aquatic macro-habitats, modified by beaver activities?
2. How are components of aquatic-terrestrial connectivity, in particular shoreline length, incision depth and variance of water body width, modified by beaver activities?
3. How are micro-habitat quantity, diversity and heterogeneity, as key components for benthic assemblages, modified by beaver activities?

Study area

The study took place in the Hürtgenwald region (50°44`N, 6°20`E), a 120 km² state forest (<https://www.wald-und-holz.nrw.de>, 2022) in western Germany, located in the federal state of North-Rhine Westphalia, which is adjacent to the Netherlands and Belgium. The area is situated within the Rhenish Massif, which is characterized by elevations ranging from 240 to 450 meters above sea level and by moderate Atlantic climate with cool summers and mild winters. It has an average temperature of 8.5 °C (<https://cdc.dwd.de/portal>) and an annual precipitation of 1062 mm (<https://www.elwasweb.nrw.de>). Due to the combination of high precipitation, steep terrain, and low soil permeability, the region features a complex and dense network of streams. Eurasian beavers (*Castor fiber*) were reintroduced to the area between 1981 and 1989 (Naumann 1991). The current estimated population size of European beavers in the federal state of North-Rhine Westphalia exceeds 1200 individuals (Dalbeck 2021). In the study area, there are approximately five beaver territories per 10 square kilometres (Dalbeck 2022), and the density of beaver dams in the small watercourses is approximately four dams per kilometre (Dalbeck et al. 2014).

Methods

The study was conducted in spring (March, April) 2019. We paired sections in beaver territories with sections located ≥ 200 m upstream with no beaver activities (“non-beaver territories”).

The

paired sections were distributed in three streams similar in elevation, stream size and slope (Fig. 1a). Each section was 200 m long.

Data on macro-habitats were collected through transect mapping (Jähnig et al. 2009) by investigating ten equally spaced transects across to the watercourse (Fig. 1c). Here, we measured the width of the water body and the bank height on each side of the shore to calculate incision depth. Furthermore, 10 points were distributed evenly over the transects' width, at which we recorded water depth, substrate type and flow pattern (Fig. 2). In total, 10 transects with 100 data points were generated per section (60 transects and 600 data points for the overall study). The categorization of substrate types coincide with the multi-habitat sampling protocol of Hering et al. (2003), and categorization of the flow patterns with Jähnig et al. (2009). We measured water depth with a folding ruler. In beaver ponds we used an amplified centimetre scale attached to a telescoping rod, which enabled depth measurement from the shore. A perforated plastic disc at the bottom of the scale prevented the rod from sinking into fine sediment layers that were covering parts of the bed of the beaver ponds. If a side channel was present within a transect, we recorded water depth and width, substrate type and flow pattern at one point within the channel. In combination with transect mapping, we took aerial pictures of the sections by drone (DJI Mavic Air, 12 megapixels).

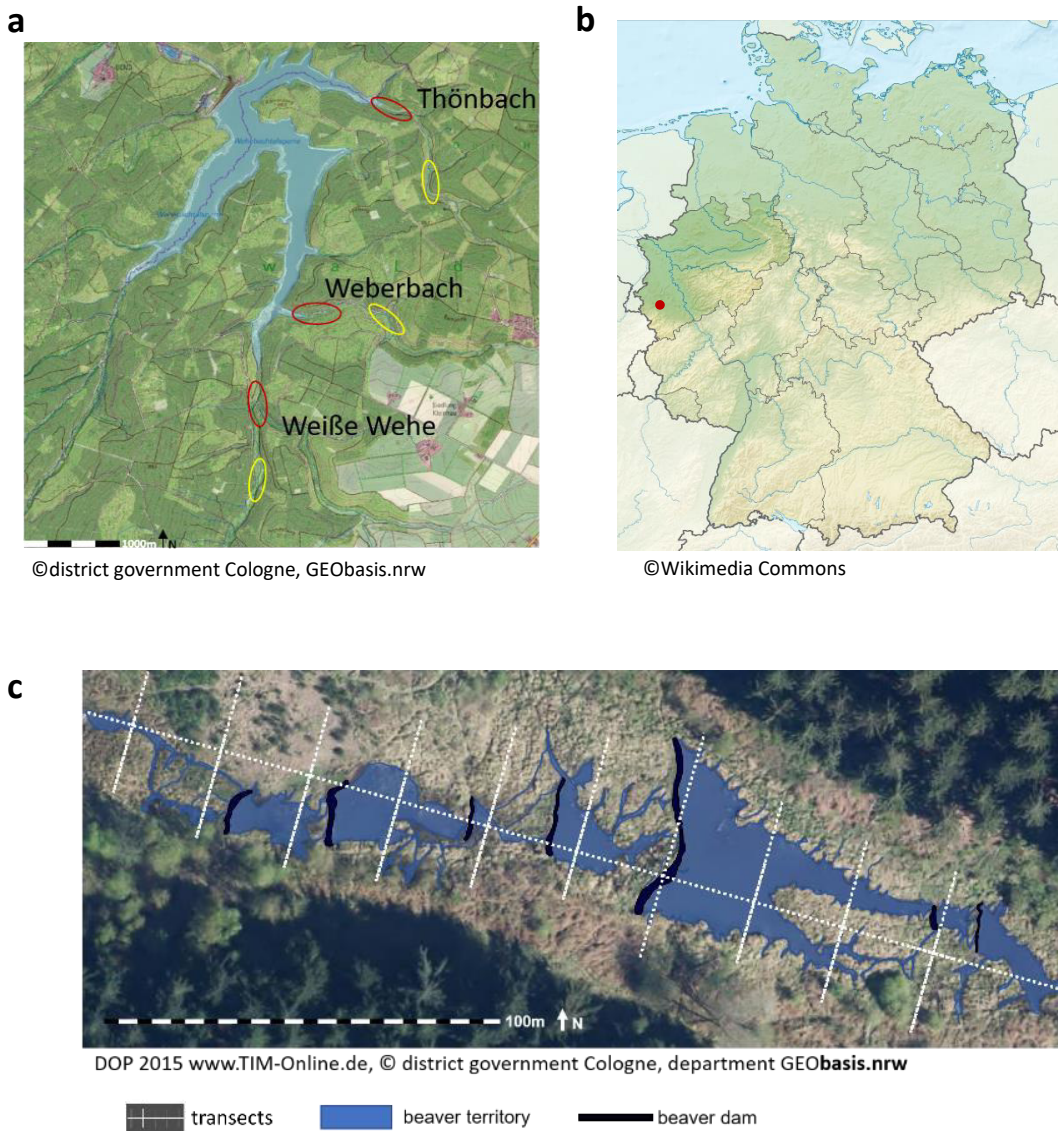


Figure 1 a) Location of the study streams Thönbach, Weberbach and Weiße Wehe within Germany (b). Study sections are indicated with coloured circles, in red the beaver territories, in yellow the non-beaver territories (a). c) example of transect mapping of a 200-m stretch in a beaver territory with 10 lateral transects, marked with a white dotted line.

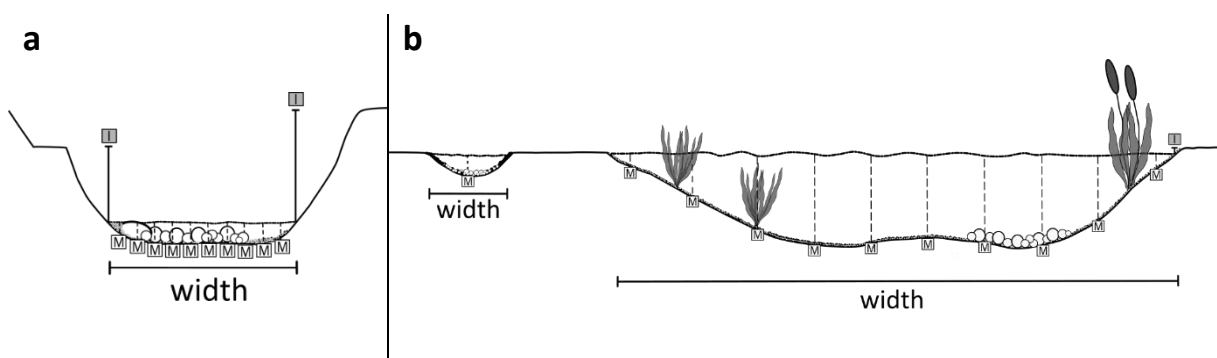


Figure 2 Cross-section of a non-beaver (a) and a beaver (b) territory with lines indicating the 10 measuring points per transect and additional measuring of the side channel.

Data analysis

To address our first question (wetted surface area and macro-habitats), we calculated the total wetted surface area (m^2) as well as areas of the individual macro-habitats (m^2) using the aerial photographs and the geometry function in QGIS 3.24 (<http://qgis.osgeo.org>) for each study site ($n= 6$). For validation, we synchronized the aerial data with the data we measured in the field via transect mapping.

To address the second question (stream-floodplain connectivity), we also applied the geometry function in QGIS 3.24 (<http://qgis.osgeo.org>) to calculate the length (m) of the shoreline (1a) of the studied stream sections. Furthermore, we calculated the incision depth (1b) in beaver and non-beaver territories, as well as the variance of water depth (1c) and waterbody width (1d) using the data from the transect mapping. We present the results (1b-d), as boxplots. To compare the variance of incision depth, water depth and width of water bodies (1b-d) we calculated the coefficient of variation (cv) for beaver and non-beaver territories.

To address question 3 (instream micro-habitat quantity, diversity and heterogeneity), we calculated the area coverage (m^2) of the different substrate types for each section using the data from the transect mapping and the data from the area calculations. First, we pooled data from the transects that ran through a certain macro-habitat type (e.g., beaver pond, downstream dam). Then, we calculated the corresponding shares of the micro-habitats per macro-habitat using the data from the area calculations. We expressed changes in substrate composition and quantity as percentages (Table 2). To address substrate diversity, we calculated the Shannon diversity index based on the number and share of substrate types per territory type. Finally, we calculated substrate heterogeneity as the sequences of substrate types within a transect (patch richness) and compared for beaver and non-beaver territories via the coefficient of variance (cv).

Results

Wetted surface area and macro-habitats

The number of macro-habitats increased due to beaver activities, adding four more habitat types to the floodplain sections (i.e., ponds, side channels, beaver dams and free-flowing areas downstream of dams). Table 1 represents the average area (m^2) of the macro-habitats within the 200-m floodplain sections, thereby resulting in an increase of wetted surface by a factor of 6 due to beaver engineering. Therefore, the absolute area of lotic habitats was maintained (beaver-

territory: 231 m²; non-beaver territory: 224 m²), but the ratio of lotic to lentic area reversed in beaver territories (beaver-territory: 1:6; non-beaver territory: 5:1).

Table 1 Average area (m²) of the different habitats within the 200-m floodplain sections.

| Site | Habitats (flow condition) | Average area (m ²) within 200 m floodplain section |
|----------------------|--|--|
| beaver territory | side channel (lotic) | 35 |
| | beaver dam (lotic) | 80 |
| | free-flowing sections downstream of beaver dam (lotic) | 116 |
| | beaver pond (lentic) | 1480 |
| non-beaver territory | riffle (lotic) | 224 |
| | pool (lentic) | 47 |

Stream-floodplain connectivity

The length of the shoreline within the studied stream sections increased on average by 280% because of beaver activities (Fig.3-a), with an average shoreline length of 587 m (ranging between 490 m and 689 m) in beaver territories, compared to non-beaver territories with on average 209 m (range between 206 and 212). The incision depth (Fig. 3-b) decreased in beaver territories ($n = 58$) and ranged between 0 cm and 100 cm ($mean = 25$ cm, $SD = 29$), while in non-beaver territories ($n = 54$) incision depth ranged between 20 cm and 100 cm ($mean = 53$ cm, $SD = 22$). The variance of incision is much higher in beaver territories ($cv = 1.2$) than in non-beaver territories ($cv = 0.45$).

Water depth ranged between 1 cm and 96 cm ($mean = 21$ cm, $SD = 17$) in beaver territories ($n = 292$) (Fig. 3-c) and between one and 29 cm ($mean = 8.1$ cm, $SD = 6$; $n = 300$) in non-beaver territories. With $cv = 0.77$, there is less variance in water depth in non-beaver territories than in beaver territories ($cv = 0.83$). Waterbody width (Fig. 3-d) in beaver territories ranged between 1.7 m and 24 m ($mean = 6$ m, $SD = 5.7$ m; $n = 30$) and in non-beaver territories between 1.2 m and 4.6 m ($mean = 2.5$ m, $SD = 0.8$ m; $n = 30$). With $cv = 0.97$ there is a higher variance of waterbody-width within beaver territories, while the variance is quite small in non-beaver territories ($cv = 0.32$).

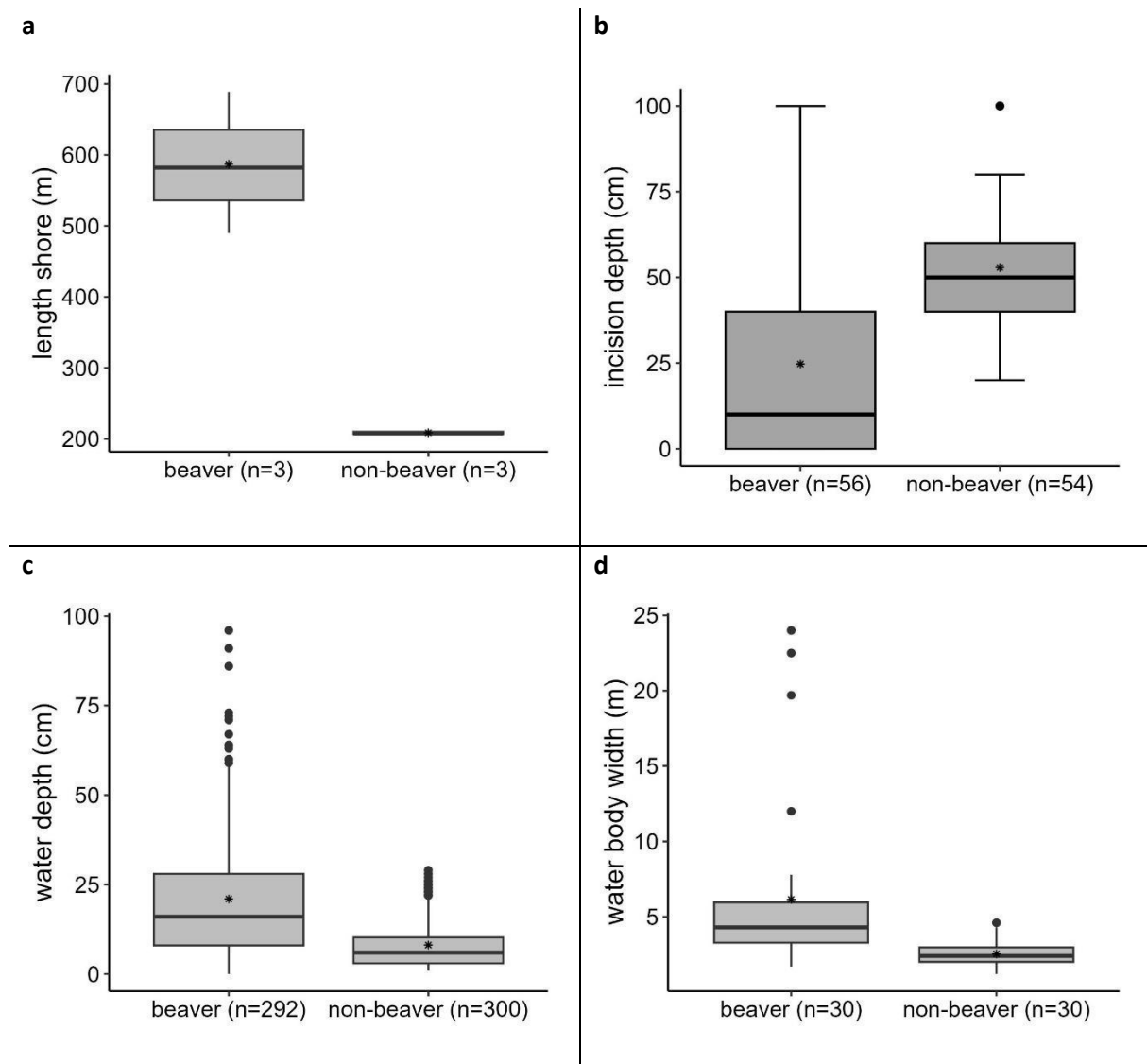


Figure 3 comparison of a) the length of the shoreline, b) the incision depth, c) the water depth, d) the waterbody width in comparison of beaver and non-beaver territories within 200 m stream section.

Instream micro-habitat quantity, diversity and heterogeneity

The number of micro-habitats increased due beaver activities, adding two more substrate types to the streams (argyllal, macrophytes), with 11 types in total. Generally, the area of certain micro-habitats increased significantly, such as “dead wood” (2,890%) or “living parts of terrestrial plants”, which indicates a stronger connection with the riparian vegetation (11,550%). Also, the amount of fine substrates, such as FPOM, increased in the ponds in beaver territories (Table2). Conversely, larger stones (≥ 6 cm), decreased (mesolithal -62 %, makrolithal -6 %) in comparison with non-beaver territories, whereas the area of smaller stones like microlithal (≤ 6 cm) increased by 163 %. In comparison, micro-habitats of non-beaver

territories consist almost entirely of stony substrate types (mesolithal, microlithal and akal), organic substrate types are completely absent or only occur in small quantities (Table. 2).

Table 2 Total area (m²) of substrate types in beaver territories and non-beaver territories and the sum of the areas in the three beaver territories / non-beaver territories (200-m stream length per territory). Changes are expressed as percentage (%).

| substrate type | Substrate definition | change (%) of quantity from non-beaver to beaver territory | Area (m ²) beaver territories | Area (m ²) non-beaver territory |
|----------------------|--|--|---|---|
| Akal | gravel, size range > 0.2 cm – 6 cm | +268 % | 273 | 102 |
| Argyllal | Loam and clay, cohesive material (e.g., alluvial loam) | only detected in beaver territories | 6 | 0 |
| CPOM | Coarse particular organic matter (e.g., leaf litter) | +1,457 % | 1268 | 87 |
| Emergent macrophytes | Emergent macrophytes (e.g., <i>Typha</i> , <i>Carex</i> , <i>Phragmites</i>) | only detected in beaver territories | 311 | 0 |
| FPOM | Fine particular organic matter | +6793 % | 1902 | 28 |
| LPTP | Living parts of terrestrial plants (e.g., roots, floating riparian vegetation) | +11,550 % | 231 | 2 |
| Makrolithal | Stones, size range > 20 cm – 40 cm | -6 % | 15 | 16 |
| Mesolithal | Stones, size range > 6 cm – 20 cm | -62 % | 121 | 318 |
| Mikrolithal | Stones, size range > 2 cm – 6 cm | +163 % | 356 | 219 |
| Psammal | Sand and/or mud, size range > 6 µm – 2 mm | 0 % | 18 | 18 |
| Dead wood | Dead wood | +2,890 % | 636 | 22 |
| Total Area | | + 632 % | 5135 | 813 |

Substrate diversity (number of substrate types per transect), calculated as Shannon-diversity index, was higher in beaver territories (1.9) than in non-beaver territories (1.6). Substrate heterogeneity (the sequence of substrate types per transect or patch richness) ranged between 3 and 8 (*mean* = 5, *SD*= 1.4; *n*= 30) in non-beaver territories. In beaver territories, the sequence of substrate types was higher and ranged between of 2 and 10 (*mean* = 6, *SD*= 2; *n*= 30). The coefficient of variance was higher in beaver territories (*cv* = 0.36) than in non-beaver territories (*cv* = 0.29).

Discussion

Wetted surface and macro-habitats

Shallow wetlands with open water are increasingly at risk, are being reduced in size and depth or disappearing completely due to drought and warming temperatures (Hood and Bayley 2008). Beaver activities may counteract these tendencies. For example, in an area of open water wetlands in morainal landscape in east-central Alberta (Canada) the wetted surface increased 9-fold when beavers were present, and the ponds also had a higher resistance to desiccation (Hood and Bayley 2008). In our study, the open wetted surface also increased greatly by a factor of six, while the pond area ranged between 0.3 m² and 1176 m². Dalbeck et al. (2013) surveyed 149 dams within the same study and described an average associated pond size of 117.6 m²

(max. 1200 m²) per dam. Kaphegyi and Christoffers (2014) discovered an average increase of wetted surface of 2,570,000 m² in a peatland, with a retention of 40,000 m² of water, per dam, on average. These findings demonstrate that water retention by beaver dams depends highly on the topography (Johnston and Naiman 1987) and that in flat terrain, even small dams can create large-scale ponds (Kaphegyi and Christoffers 2014; Johnston and Naiman 1987).

Beaver ponds, as lentic habitats, act as longitudinal discontinuities in stream ecosystems and typically are associated with greater upstream lateral connectivity of water and sediment storage (Kondolf et al. 2006). Furthermore, beaver ponds represent wetlands that are important for wildlife (Brown et al. 1996; Dalbeck 2020) and beaver dam complexes are likely to create more spatially complex flow (Green and Westbrook 2009).

However, our study highlights that lotic habitats did not disappear; rather the ratio of lotic to lentic area is reversed. Despite this reversal, the area of lotic habitats was still maintained in free-flowing sections downstream of dams, in beaver dams themselves and side channels. These areas are characterized by unique habitat features that distinguish them from lotic areas in non-beaver territories. Law et al. (2016) described areas downstream of dams as unmodified sections of streams between successive beaver impoundments, characterised by water flowing over and through the dam. These areas are influenced by upstream pond morphology, dam height and phytoplankton spillover (Fuller and Peckarsky 2011a). Downstream effects of beaver ponds on nutrients, resources and consumers depend on variation in pond morphology and annual hydrologic variation (Fuller and Peckarsky 2011a). Additionally, cold pore water infiltrates this area because of the downward pressure exerted by the pond above, which then diminishes further downstream of the dams (White 1990; Dittbrenner et al. 2022). This process affects the temperature regime of streams in beaver territories (White 1990; Dittbrenner et al. 2022) and eventually the life cycle of aquatic invertebrates, which Fuller and Peckarsky (2011b) showed for the size and time of emergence of *Baetis* sp. (Ephemeroptera).

Beaver dams are lotic habitats and the flow velocity within dams can be very high and variable (Woo and Waddington 1990; Rolauffs et al. 2001). These dams are able to create lotic conditions in lowland streams where otherwise lentic conditions prevail (Clifford et al. 1993). Therefore, the size and shape of beaver dams varies greatly (Ronnquist and Westbrook 2021; Warren 1932; Burchsted et al. 2010), and construction activities by beavers are exclusively determined by geomorphological and hydrographic settings (Danilov et al. 2011). Logs of varying length, stones and mud are the main building materials of beaver dams (Butler and Malanson 1995; Müller-Schwarze 2011; Rolauffs et al. 2001). As in-stream structures, beaver dams have a large internal surface area resulting in a network of interstitial spaces easily

accessible to organisms (Rolauuffs et al. 2001). They provide a wide variety of environmental conditions and habitat types within a very small area and undergo a distinct succession, which further enhances the variability of micro-habitats per dam (Schloemer et al. 2023). Individual site characteristics affect the number of dams within a territory and can range between 0.1 dam/km (McComb et al. 1990) and 19 dams/km (Woo and Waddington 1990). The number and sizes of the beaver dams in our study were consistent with the data observed in comparable regions. In our study, beaver activities led to the development of side channels which added flow length to the stream and connected aquatic habitats with terrestrial ones. The creation of side channels due to beaver activities and their positive effects on hydromorphology are very frequently described. Side channels enhance the total water flow length by diverting water onto the floodplain, thus resulting in a multi-channel drainage network and increase channel complexity (John and Klein 2003; Polvi and Wohl 2012; Green and Westbrook 2009).

Connectivity of the stream-floodplain complex

The shoreline of beaver ponds is radial, which additionally increases habitat heterogeneity (Hood and Larson 2015). The shoreline includes inlets and outlets created by frequent use by beavers or excavated channels by beavers used to connect ponds and aid in transportation of food and building materials (Hood and Larson 2015). Due to these structures and additional side channels, we found that the length of the shoreline was on average three times longer in beaver territories than in non-beaver territories. According to Iwata et al. (2003), lengthening of the shoreline due to greater sinuosity correlates with greater abundance of aquatic insects because the space near the edge of the stream and also the stream surface is increase. Likewise, the higher variance of the width of the waterbody within beaver territories ($cv = 0.97$; non-beaver territories $cv = 0.32$) increases the aquatic-terrestrial interface. Stream patterns, such as length and width influence abundance, influence the distribution and flux rate of aquatic insects (Iwata et al. 2003; Power and Rainey 2000). According to Iwata et al. (2003), the boundary shape, delimited by stream geomorphology, is a spatial feature that strongly affects the degree of trophic connectivity between forest and stream.

Stream incision disrupts the hydrological connection between the aquatic and riparian area. In our study, the incision depth of the streams within beaver territories was greatly reduced due to water elevation and reconnection to the shore by beaver activities. However, incision depth varied within beaver territories and, in exceptional cases, at free-flowing sections the same maximum depth was the same as that found in non-beaver territories.

Number and availability of micro-habitats

Beavers are important drivers of ecological change, because they actively transport materials across the terrestrial/aquatic boundary, which results in substantial inputs of organic matter and nutrients to the aquatic ecosystem (Johnston and Naiman 1987). In our study, the amount of deadwood highly increased, especially due to dam-building, which promotes an increase in benthic invertebrate abundance and diversity by providing habitat for attachment substrate, shelter or food sources, and as a place for oviposition or pupation (Flores et al. 2017; Hoffmann and Hering 2000). Furthermore, beaver dams induce the reconnection to the riparian area, which increases the presence of riparian vegetation (“living parts of terrestrial plants”, e.g. roots). Substrate types, including roots and bryophytes, display high micro-heterogeneity and enhance taxonomic richness of benthic invertebrates (Beisel et al. 1998). Furthermore, beaver dams positively affect material retention, habitat formation and productivity (Naiman et al. 2002), thereby creating areas with low flow and fine-scale substrate types (Rurek 2021). We also determined that the amount of fine and coarse organic matter and other fine scaled substrates (akal) increased in beaver territories, as well as the area of smaller stones (≤ 6 cm). However, the presence of middle-sized stones decreased. There were two substrate types that only occurred in beaver territories, these were aquatic vegetation (emergent macrophytes) and argyllal (e.g. alluvial loam). These findings are important because plants provide food, habitat, and refuge for benthic invertebrates; therefore, their presence positively affects abundance and diversity of many aquatic taxa (Beisel et al. 1998; Carpenter and Lodge 1986). According to Duan et al. (2009), the diversity, of benthic invertebrates is directly proportional to the availability of different micro-habitats. Beaver ecosystem engineering clearly promotes substrate diversity and heterogeneity and, therefore, micro-habitat complexity in stream ecosystems.

Conclusions

Our study examined the impact of beaver activities on aquatic ecosystems, with a specific focus on changes in total wetted surface, macro-habitats and connectivity of the stream-floodplain complex. Our findings revealed that beaver activities dramatically increased wetted surface area, and created a diverse complex of lentic, lotic and semi-aquatic habitats. Furthermore, beaver activities played a crucial role in increasing the connectivity of the stream-floodplain complex, due to lengthening the shoreline, thus reducing incision depth and consequently enhancing hydrological connections between the aquatic and riparian habitats. Additionally, our study highlights the increase in number, diversity and heterogeneity of micro-habitats within beaver territories. The presence of deadwood, riparian vegetation and diverse substrates in beaver territories contributes to higher habitat complexity and biotic diversity. Overall, our research underscores the positive ecological effects of beaver activities, including habitat creation, connectivity enhancement and increased micro-habitat availability. Given challenges posed by climate change and the continual decline of aquatic ecosystems, beaver activities should be incorporated into existing and future conservation and restoration strategies.

References

- Beisel, J.-N.; Usseglio-Polatera, P.; Thomas, S.; Moreteau, J.-C. (1998): Stream community structure in relation to spatial variation: The influence of mesohabitat characteristics. In *Hydrobiologia* 389 (1/3), pp. 73–88. DOI: 10.1023/A:1003519429979.
- Billings, W. D.; Golley, F.; Lange, O. L.; Olson, J. S.; Remmert, H.; Turner, Monica Goigel (Eds.) (1987): *Landscape Heterogeneity and Disturbance*. New York, NY: Springer New York (Ecological Studies).
- Brown, D. J.; Hubert, W. A.; Anderson, S. H. (1996): Beaver ponds create wetland habitat for birds in mountains of southeastern Wyoming. In *Wetlands* 16 (2), pp. 127–133. DOI: 10.1007/BF03160686.
- Burchsted, D.; Daniels, M.; Thorson, R.; Vokoun, J. (2010): The River Discontinuum: Applying Beaver Modifications to Baseline Conditions for Restoration of Forested Headwaters. In *BioScience* 60 (11), pp. 908–922. DOI: 10.1525/bio.2010.60.11.7.
- Burchsted, D.; Daniels, M. D. (2014): Classification of the alterations of beaver dams to headwater streams in northeastern Connecticut, U.S.A. In *Geomorphology* 205, pp. 36–50. DOI: 10.1016/j.geomorph.2012.12.029.

- Butler, D. R.; Malanson, G. P. (1995): Sedimentation rates and patterns in beaver ponds in a mountain environment. In *Geomorphology* 13, pp. 255–269.
- Butler, D. R.; Malanson, G. P. (2005): The geomorphic influences of beaver dams and failures of beaver dams. In *Geomorphology* 71 (1-2), pp. 48–60. DOI: 10.1016/j.geomorph.2004.08.016.
- Carpenter, S. R.; Lodge, D. M. (1986): Effects of submersed macrophytes on ecosystem processes. In *Aquatic Botany* 26, pp. 341–370. DOI: 10.1016/0304-3770(86)90031-8.
- Clifford, H. F.; Wiley, G. M.; Casey, R. J. (1993): Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. In *Can. J. Zool.* 71 (7), pp. 1439–1447. DOI: 10.1139/z93-199.
- Dalbeck, L. (2020): A review of the influence of beaver *Castor fiber* on amphibian assemblages in the floodplains of European temperate streams and rivers. In *HJ* (Volume 30, Number 3), pp. 135–146. DOI: 10.33256/hj30.3.135146.
- Danilov, p.; Kanshiev, V.; Fyodorov, F. (2011): Characteristics of North American and Eurasian beaver ecology in Karelia. In: *Restoring the European beaver: 50 years of experience*, Chapter 6. Sofia: Pensoft, pp. 55–72.
- Dauwalter, D. C.; Walrath, J. D. (2018): Beaver dams, streamflow complexity, and the distribution of a rare minnow, *Lepidomeda copei*. In *Ecology of Freshwater Fish* 27 (2), pp. 606–616. DOI: 10.1111/eff.12374.
- Dittbrenner, B. J.; Pollock, M. M.; Schilling, J. W.; Olden, J. D.; Lawler, J. J.; Torgersen, C. E. (2018): Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation. In *PloS one* 13 (2), e0192538. DOI: 10.1371/journal.pone.0192538.
- Dittbrenner, B. J.; Schilling, J. W.; Torgersen, C. E.; Lawler, J. J. (2022): Relocated beaver can increase water storage and decrease stream temperature in headwater streams. In *Ecosphere* 13 (7). DOI: 10.1002/ecs2.4168.
- Duan, X.; Wang, Z.; Xu, M.; Zhang, K. (2009): Effect of streambed sediment on benthic ecology. In *International Journal of Sediment Research* 24 (3), pp. 325–338. DOI: 10.1016/S1001-6279(10)60007-8.
- Flores, L.; Giorgi, A.; González, J. M.; Larrañaga, A.; Díez, J. R.; Elosegi, A. (2017): Effects of wood addition on stream benthic invertebrates differed among seasons at both habitat and reach scales. In *Ecological Engineering* 106, pp. 116–123. DOI: 10.1016/j.ecoleng.2017.05.036.

- Fuller, M. R.; Peckarsky, B. L. (2011a): Does the morphology of beaver ponds alter downstream ecosystems? In *Hydrobiologia* 668 (1), pp. 35–48. DOI: 10.1007/s10750-011-0611-x.
- Fuller, M. R.; Peckarsky, B. L. (2011b): Ecosystem engineering by beavers affects mayfly life histories. In *Freshwater Biology* 56 (5), pp. 969–979. DOI: 10.1111/j.1365-2427.2010.02548.x.
- Garcia, X.-F.; Schnauder, I.; Pusch, M. T. (2012): Complex hydromorphology of meanders can support benthic invertebrate diversity in rivers. In *Hydrobiologia* 685 (1), pp. 49–68. DOI: 10.1007/s10750-011-0905-z.
- Green, K. C.; Westbrook, Ch. J. (2009): Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams. In *JEM*. DOI: 10.22230/jem.2009v10n1a412.
- Hering, D.; Buffagni, A.; Moog, O.; Sandin, L.; Sommerhäuser, M.; Stubauer, I. et al. (2003): The Development of a System to Assess the Ecological Quality of Streams Based on Macroinvertebrates - Design of the Sampling Programme within the AQUEM Project. In *Internat. Rev. Hydrobiol.* 88 (3), pp. 345–361.
- Hoffmann, A.; Hering, D. (2000): Wood-Associated Macroinvertebrate Fauna in Central European Streams. In *Internat. Rev. Hydrobiol.* 85 (1), pp. 25–48.
- Hood, G. A.; Bayley, S. E. (2008): Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. In *Biological Conservation* 141 (2), pp. 556–567. DOI: 10.1016/j.biocon.2007.12.003.
- Hood, G. A.; Larson, D. G. (2014): Beaver-Created Habitat Heterogeneity Influences Aquatic Invertebrate Assemblages in Boreal Canada. In *Wetlands* 34 (1), pp. 19–29. DOI: 10.1007/s13157-013-0476-z.
- Hood, G. A.; Larson, D. G. (2015): Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. In *Freshw Biol* 60 (1), pp. 198–208. DOI: 10.1111/fwb.12487.
- Iwata, T.; Nakano, Sh.; Murakami, M. (2003): Stream meanders increase insectivorous bird abundance in riparian deciduous forests. In *Ecography* 26 (3), pp. 325–337. DOI: 10.1034/j.1600-0587.2003.03355.x.
- Jähnig, S. C.; Brunzel, St.; Gacek, S.; Lorenz, A. W.; Hering, D. (2009): Effects of re-braiding measures on hydromorphology, floodplain vegetation, ground beetles and benthic invertebrates in mountain rivers. In *Journal of Applied Ecology* 46 (2), pp. 406–416. DOI: 10.1111/j.1365-2664.2009.01611.x.

- John, St.; Klein, A. (2003): Beaver pond development and its hydrogeomorphic and sedimentary impact on the Jossa floodplain in Germany. In *Lutra* 46 (2), pp. 183–188.
- Johnston, C. A.; Naiman, R. J. (1987): Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. In *Landscape Ecology* 1 (1), pp. 47–57.
- Kaphegyi, T.; Christoffers, Y. (2014): Vom Prozessschutz zu adaptiven Naturschutzstrategien in Kulturlandschaften. Die Rückkehr des Bibers (*Castor fiber*) als Motor neuer Managementkonzepte für Schutzgebiete. Der Biber als Faktor im Moorschutz. Edited by Albert-Ludwigs-Universität Freiburg Professur für Landespflege.
- Kaufmann, P. R.; Faustini, J. M. (2012): Simple measures of channel habitat complexity predict transient hydraulic storage in streams. In *Hydrobiologia* 685 (1), pp. 69–95. DOI: 10.1007/s10750-011-0841-y.
- Kovalenko, K. E.; Thomaz, S. M.; Warfe, D. M. (2012): Habitat complexity: approaches and future directions. In *Hydrobiologia* 685 (1), pp. 1–17. DOI: 10.1007/s10750-011-0974-z.
- Kroes, D. E.; Bason, Ch. W. (2015): Sediment-trapping by Beaver Ponds in Streams of the Mid-Atlantic Piedmont and Coastal Plain, USA. In *Southeastern Naturalist* 14 (3), pp. 577–595.
- Law, A.; McLean, F.; Willby, N. J. (2016): Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. In *Freshwater Biology* 61 (4), pp. 486–499. DOI: 10.1111/fwb.12721.
- McComb, W. C.; Sedell, J. R.; Buchholz, T. D. (1990): Dam-Site selection by beavers in an eastern Oregon basin. In *Great Basin Naturalist* 50 (3), pp. 273–281.
- Mocq, J.; Soukup, P. R.; Näslund, J.; Boukal, D. S. (2021): Disentangling the nonlinear effects of habitat complexity on functional responses. In *The Journal of Animal Ecology* 90 (6), pp. 1525–1537. DOI: 10.1111/1365-2656.13473.
- Müller-Schwarze, D. (2011): *The beaver. Its life and impact*. 2nd ed. Ithaca: Comstock Pub. Associates. Available online at <http://site.ebrary.com/lib/alltitles/docDetail.action?docID=10468066>.
- Naiman, R. J.; Bailan, E.; Bartz, K.; Bilby, R.; Latterell, J. (2002): Dead wood dynamics in stream ecosystems. In *USDA Forest Service General Technical Report* 181.
- Polvi, L. E.; Wohl, E. (2012): The beaver meadow complex revisited - the role of beavers in post-glacial floodplain development. In *Earth Surf. Process. Landforms* 37 (3), pp. 332–346. DOI: 10.1002/esp.2261.

- Power, M. E.; Rainey, W. E. (2000): Food webs and resources sheds: towards spatially delimiting trophic interactions. In *Ecological consequences of habitat heterogeneity*, pp. 291–314.
- Pringle, C.; Naiman, R. J.; Bretschko, G.; Karr, J. R.; Oswood, M. W.; Webster, J. R. et al. (1988): Patch dynamics in lotic systems: the stream as a mosaic. In *J. N. Am. Benthol. Soc.* 7 (4), pp. 503–524.
- Reice, S. R. (1974): Environmental Patchiness and the Breakdown of Leaf Litter in a Woodland Stream. In *Journal of Wildlife Management* 55 (6), pp. 1271–1282. DOI: 10.2307/1935455.
- Rolauffs, P.; Hering, D.; Lohse, S. (2001): Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. In *Hydrobiologia* (459), pp. 201–212.
- Ronnquist, A. L.; Westbrook, Ch. J. (2021): Beaver dams: How structure, flow state, and landscape setting regulate water storage and release. In *The Science of the total environment* 785, p. 147333. DOI: 10.1016/j.scitotenv.2021.147333.
- Rurek, M. (2021): Characteristics of Beaver Ponds and Landforms Induced by Beaver Activity, S Part of the Tuchola Pinewoods, Poland. In *Water* 13 (24), p. 3641. DOI: 10.3390/w13243641.
- Schloemer, S.; Hörren, Th.; Lorenz, A. W.; Hering, D. (2023): The macroinvertebrate fauna of maintained and abandoned beaver dams. In *Hydrobiologia* 850 (8), pp. 1763–1778. DOI: 10.1007/s10750-023-05176-9.
- Visscher, M. de; Nyssen, J.; Pontzele, J.; Billi, P.; Frankl, A. (2012): Spatio-temporal sedimentation patterns in beaver ponds along the Chevral River, Ardennes, Belgium. In *Hydrological Processes* 28 (4), pp. 1–12.
- Warren, E. R. (1932): POSITION OF WOOD IN BEAVER DAMS. In *Science* (New York, N.Y.) 75 (1937), pp. 194–195. DOI: 10.1126/science.75.1937.194-b.
- White, D. S. (1990): Biological relationships to convective flow patterns within stream beds. In *Hydrobiologia* 196 (2), pp. 149–158. DOI: 10.1007/BF00006106.
- Woo, M.-K.; Waddington, J. M. (1990): Effects of Beaver Dams on Subarctic Wetland Hydrology. In *Arctic* 43 (3), pp. 223–230.

3.2 Species richness and abundance of benthic invertebrates are multiplied by beaver (*Castor sp.*) activities in small floodplains

Abstract

Beaver activities modify floodplains of small streams fundamentally. Prevailing lotic sections are supplemented with several additional habitats e.g., ponds, dams and side channels. While there are several investigations in the invertebrate fauna of single beaver-induced habitats, a quantification of how beavers modify aquatic invertebrate assemblages of entire floodplain sections is still missing.

We investigated three beaver territories and three upstream floodplain sections (“non-beaver territories”). We quantified the areas covered by different aquatic habitat types and collected 188 habitat-specific invertebrate samples that yielded more than 82,000 individuals. We used GLMMs with logit links and PCoA to quantify the differences between territory types in terms of aquatic habitat area, abundance, species richness, general community composition and flow preferences.

The area of aquatic habitats increased six-fold in beaver territories. The abundance of benthic invertebrates increased by factor 4.5. From species extrapolation analysis, we inferred that species richness in beaver territories increased by factor 2.7, compared to non-beaver territories. Of the 254 taxa recorded, 141 exclusively occurred in beaver territories and only four taxa in non-beaver territories. The most taxa-rich habitat type were side channels in beaver territories. Community composition was most similar between habitat types with comparable flow patterns e.g., beaver ponds and pools in non-beaver territories. In both territory types, rheophile taxa account for the largest percentage, with a median of 57 % in beaver territories and 61 % in non-beaver territories. The number of rheobiont taxa (21 in total) is higher in beaver territories (20 taxa) compared to non-beaver territories (16 taxa), while the overall proportion of rheobiont taxa is higher in non-beaver territories.

Beaver activities greatly enhance species richness and abundance of aquatic invertebrates. While a predominantly lotic community shifts to an assemblage with more heterogeneous flow preferences, almost no taxa (not even those depending on high currents) are eliminated from beaver territories. Beavers thus enhance aquatic invertebrate biodiversity, at the same time maintaining the original community.

Beaver activities are cost-effective measures to enhance the biodiversity of small floodplains and should be integral part of restoration plans.

Introduction

Beavers significantly impact the floodplains of small streams and change hydrology and morphology fundamentally (Naiman et al. 1986; Wegener et al. 2017; Stout et al. 2017). While the primary purpose of their dam-building activities is to ensure underwater access to their lodges, this process also creates a diverse array of habitats within the stream and floodplain ecosystems, including dams, ponds, side channels, and beaver meadows (Laurel and Wohl 2019). These modifications lead to an expansion of the overall watercourse length as a single stream transforms into a multi-braided network (Green and Westbrook 2009; John and Klein 2003; Polvi and Wohl 2012). Shading of the riparian area is reduced, vegetation height and composition is modified (Orazi et al. 2022) with far-reaching consequences on adjacent terrestrial ecosystems and terrestrial-aquatic interactions (Naiman et al. 1988; McCaffery and Eby 2016). Furthermore, beaver dams modify hydrological processes by creating ponds, raising the groundwater level (Westbrook et al. 2006; Dittbrenner et al. 2022) and enhance the storage of ground and surface water (Hood and Bayley 2008; Dittbrenner et al. 2022). These alterations confer increased resistance to drought (Hood and Bayley 2008) and fire events (Fairfax and Whittle 2021) within beaver wetlands. Finally, beavers play a crucial role in augmenting the diversity of deadwood substrates, acting as facilitators for the accumulation of coarse and fine woody debris in aquatic ecosystems and their adjoining floodplains (Thompson et al. 2016). Consequently, beavers can transform a valley that was previously characterized by a small stream with a narrow riparian gallery forest into a multi-channelled stream network, complemented by large ponds and swamps with large amounts of deadwood.

While modifying floodplain hydrology and morphology, beavers have significant effects on biodiversity patterns. Beaver wetlands have been described as potential agents in stabilizing β -diversity and regional diversity in the face of wetland loss due to climate change and human impacts (Bush et al. 2019). By comparing beaver ponds with river and forest habitats, Orazi et al. (2022) demonstrated that beaver activities introduce components to the riparian ecosystem that multiplied abundance and species diversity. Particularly, species richness of birds, beetles, and true bug communities were promoted. However, an analysis of comparable quality is lacking for aquatic invertebrates. A comparison of habitat composition between beaver territories (including ponds, swamps, beaver dams and short stream sections) with non-beaver territories, where aquatic habitats are limited to streams, already leads to the conjecture of fundamental effects on aquatic life. Thereby, it is assumed that lotic species are replaced with lentic species due to beaver activities (Arndt and Domdei 2011; McDowell and Naiman 1986;

Pliūraitė and Kesminas 2012) as their habitats might be significantly reduced or disappear completely and it is unclear if the remains still support populations of lotic taxa.

In this study, we investigated the benthic invertebrate communities in three beaver territories and compared them to three nearby floodplain sections unaltered by beavers (non-beaver territories). In both sites, we quantified the areas of different aquatic habitat types, based on the flow conditions and substrate types, and took habitat specific invertebrate samples. From these, we inferred patterns of the overall benthic invertebrate communities in the sections. We explored the following hypotheses:

1. Beaver activities multiply the abundance of aquatic invertebrates that occur in a floodplain section, mainly by multiplying the area of aquatic habitats.
2. Beaver activities greatly enhance the number of aquatic invertebrate species by providing additional niches in beaver ponds, side channels and within and downstream of beaver dams.
3. There is a general shift in community composition, caused by different environmental conditions (e.g., flow velocities) in beaver and non-beaver territories.
4. The benthic invertebrate community of beaver territories contains comparatively more limnophile taxa, while the typical rheophile invertebrate fauna of floodplain sections unaltered by beavers remains.

Study area

We examined floodplain sections of three 2nd to 3rd order streams in the Hürtgenwald (50°44`N, 6°20`E), a 120 km² state forest (<https://www.wald-und-holz.nrw.de>, 2022) in the western part of Germany and the federal state of North Rhine-Westphalia, adjacent to the Netherlands and Belgium. The area, situated at an elevation of 240-450 m a.s.l., has a moderate atlantic climate characterised by cool summers and mild winters, and belongs to the Rheinisch Massif. The average temperature in this area is 8.5 °C (<https://cdc.dwd.de/portal>) and the annual precipitation is 1062 mm (<https://www.elwasweb.nrw.de>). Promoted by high precipitation, a steep relief and low permeability of the subsoil, the area is characterised by an intricately branched and dense network of streams. The European beaver (*C. fiber*) was reintroduced to this area between 1981 to 1989 (Naumann 1991). The current total population size in the federal state of North Rhine-Westphalia is estimated to exceed 1200 individuals (Dalbeck 2021). In the study area, the estimated average density is 4.95 territories per 10 km (Dalbeck 2022), with a dam density in the small watercourses of 4 dams per km (Dalbeck et al. 2014).

Methods

In spring 2019, three beaver territories and three non-beaver territories located ≥ 200 m upstream were investigated in the floodplains of the streams Thönbach, Weberbach and Weiße Wehe (Figure 1a). The paired sites were selected to ensure similarity in terms of elevation, stream size, slope and each investigated section spanned a length of 200 m.

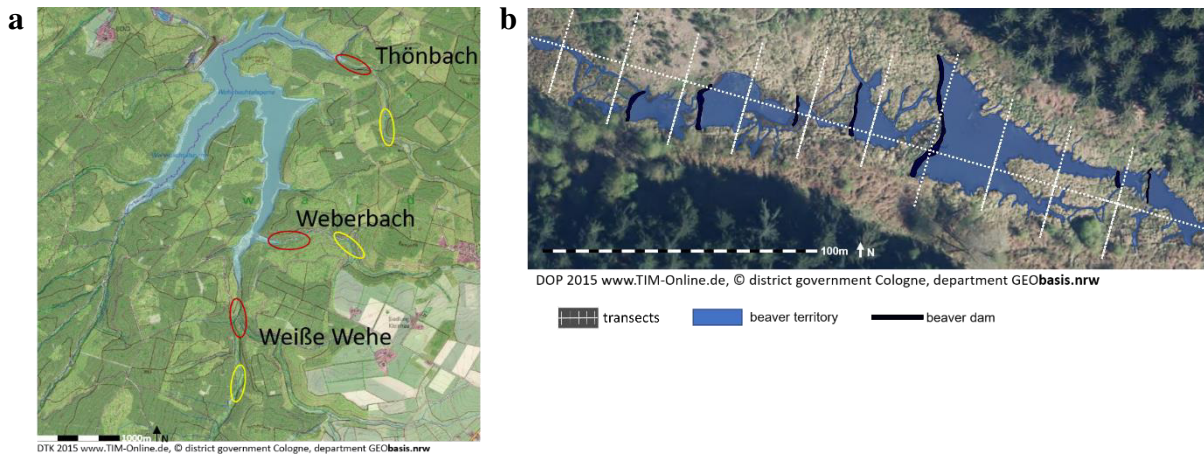


Figure 1 a) location of the studied streams Thönbach, Weberbach and Weiße Wehe. The study sections are indicated with coloured circles, in red the beaver territories, in yellow the non-beaver territories. b) example of transect mapping of a 200 m stretch in a beaver territory within the Thönbach stream.

In both territory types, we distinguished free-flowing (lotic) and slow-flowing (lentic) habitats based on flow patterns. In non-beaver territories, slow-flowing habitats include pools close to watercourse margins and upstream of obstacles. Within the beaver territories, side channels, beaver dams and sections directly downstream of the dams were considered as lotic and the beaver ponds as lentic habitats (Table 1). We recorded them by transect mapping (Jähnig et al. 2009): We targeted floodplain sections of 200 m length and measured habitat width at 10 m intervals laterally to the watercourse (Figure 1b). At these sections, the width of water bodies was measured, and 10 points were distributed evenly over the water bodies' width, at which water depth, substrate type and flow pattern were recorded. The substrate types used in the multi-habitat sampling protocol of Hering et al. (2003) were recorded, and flow patterns according to Jähnig et al. (2009). Water depth was measured with a folding rule, with exception of the beaver ponds, where we attached the centimetre scale to a wooden strip with a round plastic disc with holes fixed to the end. The disc prevents the stick from sinking into fine sediment layers that are present in large parts of the beaver ponds. To be able to operate the measurement stick from the shore, we also attached a telescopic rod. The transect was extended to the riparian area across the entire floodplain width, to record the same parameters for the side

channels and to measure their position in relation to the main channel. In combination with the transect mapping, we took aerial pictures of the sections by drone. All data combined were transferred to QGIS 3.24 (<http://qgis.osgeo.org>), which was then used to calculate the area of different habitat types.

Table 1 Number of macroinvertebrate samples taken in the individual habitats.

| Site | Habitat | Sampling design | Total number of samples |
|----------------------|----------------------------------|---|--------------------------------|
| Beaver territory | side channel (lotic) | 3 per territory | 9 |
| | beaver pond (lentic) | 3 per territory | 9 |
| | downstream of beaver dam (lotic) | 3 per territory | 9 |
| | beaver dam (lotic) | 9 samples per dam in altogether 16 dams | 144 |
| Non-beaver territory | riffle (lotic) | 3 per territory | 9 |
| | pool (lentic) | 3 per territory | 9 |

We sampled macroinvertebrates in all habitats, except beaver dams, with a kick-net-sampler with a square opening of 0.25 * 0.25 m and a mesh size of 500 μ m. We took three samples of each type of habitat per territory, resulting in a total of nine samples per habitat for beaver territories and non-beaver territories, respectively (Table 1). Beaver dams were sampled with a vacuum sampler (Schloemer and Hoffmann 2018). We sampled nine different areas of a dam (0.25 m² streamside areas and 1 m² pondside areas) and in total 16 dams were sampled within the three beaver territories (Table 1). Samples were filtered through a 500 μ m sieve in the field. Sampling was carried out in spring from mid-March to mid-April 2018 (beaver dams) and 2019 (all other habitats); this sampling season ensures that a large proportion of merolimnic organisms were recorded before they emerged. After collection, all samples were transferred into containers and preserved in 96 % ethanol for further processing. In the laboratory, each sample was rinsed with water through a 2 mm mesh following the method of Meier et al. (2006), before the sample was divided into small amounts, which were ultimately transferred into a tray for sorting. Identification was generally on species level, except for most Diptera that were identified to genus or family level.

Data analysis

To address the first hypothesis (beaver activities multiply the abundance, mainly by multiplying the area of aquatic habitats) we calculated the average abundance per habitat type in beaver territories and non-beaver territories. Based on these data, we applied a GLMM with the assumption of negative binomial errors and log link, and corrected for the difference in the sampled areas. The dependent variable was the abundance regressed on the beaver and non-beaver territories. The differences between beaver- and non-beaver territories were assessed with a t-test over the $\log(\text{odds})$.

To address the difference of the average abundances taking in account an area of 200 m in beaver and non-beaver territories, we applied 10^6 Monte-Carlo simulations from two negative binomial distributions using the mean abundance of the two groups and the methods-of-moments to calculate the size parameter. These simulations were multiplied with the area (beaver territory: 5241 m²; non-beaver territory 813 m²) and the $\log(\text{odds})$ were estimated; the p-value was obtained from the t-test. The areas were calculated using the transect mapping data in QGIS 3.24 (<http://qgis.osgeo.org>).

To address the second hypothesis (beaver activities enhance the number of species by providing additional habitats), we first estimated the difference in the average number of species per square metre in the individual habitat types recorded in beaver and non-beaver territories. We used a Generalized Linear Mixed Model (GLMM) with the assumption of negative binomial distributed errors and log link. Since the sampled areas were unequal in size in the beaver dams as compared to all other habitats, we applied an offset on the log of the area to correct the sampled areas. The dependent variables were the number of species regressed on the beaver and non-beaver territories. Random effects included the streams (Weiße Wehe, Weberbach and Thönbach), and nested under this the different habitats (e.g., pond, dam, riffle) to model the variance within territories and habitats separately. The difference in means was assessed with the t-test over the $\log(\text{odds})$. To calculate the overall number of species in beaver and non-beaver territories, we had to account for the different number of samples taken in the two territory types, as the number of recorded species is expected to increase with the number of samples as a saturation curve. Therefore, the number of species was analysed based on the rarefaction and extrapolation methodology of Chao et al. (2014) and Hsieh et al. (2016), using species frequency to estimate overall species richness within the territories and the associated 95% confidence intervals. In addition, we compared how many species occurred exclusively in the beaver territories, exclusively in non-beaver territories and in both territory types. The results of this analysis were displayed in a Venn diagram.

For testing the third hypothesis (shift in community composition) we analysed the dissimilarity of species composition among the samples with a Principal Coordinate Analysis (PCoA). The abundance in the community matrix were relative rank transformed and Bray-Curtis metric was used as a dissimilarity matrix.

To address the last hypothesis (flow preference of benthic invertebrate communities differ between territory types), we used the trait data for current preferences compiled by Schmidt-Kloiber and Hering (2015) that were originally assembled by Schmedtje and Colling (1996). The traits encompass seven flow preferences, ranging from limnobionts that depend on stagnant water to rheobionts relying on fast flow velocity. We added an additional category, “semiaquatic taxa”, to account for taxa that are not covered by Schmidt-Kloiber and Hering (2015). For each sample, the proportion of flow preferences of the community were calculated. Then, we calculated the difference in flow preferences between beaver and non-beaver territories by using a GLMM and assumed beta distributed errors and logit link. The dependent variables were the fraction of flow preference group regressed on the beaver and non-beaver territories. The random effect of the habitat was nested on the territory and was corrected for the sampled area using the logit function of the area $\log(x/(1-x))$. The difference in means was assessed with the t-test in over the $\log(\text{odds})$ between each flow preference group comparing beaver and non-beaver territories.

All analysis were performed in Rstudio (RStudio Team, 2023) and significance from the null was assumed at $p < .05$ for all tests. The GLMMs were fitted using the `glmmTMB` package for R (Brooks et al., 2017). The t-test over the $\log(\text{odds})$ was applied using the `emmeans` package (Lenth, 2023) for with exception of the Monte-Carlo permutations where $p = P(|Z| > |z|)$, $z = \log(\text{odds})/SE$. Species richness was extrapolated with the `iNEXT` package (Hsieh et al., 2022), resulting in rarefaction/extrapolation curves. The PCoA was applied with the `vegan` package (Oksanen et al., 2017). Residuals of each model were checked and all figures were created using `ggplot2` and `cowplot` (Wilke, 2019).

Results

Overview

In total, 254 taxa with 82,128 individuals were sampled. 109 taxa occurred in both, beaver territories and non-beaver territories, while 141 taxa were found exclusively in beaver territories and only four taxa in non-beaver territories (Figure 3a). Numerous taxa occurred exclusively in certain habitat types. For example, 87 taxa (see Appendix Table S1) were found exclusively in beaver dams, including species such as the beetle *Dianous coerulescens* (Gyllenhal, 1810) (Coleoptera: Staphilinidae), the larvae of *Lipsothrix* sp. (Diptera: Limoniidae), the larvae of *Thaumastoptera calceata* Myk, 1866 (Diptera: Limoniidae) and the larvae of the caddisfly *Rhyacophila laevis* Pictet, 1834 (Trichoptera: Rhyacophilidae). Four taxa exclusively occurred in the free-flowing sections downstream of beaver dams, such as the beetle *Hydrochus elongatus* (Schaller, 1783) (Coleoptera: Hydrochidae), and the caddisfly larvae *Silo nigricornis* (Pictet, 1834) (Trichoptera: Goeridae). Eight taxa were unique to side channels, such as the caddisfly larvae *Rhyacophila praemorsa* McLachlan, 1879 (Trichoptera: Rhyacophilidae) and *Silo piceus* (Brauer, 1857) (Trichoptera: Goeridae), as well as the beetle *Laccobius bipunctatus* (Fabricius, 1775) (Coleoptera: Hydrophilidae). Nine taxa exclusively occurred in beaver ponds such as the beetle *Dryops ernesti* Des Gozis, 1886 (Coleoptera: Dryopidae) and the dragonfly *Libellula depressa* Linnaeus, 1758 (Odonata: Libellulidae). In non-beaver territories, only in riffle habitats four exclusive species were present, like the beetle *Elmis aenea* (Müller, 1806) (Coleoptera: Elmidae) and the mayfly *Baetis alpinus* (Pictet, 1843) (Ephemeroptera: Baetidae). Furthermore, the snail *Bythinella dunkeri* (Frauenfeld, 1857) (Gastropoda: Hydrobiidae) and the caddisfly *Lithax niger* (Hagen, 1859) (Trichoptera: Goeridae) were found solely in non-beaver territories.

Abundance and overall number of individuals

The number of individuals differs between habitats (see Appendix Table S1). In general, highest abundance were found in non-beaver territories, which can be traced back to the high abundance of *Gammarus fossarum* Koch, 1835 (Gammaridae: Crustacea), especially in the pool habitat (see Appendix Table S2). Excluding this species from the dataset, the average abundances do not differ between habitat types, with the exception of side channels, where abundance is nearly twice as high as in every other habitat (see Appendix Table S2). According to the GLMM (Figure 2a) and including *G. fossarum*, the estimated abundance and the standard error are a bit higher in non-beaver territories. Log(odds) is close to zero (-0.35), indicating that mean abundance is not significantly different from null when comparing beaver- and non-beaver

territories. However, if we consider the abundance within floodplain sections of 200 m length (Figure 3b), it increased by factor 4.5 in beaver territories. This result is significantly different from null and the log(odds) of 1.53 is far from zero (Figure 2b). Table 2 shows the average area (m²) of the habitats within the 200 m floodplain sections, resulting in an increase of aquatic habitat area by factor 6 due to beaver engineering. Thereby, the area of lotic habitats (Table 2) stays the same (beaver-territory: 231 m²; non-beaver territory: 224 m²), but the ratio of lotic to lentic area reverses in beaver territories (beaver-territory: 1:6; non-beaver territory: 5:1).

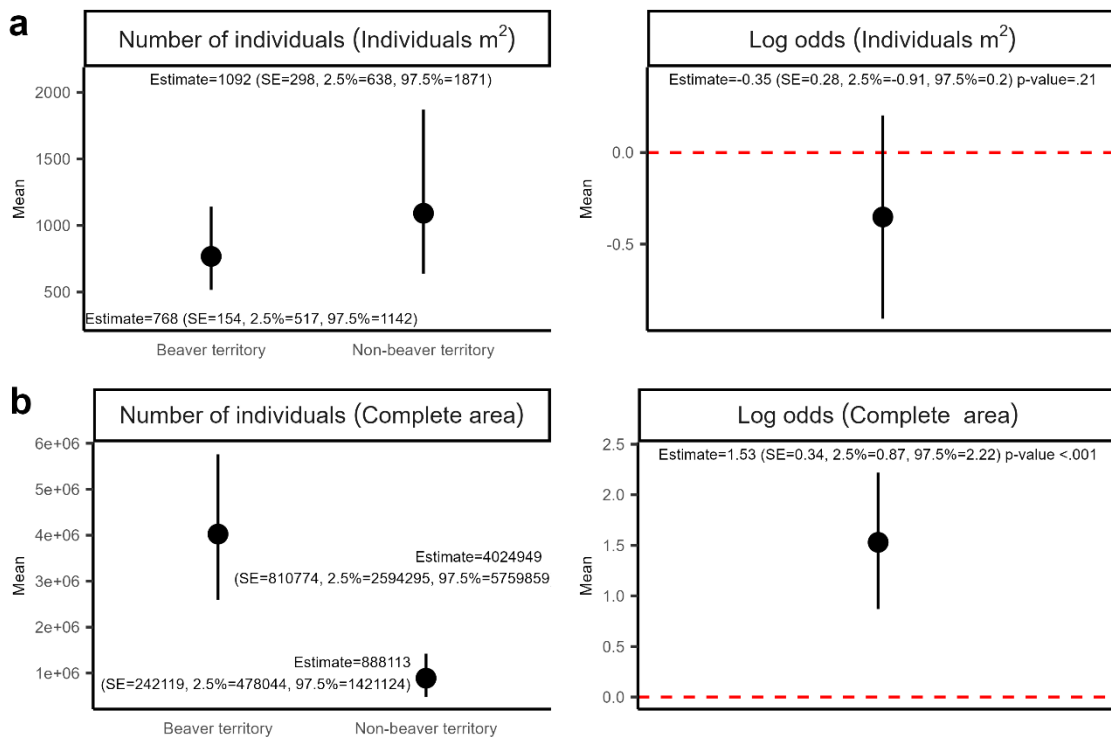


Figure 2 a) GLMM of abundance (number of individuals/m²) with log(odds). b) GLMM of number of individuals of the entire floodplain sections (200 m length) with log(odds). Points represent the point estimation and the intervals the confidence intervals at 95 %

Table 2 Average area (m²) of the different habitats within 200 m floodplain sections.

| Site | Habitats (flow condition) | Average area [m ²] |
|----------------------|--|--------------------------------|
| beaver territory | side channel (lotic) | 35 |
| | beaver dam (lotic) | 80 |
| | free-flowing sections downstream of beaver dam (lotic) | 116 |
| | beaver pond (lentic) | 1480 |
| non-beaver territory | riffle (lotic) | 224 |
| | pool (lentic) | 47 |

Number of taxa

Most taxa were found in beaver territories (see Appendix Table S1) with 250 taxa in comparison to 113 taxa in non-beaver territories. Extrapolation resulted in 340 taxa in beaver territories and 128 taxa in non-beaver territories (see Appendix Table S3), which represents an increase of species richness by the factor 2.7 (Figure 3b).

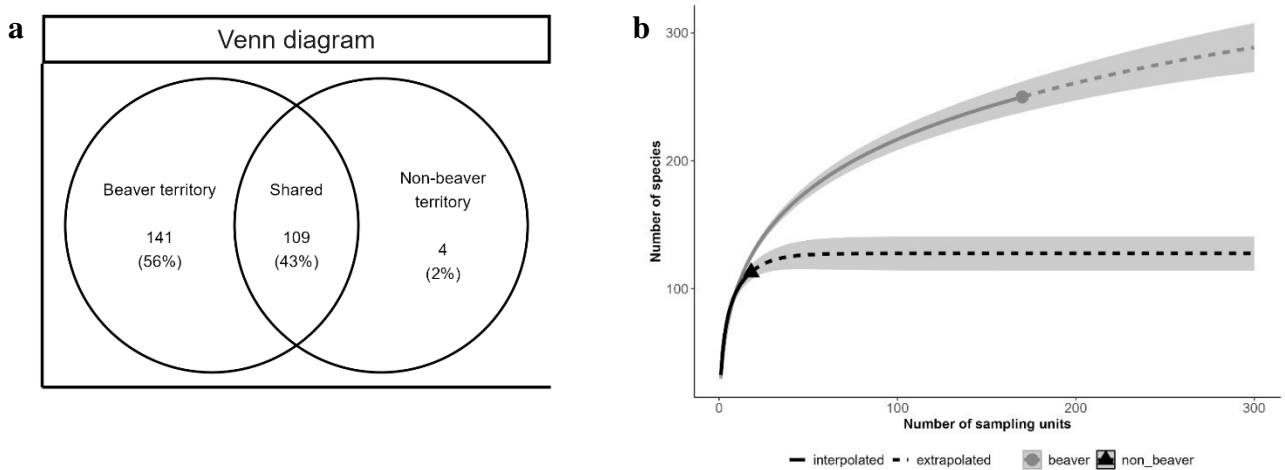


Figure 3 a) Venn diagram with the number of shared taxa and number of taxa exclusively occurring in beaver or non-beaver territories. b) rarefaction/extrapolation curve for species richness up to nearly double the maximum sample size of macro invertebrates in beaver and non-beaver territories. The transparent shading represents the 95 % confidence intervals and the solid lines the actual sample size, while the dashed lines show the results of the extrapolation.

In general, lotic habitats were most taxa-rich (see Appendix Table S2), led by beaver dams, where we found in total 210 taxa (on average 29 per sample). Nevertheless, the highest average number of taxa was found in the side channels (in total 110, on average 42 per sample), riffle habitats (in total 91, on average 40 per sample) and in free-flowing sections downstream of dams (in total 101, on average 35 per sample). Slightly fewer taxa were recorded in lentic habitats such as pool areas (in total 63, on average 25 per sample) and beaver ponds (in total 64, on average 19 per sample).

According to the GLMM (Figure 4), the estimated average number of taxa/m² is higher in non-beaver territories (65 taxa/m²) than in beaver territories (55 taxa/m²). The difference, however, is very small (log-odds= -0.16) and not much different from null (p-value= 0.22).

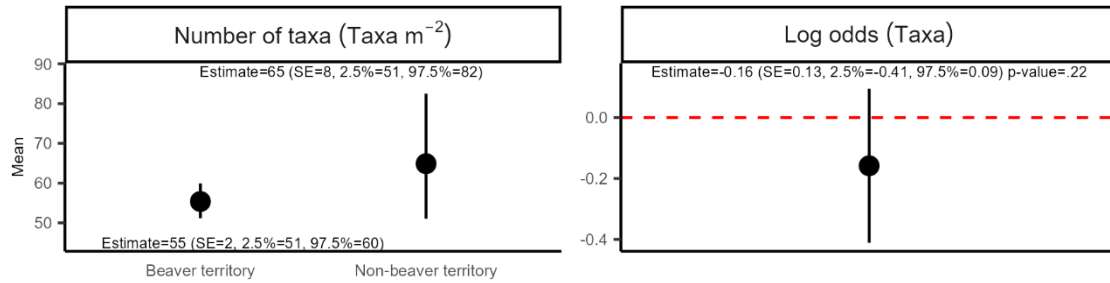


Figure 4 GLMM for the number of taxa/m² with log(odds).

Community composition

In general, the PCoA (Figure 5) shows only minor differences in community composition between beaver and non-beaver territories. The taxa assemblages were most similar in habitats with comparable flow patterns, regardless of the beaver influence. Here, sample points of the lentic habitats (pools and ponds) overlap strongly as well as riffles and sections downstream of dams as lotic habitats. Especially for the lentic habitats, the taxa resemblance is striking (see Appendix Table S1), showing the typical species spectrum of lentic areas in small streams, such as *Ephemera danica* Müller, 1764 (Ephemeroptera: Ephemeridae) and *Sialis sp.* (Megaloptera: Sialidae). Main differences exist between habitats of non-beaver territories (riffle, pool) and dam habitats, which do not overlap at all.

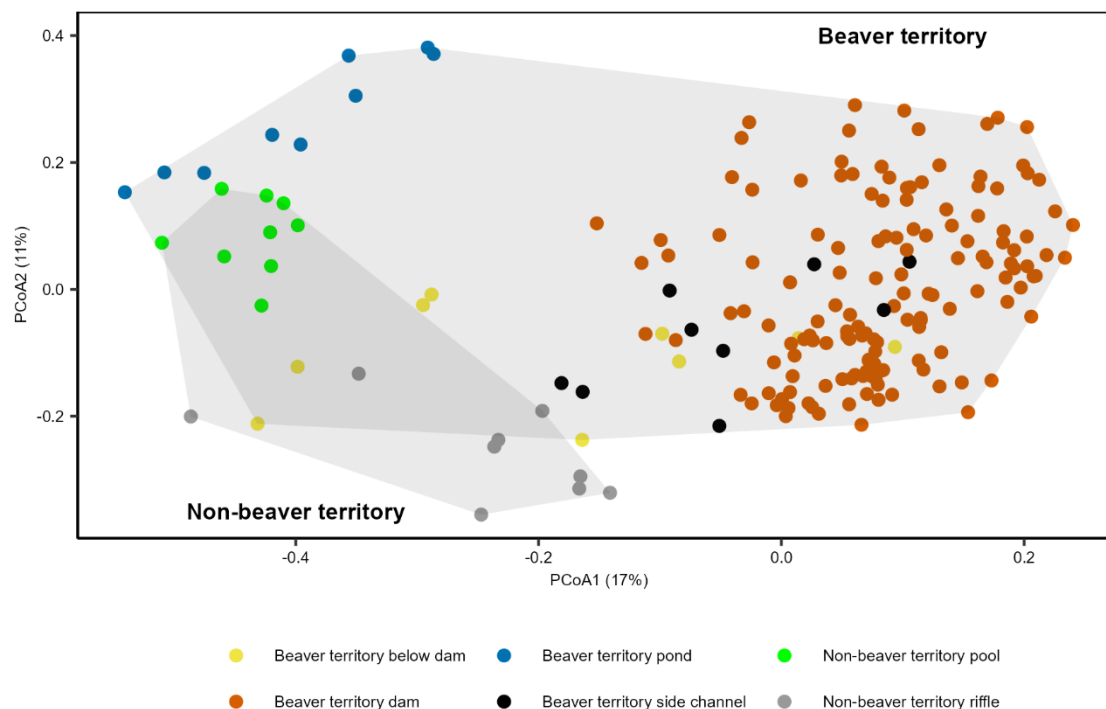


Figure 5 PCoA of community composition for samples taken in habitats of beaver and non-beaver territories, based on Bray-Curtis dissimilarities.

Flow preferences

Information on the flow preferences was available for 198 taxa (see Appendix Table S4), thus 78 % of the taxa could be included in the calculation. There is no obvious difference in the median percentages of flow preferences between territory types (Figure 6a). In both communities, rheophile taxa account for the largest percentage, with a median of 57 % in beaver territories and 61 % in non-beaver territories. The results of the GLMM confirms these findings and do not indicate much difference between the mean percentage of flow preferences in beaver

and non-beaver territories (Figure 6b), with the exception of rheobionts. The median percentage of rheobionts in beaver territories is 4 %, while in non-beaver territories it is 8 %. The log(odds) of the mean number of rheobiont percentage (Figure 6c) is far from zero (log odd -1.44; p-value= 0.001).

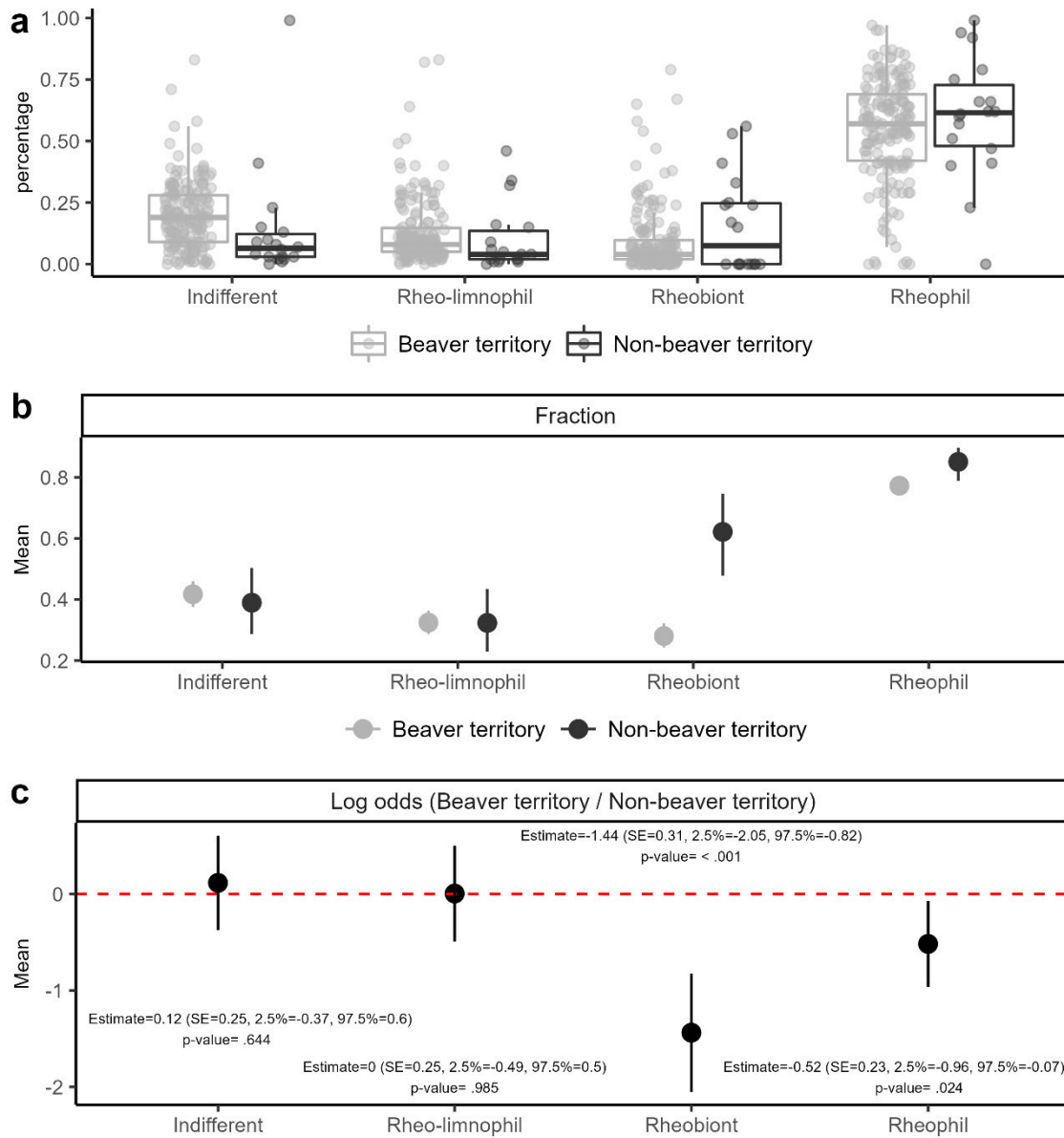


Figure 6 a) GLMM of percentages in flow preferences of invertebrate communities in beaver and non-beaver territories. b) mean percentage of flow preferences of beaver and non-beaver territories. c) log(odds) of the difference in means of flow preferences of beaver and non-beaver territories.

Discussion

We expected that beaver activities multiply the abundance of aquatic invertebrates, mainly by multiplying the area of aquatic habitats (hypothesis 1). The data supports this hypothesis. In terms of single habitats, we found most individuals per square metre in the side channels (3,108 Ind./m²) of beaver territories and in pool areas in non-beaver territories (3,199 Ind./m²). According to the GLMM the abundance (Ind./m²) in non-beaver territories was comparable or even slightly higher than in beaver territories (Figure 2a). However, when quantifying the abundance for entire stream sections (200 m), the habitat area increased sixfold due to beaver activities, while the abundance increased 4.5-fold (Figure 2b). Other studies found an increased abundance of benthic organisms in beaver induced habitats (Law et al. 2016; Rolauffs et al. 2001; McDowell and Naiman 1986) or no change in abundance (Arndt & Domdei 2011; Bylak & Kukula 2022). Thereby, the numbers naturally vary depending on habitat, successional state and season. For example, Law et al. (2016) sampled the vegetated areas within beaver territories, which turned out to be the habitat with the highest abundance. Rolauffs et al. (2001) found the highest abundance in beaver dams, which was 3.2 times higher than in unmodified riffle areas and 5.5 times higher than in beaver ponds.

We expected that beaver activities greatly enhance the number of aquatic invertebrate species by providing additional niches (hypothesis 2); this hypothesis was supported as well. We found that 56 % of the taxa in the study area were exclusive to beaver territories, while only 2 % occurred exclusively in non-beaver territories. Specifically, there was a higher species number of Coleoptera, Trichoptera and Diptera taxa within beaver territories (see Appendix Table S4). While the number of taxa per square metre did not differ largely between beaver and non-beaver territories (Figure 4), the former offered a greater number of additional habitats and niches that supported several species not found in the absence of beaver activities. Especially beaver dams, constructed mainly from wood, exhibited high flow diversity due to their structural arrangement (Rolauffs et al. 2001; Ronnquist and Westbrook 2021) resulting in a rich diversity of species and providing habitats for specialized taxa (Rolauffs et al. 2001; Schloemer et al. 2023). A detailed study of invertebrate colonization in beaver dams (Schloemer et al. 2023) revealed that these habitats, serving as an aquatic-terrestrial interface, support rheophile species as well as those colonising springs, hygropetric areas and deadwood. Free flowing sections downstream of dams are interesting and diverse habitats, representing transitional zones between running water and ponds. Therefore, these sections attract taxa characteristic of both vegetated open-canopy waters, such as the before mentioned beetle *H. elongatus* (Spitzenberg et al. 2021), and riffle areas in cool, lotic environments, exemplified by caddisfly larvae *S. nigricornis* (Eiseler

2020). Additionally, the cold pore water infiltrates this area as a result of the downward pressure exerted by the pond above, which diminishes further downstream of the dams (White 1990; Dittbrenner et al. 2022). This effects the temperature regime in beaver territories in general (White 1990; Dittbrenner et al. 2022) and the life cycle of aquatic invertebrates, like Fuller and Peckarsky (2011) showed for the size and time of emergence of *Baetis sp.* (Ephemeroptera). Side channels provide permanent or temporary habitats for some species (Harthun 1998), and facilitate the movement of aquatic organisms across dams (Pollock et al. 2022). In our study, side channels were richest in taxa compared to all other habitats in beaver or non-beaver territories. Thereby, we found typical taxa of lotic environments unique to side channels such as the aforementioned caddisfly larvae *S. piceus* and *R. praemorsa*, both adapted to well-oxygenated streams with lithal substrates, while the latter is often the most common Rhyacophilidae in cool spring brooks and headwaters (Eiseler 2020). Ponds, the most prominent habitats in beaver territories, underwent various successional stages with distinct features (Nummi et al. 2021; Dalbeck et al. 2014; Johnston 2017), which are rare in forest mountain streams without beavers (Dalbeck et al. 2014). We found nine taxa exclusively in beaver ponds including the beetle *D. ernesti*, commonly found at the edge of stagnant water bodies in damp moss or plant assemblages (Spitzenberg et al. 2021), and *L. depressa*, considered a pioneer species and one of the first dragonflies to colonise newly formed water bodies (Sternberg and Buchwald 2000).

Our hypothesis regarding a general shift in community composition between beaver and non-beaver territories (hypothesis 3) was only partially supported. The composition of invertebrate communities in beaver and non-beaver territories (PCoA, Figure 5) showed differences and similarities depending on the habitats compared. A clear shift is only observed if, for example, solely pond and riffle samples (Figure 5) are compared, like most studies did. However, if other beaver created habitats are included in the consideration, it becomes clear that there are strong similarities between the communities of beaver and non-beaver territories, primarily driven by the flow regime. Therefore, the taxa composition within lotic areas and particularly within lentic areas (ponds vs. pools) is most similar to each other. Beaver dams, in contrast represent a distinct group in the PCoA, which underlines their special habitat character as aquatic-terrestrial interface within the stream ecosystem.

Our final hypothesis, that the benthic invertebrate community of beaver territories contain a higher proportion of limnophile taxa while maintaining the typical rheophile invertebrate fauna of floodplain section unaltered by beavers, was also partly supported. Both beaver and non-beaver territories had a similar composition of approximately 60 % rheophile taxa. The

remaining 40 % consisted of mainly three other flow types (rheobiont, rheo-limnophil, indifferent), with a twice as high mean percentage of rheobionts in the invertebrate community of non-beaver territories (8 %). Although rheobionts make up a higher proportion of the species community in non-beaver territories, the number of rheobiont taxa (21 in total) is higher in beaver territories (20 taxa) compared to non-beaver territories (16 taxa) (see Appendix Table S4). A study of Robinson et al. (2020) indicates, that the flow preferences of the species community within a beaver territory also depend on topography, and that a lotic species community with additional lentic species predominates at higher gradients. Our findings support the conjecture that the array of ecological traits e.g., flow preferences, is enhanced by beaver activities, while taxa representing the originally occurring traits remain.

Conclusion

Beaver activities have the potential to modify benthic communities in small streams. Through their dam building and associated habitat creation, beavers reintroduce habitat features that were once characteristic of natural stream ecosystems and that are missing in most contemporary European streams (Hering et al. 2001). This includes the expansion of lentic habitats, the establishment of side channels, and the construction of dams, which collectively contribute to the structural diversity and functionality of the stream environment. Focusing solely on specific habitats, e.g., ponds, may lead to incomplete or incorrect conclusions, potentially resulting in inadequate management and restoration plans. By considering the full range of habitats created by beavers, we can ensure more accurate assessments and make informed decisions for conservation and restoration efforts. In our study, we were able to show that, the effect of beaver activities did not result in a loss of rheophile species assemblages. On the contrary, the presence of beaver dams, free flowing sections downstream of the dams, and side channels provides suitable habitats that support rheophile species and dramatically increase the overall species richness and abundance. Beavers play a vital role in restoring and maintaining the ecological integrity of small streams, aligning them more closely with their “potentially natural” state. Therefore, beaver activities should be promoted whenever possible and implemented in future restoration plans.

References

- Arndt, E. and Domdei, J. (2011). Influence of beaver ponds on the macroinvertebrate benthic community in lowland brooks. *Polish Journal of Ecology*, 59(4), 799–811.
- Brooks, M. E., Kristensen, K., Benthem, K. J., van Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J.* 9, 378. <https://doi.org/10.32614/RJ-2017-066>
- Burchsted, D., Daniels, M., Thorson, R. and Vokoun, J. (2010). The River Discontinuum: Applying Beaver Modifications to Baseline Conditions for Restoration of Forested Headwaters. *BioScience*, 60(11), 908–922. doi: 10.1525/bio.2010.60.11.7.
- Bush, B.M., Stenert, C., Maltchik, L. and Batzer, D.P. (2019). Beaver-created successional gradients increase β -diversity of invertebrates by turnover in stream-wetland complexes. *Freshwater Biology*, 64(7), 1265–1274. doi: 10.1111/fwb.13302.
- Chao, A., Gotelli, N. J., Hsieh, T. C.; Sander, E. L., Ma, K. H., Colwell, R. K., Ellison, A. M. (2014): Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. In *Ecological Monographs* 84 (1), pp. 45–67. DOI: 10.1890/13-0133.1.
- Dalbeck, L. (2021). Bestandsentwicklung des Bibers am Beispiel des Kreises Düren. in *Wald und Holz NRW* (ed.) 40 Jahre Biber-Wiederansiedlung in Nordrhein-Westfalen, 14–17.
- Dalbeck, L. (2022). Ergebnisse der Bibererfassung im Kreis Düren in 2022. Düren.
- Dalbeck, L., Janssen, J. and Luise Völsgen, S. (2014). Beavers (*Castor fiber*) increase habitat availability, heterogeneity and connectivity for common frogs (*Rana temporaria*). *Amphibia-Reptilia*, 35(3), pp. 321–329. doi: 10.1163/15685381-00002956.

- Dittbrenner, B.J., Schilling, J.W., Torgersen, C.E. and Lawler, J.J. (2022). Relocated beaver can increase water storage and decrease stream temperature in headwater streams. *Ecosphere*, 13(7). doi: 10.1002/ecs2.4168.
- Eiseler, B. (2020). Bestimmungshilfen - Makrozoobenthos (3) Köcherfliegenlarven: LANUV-Arbeitsblatt 46. Recklinghausen.
- Fairfax, E. and Whittle, A. (2021). Smokey the Beaver: Beaver-Dammed Riparian Corridors Stay Green During Wildfire Throughout the Western USA. *The Bulletin of the Ecological Society of America*, 102(1). doi: 10.1002/bes2.1795.
- Fuller, M.R. and Peckarsky, B.L. (2011). Ecosystem engineering by beavers affects mayfly life histories. *Freshwater Biology*, 56(5), 969–979. doi: 10.1111/j.1365-2427.2010.02548.x.
- Green, K.C. and Westbrook, C.J. (2009). Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams', *Journal of Ecosystems and Management*. doi: 10.22230/jem.2009v10n1a412.
- Harthun, M. (1998). Biber als Landschaftsgestalter: Einfluß des Bibers (*Castor fiber albicus* Matschie, 1907) auf die Lebensgemeinschaft von Mittelgebirgsbächen. Zugl.: Diplomarbeit. (Schriftenreihe der Horst-Rohde-Stiftung). München: Maecenata Verl.
- Hering, D., Buffagni, A., Moog, O., SANDIN, L., Sommerhäuser, M., Stubauer, I., Feld, C., Johnson, R., Pinto, P., Skoulikidis, N., Verdonschot, P. and Zahradkova, S. (2003). The Development of a System to Assess the Ecological Quality of Streams Based on Macroinvertebrates - Design of the Sampling Programme within the AQUEM Project. *Internat. Rev. Hydrobiol.*, 88(3), 345–361.
- Hering, D., GERHARD, M., Kiel, E., Ehlert, T. and Pottgießer, T. (2001). Review Study on Near-natural Conditions of Central European Mountain Streams, with Particular Reference to Debris and Beaver Dams: Results of the "REG Meeting" 2000. *Limnologica*, 31, 81–92.
- Hood, G.A. and Bayley, S.E. (2008). Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation*, 141(2), 556–567. doi: 10.1016/j.biocon.2007.12.003.
- Hsieh, T. C., Ma, K. H., Chao, A. (2016): iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). In *Methods in Ecology and Evolution* 7 (12), pp. 1451–1456. DOI: 10.1111/2041-210X.12613.

- Hsieh T. C., Ma KH, Chao, A. (2022). iNEXT: Interpolation and Extrapolation for Species Diversity. R package version 3.0.0, http://chao.stat.nthu.edu.tw/wordpress/software_download/.
- Jähnig, S.C., Brunzel, S., Gacek, S., Lorenz, A.W. and Hering, D. (2009). Effects of re-braiding measures on hydromorphology, floodplain vegetation, ground beetles and benthic invertebrates in mountain rivers. *Journal of Applied Ecology*, 46(2), 406–416. doi: 10.1111/j.1365-2664.2009.01611.x.
- John, S. and Klein, A. (2003). Beaver pond development and its hydrogeomorphic and sedimentary impact on the Jossa floodplain in Germany. *Lutra*, 46(2), 183–188.
- Johnston, C.A. (ed.) (2017). *Beavers: Boreal Ecosystem Engineers*. Cham: Springer International Publishing.
- Laurel, D. and Wohl, E. (2019). The persistence of beaver-induced geomorphic heterogeneity and organic carbon stock in river corridors. *Earth Surface Processes and Landforms*, 44(1), 342–353. doi: 10.1002/esp.4486.
- Lenth, R. V., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., Singmann, H. (2023). emmeans: Estimated Marginal Means, aka Least-Square Means. <https://github.com/rvlenth/emmeans>.
- McCaffery, M. and Eby, L. (2016). Beaver activity increases aquatic subsidies to terrestrial consumers. *Freshwater Biology*, 61(4), 518–532. doi: 10.1111/fwb.12725.
- McDowell, D.M. and Naiman, R.J. (1986). Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia*, 68, 481–489.
- Meier, C., Böhmer, J., Biss, R., Feld, C., Haase, P., Lorenz, A., Rawer-Jost, C., Rolauffs, P., Schindehütte, K., Schöll, F., Sundermann, A., Zenker, A. and Hering, D. (2006). *Weiterentwicklung und Anpassung des nationalen Bewertungssystems für Makrozoobenthos an neue internationale Vorgaben*. Essen.

- Naiman, R.J., Johnston, C.A. and Kelley, J.C. (1988). Alteration of North American Streams by Beaver. *BioScience*, 38(11), 753-762.
- Naiman, R.J., Melillo, J.M. and Hobbie, J.E. (1986). Ecosystem Alteration of Boreal Forest Streams by Beaver (*Castor Canadensis*). *Journal of Wildlife Management*, 67(5), 1254–1269. doi: 10.2307/1938681.
- Naumann, G. (1991). Aussetzen von Bibern in der Eifel - Ein Beispiel für die Problematik von Wiedereinbürgerungen. *Naturschutz im Rheinland, Rheinischer Verein für Denkmalpflege und Landschaftsschutz, Jahrbuch 1989-1991*, 137–150.
- Nummi, P., Liao, W., van der Schoor, J. and Loehr, J. (2021). Beaver creates early successional hotspots for water beetles. *Biodiversity and Conservation*, 30(10), 2655–2670. doi: 10.1007/s10531-021-02213-8.
- Oksanen, J., Guillaume, F.B., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. *vegan: Community Ecology Package*. R Package Version 24-5.
- Orazi, V., Hagge, J., Gossner, M.M., Müller, J. and Heurich, M. (2022). A Biodiversity Boost from the Eurasian Beaver (*Castor fiber*) in Germany’s Oldest National Park. *Frontiers in Ecology and Evolution*, 10. doi: 10.3389/fevo.2022.873307.
- Pliūraitė, V. and Kesminas, V. (2012). Ecological impact of Eurasian beaver (*Castor fiber*) activity on macroinvertebrate communities in Lithuanian trout streams. *Open Life Sciences*, 7(1), 101–114. doi: 10.2478/s11535-011-0084-y.
- Pollock, M.M., Witmore, S. and Yokel, E. (2022). Field experiments to assess passage of juvenile salmonids across beaver dams during low flow conditions in a tributary to the Klamath River, California, USA. *PloS One*, 17(5), e0268088. doi: 10.1371/journal.pone.0268088.
- Polvi, L.E. and Wohl, E. (2012). The beaver meadow complex revisited - the role of beavers in post-glacial floodplain development. *Earth Surface Processes and Landforms*, 37(3), 332–346. doi: 10.1002/esp.2261.
- Robinson, C.T., Schweizer, P., Larsen, A., Schubert, C.J. and Siebers, A.R. (2020). Beaver effects on macroinvertebrate assemblages in two streams with contrasting morphology. *The Science of the Total Environment*, 722. doi: 10.1016/j.scitotenv.2020.137899.

- Rolauffs, P., Hering, D. and Lohse, S. (2001). Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. *Hydrobiologia* (459), 201–212.
- RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL <http://www.rstudio.com/>
- Schloemer, S. and Hoffmann, A. (2018). The Beaver Dam Vacuum Sampler - a new sampling method to investigate the invertebrate fauna in beaver dams. *Lauterbornia* (85), 117–121.
- Schloemer, S., Hörren, T., Lorenz, A.W. and Hering, D. (2023). The macroinvertebrate fauna of maintained and abandoned beaver dams. *Hydrobiologia*, 850(8), 1763–1778. doi: 10.1007/s10750-023-05176-9.
- Schmedtje, U. and Colling, M. (1996). *Ökologische Typisierung der aquatischen Makrofauna*. München (Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 4). Available at: https://www.gewaesser-bewertung-berechnung.de/files/downloads/perlodes/PerlodesOnline_Dokumentation_Teil_III_Beschreibung_Indizes.pdf (Accessed: 26 October 2021).
- Schmidt-Kloiber, A. and Hering, D. (2015). www.freshwaterecology.info – An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, 53, 271–282. doi: 10.1016/j.ecolind.2015.02.007.
- Spitzenberg, D., Schöne, A., Klausnitzer, B. and Malchau, W. (2021). *Die wasserbewohnenden Käfer Sachsen-Anhalts*. Rangsdorf: Natur + Text.
- Sternberg, K. and Buchwald, R. (eds.) (2000). *Die Libellen Baden-Württembergs: Band 2: Großlibellen (Anisoptera)*. Stuttgart: Eugen Ulmer GmbH & Co (Die Libellen Baden-Württembergs / bearb. und hrsg. von Klaus Sternberg und Rainer Buchwald. Mit Textbeitr. von Rainer Buchwald, 2).
- Stout, T.L., Majerova, M. and Neilson, B.T. (2017). Impacts of beaver dams on channel hydraulics and substrate characteristics in a mountain stream. *Ecohydrology*, 10(1), e1767. doi: 10.1002/eco.1767.
- Thompson, S., Vehkaoja, M. and Nummi, P. (2016). Beaver-created deadwood dynamics in the boreal forest. *Forest Ecology and Management*, 360, 1–8. doi: 10.1016/j.foreco.2015.10.019.

- Wegener, P., Covino, T. and Wohl, E. (2017). Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism. *Water Resources Research*, 53(6), 4606–4623. doi: 10.1002/2016WR019790.
- Westbrook, C.J., Cooper, D.J. and Baker, B.W. (2006). Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. *Water Resources Research*, 42(6), 288. doi: 10.1029/2005WR004560.
- Wilke, C.O., 2019. cowplot: Streamlined Plot Theme and Plot Annotations for “ggplot2.” R Package Version 094 <https://CRAN.R-project.org/package=cowplot>.
- White, D.S. (1990). Biological relationships to convective flow patterns within stream beds. *Hydrobiologia*, 196(2), 149–158. doi: 10.1007/BF00006106.

Appendix - Supplementary material

Table S1 Taxa and number of individuals in the single habitats, with (n= number of samples)

| Taxa | Side channel (n=9) | Downstream dam (n=9) | Dam (n=143) | Pond (n=9) | Riffle (n=9) | Pool (n=9) |
|--|-----------------------|-------------------------|-------------|------------|--------------|------------|
| Pisidium sp. | 50 | 17 | 121 | 448 | 5 | 74 |
| Acupalpus dubius Ad. (Schilsky, 1888) | 0 | 0 | 1 | 0 | 0 | 0 |
| Agabus biguttatus Ad. | 0 | 0 | 1 | 0 | 0 | 0 |
| Agabus paludosus Ad. (Fabricius, 1801) | 0 | 0 | 5 | 0 | 0 | 0 |
| Agabus sp. Lv. | 1 | 0 | 0 | 0 | 0 | 0 |
| Agriotes obscurus Ad. (Linnaeus, 1758) | 0 | 0 | 1 | 0 | 0 | 0 |
| Agriotes sp. Lv. | 0 | 0 | 1 | 0 | 0 | 0 |
| Anacaena globulus Ad. (Paykull, 1798) | 0 | 0 | 8 | 0 | 0 | 0 |
| Anacaena globulus Lv. (Paykull, 1798) | 0 | 0 | 2 | 0 | 0 | 0 |
| Bembidion guttula Ad. (Fabricius, 1792) | 0 | 0 | 1 | 0 | 0 | 0 |
| Byrrhus sp. Lv. | 0 | 0 | 1 | 0 | 0 | 0 |
| Cantharis sp. Lv. | 0 | 0 | 1 | 0 | 0 | 0 |
| Cercyon analis Ad. (Paykull, 1798) | 0 | 0 | 1 | 0 | 0 | 0 |
| Cercyon ustulatus Ad. (Preysslner, 1790) | 0 | 0 | 2 | 0 | 0 | 0 |
| Cyphon sp. Lv. | 0 | 0 | 1 | 0 | 0 | 0 |
| Datonychus melanostictus Ad. (Marsham, 1802) | 0 | 0 | 1 | 0 | 0 | 0 |
| Dianous coerulescens Ad. (Gyllenhal, 1810) | 0 | 0 | 381 | 0 | 0 | 0 |
| Dianous coerulescens Lv. (Gyllenhal, 1810) | 0 | 0 | 1 | 0 | 0 | 0 |
| Dryops ernesti Ad. (Des Gozis, 1886) | 0 | 0 | 0 | 3 | 0 | 0 |
| Dryops luridus Ad. (Erichson, 1847) | 0 | 0 | 37 | 0 | 0 | 0 |
| Dryops sp. Ad. | 8 | 0 | 0 | 0 | 0 | 0 |
| Dryops sp. Lv. | 11 | 0 | 4 | 0 | 0 | 0 |
| Dytiscidae Gen. sp. | 3 | 0 | 0 | 0 | 0 | 0 |
| Elmis aenea Ad. (Müller, 1806) | 0 | 0 | 3 | 0 | 2 | 0 |
| Elmis aenea/mauguetii Ad. | 0 | 0 | 33 | 1 | 0 | 0 |
| Elmis mauguetii Ad. (Latreille, 1802) | 6 | 4 | 59 | 0 | 0 | 0 |
| Elmis sp. Ad. | 12 | 12 | 0 | 0 | 2 | 0 |

| Taxa | Side channel (n=9) | Downstream dam (n=9) | Dam (n=143) | Pond (n=9) | Riffle (n=9) | Pool (n=9) |
|---|-----------------------|-------------------------|-------------|------------|--------------|------------|
| <i>Elmis</i> sp. Lv. | 19 | 3 | 64 | 0 | 5 | 0 |
| <i>Elodes marginata</i> Lv. (Fabricius, 1798) | 4 | 1 | 0 | 0 | 35 | 0 |
| <i>Elodes</i> sp. Lv. | 382 | 8 | 3,016 | 4 | 5 | 4 |
| <i>Esolus angustatus</i> Ad. (Müller, 1821) | 1 | 6 | 2 | 0 | 0 | 0 |
| <i>Esolus parallelepipedus</i> Ad. (Müller, 1806) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Esolus</i> sp. Lv. | 0 | 3 | 0 | 0 | 0 | 0 |
| <i>Gabrius appendiculatus</i> Ad. (Sharp, 1910) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Gyrinus substriatus</i> Ad. (Stephens, 1829) | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Haliphus ruficollis</i> Ad. (De Geer, 1774) | 0 | 0 | 2 | 1 | 0 | 0 |
| <i>Haliphus</i> sp. Lv. | 0 | 1 | 16 | 0 | 0 | 0 |
| <i>Hydraena assimilis</i> Ad. (Rey, 1885) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Hydraena gracilis</i> Ad. (Germar, 1823) | 10 | 18 | 20 | 0 | 17 | 0 |
| <i>Hydraena pygmaea</i> Ad. (Waterhouse, 1833) | 0 | 0 | 9 | 0 | 1 | 0 |
| <i>Hydrobius subrotundus</i> Ad. (Stephens, 1829) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Hydrochus angustatus</i> Ad. (Germar, 1823) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Hydrochus elongatus</i> Ad. (Schaller, 1783) | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Hydrocyphon deflexicollis</i> Lv. (Müller, 1821) | 1 | 34 | 0 | 0 | 37 | 0 |
| <i>Hydroporus neglectus</i> Ad. (Schaum, 1845) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Ilybius</i> sp. Lv. | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Laccobius bipunctatus</i> Ad. (Fabricius, 1775) | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Laccobius minutus</i> Ad. (Linnaeus, 1758) | 0 | 0 | 6 | 0 | 0 | 0 |
| <i>Lesteva longoelytrata</i> Ad. (Goeze, 1777) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Lesteva pubescens</i> Ad. (Mannerheim, 1830) | 0 | 0 | 3 | 0 | 0 | 0 |
| <i>Limnebius truncatellus</i> Ad. (Thunberg, 1794) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Limnius perrisi</i> Ad. (Dufour, 1843) | 4 | 4 | 0 | 0 | 5 | 0 |
| <i>Limnius perrisi</i> Lv. (Dufour, 1843) | 0 | 4 | 0 | 0 | 27 | 0 |
| <i>Limnius volckmari</i> Ad. (Panzer, 1793) | 9 | 26 | 6 | 0 | 9 | 0 |
| <i>Limnius volckmari</i> Lv. (Panzer, 1793) | 3 | 12 | 8 | 0 | 4 | 5 |
| <i>Ocotemnus glabriculus</i> Ad. (Gyllenhal, 1827) | 0 | 0 | 1 | 0 | 0 | 0 |

| Taxa | Side channel (n=9) | Downstream dam (n=9) | Dam (n=143) | Pond (n=9) | Riffle (n=9) | Pool (n=9) |
|---|-----------------------|-------------------------|-------------|------------|--------------|------------|
| Ocys tachysoides Ad. (Antoine, 1933) | 0 | 0 | 1 | 0 | 0 | 0 |
| Orectochilus villosus Lv. (Müller, 1776) | 2 | 7 | 26 | 0 | 3 | 2 |
| Oulimnius sp. Lv. | 1 | 0 | 0 | 0 | 0 | 0 |
| Oulimnius tuberculatus Ad. (Müller, 1806) | 0 | 2 | 1 | 0 | 0 | 0 |
| Phaedon armoraciae Ad. (Linnaeus, 1758) | 0 | 0 | 2 | 0 | 0 | 0 |
| Phyllotreta tetrastigma Ad. (Comolli, 1837) | 0 | 0 | 2 | 0 | 0 | 0 |
| Platambus maculatus Ad. (Linnaeus, 1758) | 0 | 0 | 1 | 0 | 0 | 0 |
| Platambus maculatus Lv. (Linnaeus, 1758) | 1 | 1 | 0 | 7 | 0 | 0 |
| Pterostichus diligens Ad. (Sturm, 1824) | 0 | 0 | 0 | 1 | 0 | 0 |
| Stenus clavicornis Ad. (Scopoli, 1763) | 0 | 0 | 1 | 0 | 0 | 0 |
| Stictotarsus duodecimpustulatus Ad. (Fabricius, 1792) | 0 | 0 | 1 | 0 | 0 | 0 |
| Strophosoma melanogrammum Ad. (Forster, 1771) | 0 | 0 | 1 | 0 | 0 | 0 |
| Quedius sp. Ad. | 0 | 0 | 0 | 1 | 0 | 0 |
| Xyleborus germanus Ad. (Blandford, 1894) | 0 | 0 | 1 | 0 | 0 | 0 |
| Xylomidae Gen. sp. | 0 | 0 | 1 | 0 | 0 | 0 |
| Asellus aquaticus (Linnaeus, 1758) | 0 | 0 | 244 | 0 | 0 | 0 |
| Gammarus fossarum (Koch, 1836) | 1,076 | 347 | 15,257 | 5 | 1,347 | 4,031 |
| Androprosopa sp. | 0 | 0 | 1 | 0 | 0 | 1 |
| Austrolimnophila sp. | 0 | 1 | 43 | 0 | 1 | 2 |
| Bazarella/Berdeniella sp. | 0 | 0 | 47 | 0 | 0 | 0 |
| Ceratopogoninae Gen. sp. | 18 | 5 | 95 | 124 | 12 | 41 |
| Chelifera sp. | 8 | 0 | 0 | 11 | 1 | 8 |
| Chironomidae Gen. sp. | 1,126 | 158 | 6,815 | 73 | 61 | 121 |
| Chironomus plumosus | 0 | 0 | 0 | 2 | 0 | 0 |
| Chironomus riparius | 0 | 0 | 0 | 48 | 0 | 0 |
| Chrysops sp. | 0 | 0 | 8 | 0 | 0 | 0 |
| Clinocerinae Gen. sp. | 0 | 0 | 18 | 0 | 0 | 0 |
| Coenosiinae Gen. sp. | 0 | 0 | 1 | 0 | 0 | 0 |
| Dicranomyia sp. | 0 | 1 | 42 | 0 | 0 | 0 |

| Taxa | Side channel (n=9) | Downstream dam (n=9) | Dam (n=143) | Pond (n=9) | Riffle (n=9) | Pool (n=9) |
|--|-----------------------|-------------------------|-------------|------------|--------------|------------|
| Dicranota sp. | 6 | 19 | 90 | 1 | 7 | 7 |
| Dixa sp. | 2 | 0 | 5 | 0 | 1 | 1 |
| Dolichopodidae Gen. sp. | 3 | 0 | 0 | 1 | 0 | 1 |
| Ellipteroides sp. | 0 | 0 | 2 | 0 | 2 | 0 |
| Eloeophila sp. | 3 | 6 | 21 | 4 | 2 | 22 |
| Empididae Gen. sp. | 0 | 0 | 1 | 0 | 0 | 0 |
| Fanniidae Gen. sp. | 0 | 0 | 1 | 1 | 0 | 0 |
| Helius sp. | 0 | 0 | 11 | 2 | 0 | 0 |
| Hemerodromia sp. | 0 | 0 | 5 | 0 | 0 | 0 |
| Hydrellia sp. | 0 | 0 | 1 | 0 | 0 | 0 |
| Limnophora sp. | 2 | 0 | 11 | 0 | 0 | 0 |
| Limonia sp. | 0 | 0 | 2 | 0 | 0 | 0 |
| Limoniidae Gen. sp. | 3 | 1 | 13 | 0 | 0 | 2 |
| Lipsothrix sp. | 0 | 0 | 128 | 0 | 0 | 0 |
| Lispe sp. | 0 | 0 | 67 | 0 | 1 | 0 |
| Melanogaster sp. | 0 | 0 | 1 | 0 | 0 | 0 |
| Molophilus sp. | 0 | 0 | 5 | 4 | 0 | 1 |
| Muscidae Gen. sp. | 1 | 0 | 1 | 5 | 0 | 6 |
| Mycetobia sp. | 0 | 0 | 18 | 0 | 0 | 0 |
| Neolimnomyia sp. | 0 | 0 | 4 | 0 | 0 | 0 |
| Orthocladiinae Gen. sp. | 0 | 0 | 0 | 414 | 0 | 117 |
| Pedicia sp. | 0 | 1 | 0 | 0 | 1 | 0 |
| Phylidorea sp. | 0 | 0 | 2 | 0 | 0 | 0 |
| Pilaria sp. | 8 | 1 | 3 | 1 | 0 | 1 |
| Prodiamesa olivacea (Meigen, 1818) | 0 | 1 | 4 | 31 | 0 | 3 |
| Prosimulium sp. | 1,305 | 265 | 2,696 | 1 | 489 | 0 |
| Prosimulium tomosvaryi (Enderlein, 1921) | 278 | 19 | 284 | 0 | 6 | 0 |
| Pseudolimnophila sp. | 2 | 0 | 17 | 6 | 0 | 0 |
| Psychodidae Gen. sp. | 5 | 0 | 0 | 1 | 1 | 4 |

| Taxa | Side channel (n=9) | Downstream dam (n=9) | Dam (n=143) | Pond (n=9) | Riffle (n=9) | Pool (n=9) |
|--------------------------------------|-----------------------|-------------------------|-------------|------------|--------------|------------|
| Ptychoptera sp. | 7 | 1 | 4 | 3 | 0 | 72 |
| Rhagionidae Gen. sp. | 0 | 2 | 14 | 1 | 1 | 1 |
| Rhypholophus sp. | 0 | 0 | 5 | 0 | 1 | 1 |
| Scatophagidae Gen. sp. | 0 | 0 | 2 | 0 | 0 | 0 |
| Scleroprocta sp. | 0 | 0 | 1 | 0 | 1 | 0 |
| Simulium sp. | 489 | 137 | 5,803 | 2 | 37 | 0 |
| Simulium venum-Gr. | 6 | 5 | 232 | 0 | 0 | 0 |
| Stratiomyidae Gen. sp. | 0 | 0 | 1 | 0 | 0 | 0 |
| Syrphidae Gen. sp. | 0 | 0 | 3 | 0 | 0 | 0 |
| Tabanidae Gen. sp. | 4 | 6 | 4 | 26 | 0 | 5 |
| Tanypodinae Gen. sp. | 94 | 46 | 363 | 814 | 13 | 360 |
| Tanytarsini Gen. sp. | 59 | 53 | 734 | 496 | 118 | 733 |
| Thaumaleidae Gen. sp. | 0 | 0 | 1 | 0 | 0 | 0 |
| Thaumastoptera calceata (Mik, 1866) | 0 | 0 | 18 | 0 | 0 | 0 |
| Tipula sp. | 4 | 0 | 28 | 1 | 1 | 0 |
| Trichoceridae Gen. sp. | 1 | 1 | 1 | 0 | 0 | 0 |
| Tricyphona sp. | 0 | 0 | 3 | 0 | 0 | 0 |
| Baetis alpinus (Pictet 1843) | 0 | 0 | 0 | 0 | 94 | 0 |
| Baetis fuscatus (Linnaeus, 1761) | 0 | 0 | 7 | 0 | 0 | 0 |
| Baetis muticus (Linnaeus, 1758) | 165 | 51 | 449 | 0 | 63 | 0 |
| Baetis niger (Linnaeus, 1761) | 27 | 7 | 210 | 1 | 0 | 0 |
| Baetis rhodani (Pictet, 1843) | 128 | 198 | 664 | 2 | 10 | 0 |
| Baetis scambus (Eaton, 1870) | 0 | 1 | 1 | 0 | 0 | 0 |
| Baetis sp. | 63 | 87 | 1,015 | 7 | 49 | 0 |
| Baetis vernus (Curtis, 1834) | 0 | 0 | 3 | 0 | 0 | 0 |
| Centroptilum luteolum (Müller, 1776) | 0 | 0 | 1 | 0 | 0 | 0 |
| Cloeon dipterum (Linnaeus, 1761) | 0 | 3 | 20 | 0 | 0 | 0 |
| Caenis sp. | 0 | 0 | 5 | 23 | 0 | 0 |
| Ephemera danica (Müller, 1764) | 7 | 6 | 48 | 0 | 22 | 1 |

| Taxa | Side channel (n=9) | Downstream dam (n=9) | Dam (n=143) | Pond (n=9) | Riffle (n=9) | Pool (n=9) |
|---|-----------------------|-------------------------|-------------|------------|--------------|------------|
| <i>Ecdyonurus venosus</i> -Gr. | 1 | 7 | 1 | 0 | 23 | 0 |
| <i>Epeorus assimilis</i> (Eaton, 1885) | 6 | 57 | 44 | 56 | 4 | 90 |
| <i>Rhithrogena semicolorata</i> -Gr. | 34 | 22 | 1,891 | 10 | 55 | 80 |
| <i>Habroleptoides confusa</i> (Sartori & Jacob, 1986) | 3 | 4 | 9 | 2 | 9 | 32 |
| <i>Habrophlebia lauta</i> (Eaton, 1884) | 0 | 0 | 75 | 0 | 0 | 0 |
| <i>Leptophlebia marginata</i> (Linnaeus, 1767) | 68 | 56 | 734 | 0 | 85 | 0 |
| <i>Paraleptophlebia submarginata</i> (Stephens, 1835) | 14 | 231 | 93 | 0 | 325 | 1 |
| <i>Ancylus fluviatilis</i> (Müller, 1774) | 5 | 9 | 64 | 0 | 0 | 0 |
| <i>Bythinella dunkeri</i> (Frauenfeld, 1857) | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Cochlicopa lubrica</i> (Müller, 1774) | 0 | 0 | 3 | 0 | 0 | 0 |
| <i>Discus perspectivus</i> (Megerle von Mühlfeld, 1816) | 0 | 0 | 4 | 0 | 0 | 0 |
| <i>Euconulus fulvus</i> (Müller, 1774) | 0 | 0 | 40 | 0 | 0 | 0 |
| <i>Galba truncatula</i> (Müller, 1774) | 0 | 0 | 93 | 0 | 0 | 0 |
| <i>Gyraulus</i> sp. | 0 | 0 | 97 | 4 | 0 | 3 |
| Oxychilidae sp. | 0 | 0 | 33 | 0 | 0 | 0 |
| <i>Physa fontinalis</i> (Linnaeus, 1758) | 0 | 0 | 39 | 0 | 0 | 0 |
| <i>Radix balthica</i> (Linnaeus, 1758) | 11 | 1 | 100 | 0 | 0 | 1 |
| <i>Trochulus</i> sp. | 0 | 0 | 6 | 0 | 0 | 0 |
| <i>Vertigo antivertigo</i> (Draparnaud, 1801) | 0 | 0 | 4 | 0 | 0 | 0 |
| <i>Vitrea</i> sp. | 0 | 0 | 7 | 0 | 0 | 0 |
| <i>Cymus clavicolus</i> Ad. (Fallen, 1807) | 0 | 0 | 0 | 1 | 0 | 0 |
| Gerridae Gen. sp. | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>Nepa cinerea</i> (Linnaeus, 1758) | 0 | 0 | 4 | 0 | 0 | 0 |
| <i>Glossiphonia complanata</i> (Linnaeus, 1758) | 1 | 1 | 1 | 0 | 0 | 0 |
| Hydrachnidia Gen. sp. | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Cataclysta lemnata</i> (Linnaeus, 1758) | 1 | 0 | 2 | 0 | 0 | 0 |
| <i>Elophila nymphaeata</i> (Linnaeus, 1758) | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Sialis</i> sp. | 1 | 4 | 22 | 79 | 6 | 38 |
| <i>Osmylus fulvicephalus</i> Lv. (Scopoli, 1763) | 0 | 0 | 5 | 0 | 0 | 0 |

| Taxa | Side channel (n=9) | Downstream dam (n=9) | Dam (n=143) | Pond (n=9) | Riffle (n=9) | Pool (n=9) |
|--|-----------------------|-------------------------|-------------|------------|--------------|------------|
| <i>Aeshna cyanea</i> (Müller, 1764) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Calopteryx splendens</i> (Harris, 1780) | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>Calopteryx virgo</i> (Linnaeus, 1758) | 0 | 0 | 5 | 0 | 0 | 0 |
| <i>Cordulegaster boltonii</i> (Donovan, 1807) | 2 | 1 | 14 | 5 | 0 | 3 |
| <i>Libellula depressa</i> (Linnaeus, 1758) | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>Pyrrhosoma nymphula</i> (Sulzer, 1776) | 3 | 0 | 2 | 2 | 0 | 0 |
| <i>Eiseniella tetraedra</i> (Savigny, 1826) | 9 | 4 | 266 | 0 | 4 | 0 |
| Lumbriculidae Gen. sp. | 0 | 0 | 700 | 128 | 0 | 44 |
| Naididae/Tubificidae Gen. sp. | 7 | 113 | 21 | 161 | 14 | 23 |
| Oligochaeta Gen. sp. | 64 | 177 | 0 | 0 | 140 | 0 |
| <i>Stylogrillus heringianus</i> (Claparède, 1862) | 0 | 0 | 14 | 24 | 0 | 28 |
| <i>Amphinemura</i> sp. | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Brachyptera risi</i> (Morton, 1896) | 1 | 1 | 2 | 0 | 1 | 1 |
| <i>Brachyptera seticornis</i> (Klapálek, 1902) | 2 | 0 | 3 | 0 | 2 | 0 |
| <i>Chloroperla</i> sp. | 0 | 1 | 0 | 0 | 2 | 0 |
| <i>Dinocras cephalotes</i> (Curtis, 1827) | 0 | 1 | 0 | 0 | 4 | 0 |
| <i>Isoperla</i> sp. | 7 | 2 | 25 | 0 | 16 | 0 |
| <i>Leuctra braueri</i> (Kempny, 1898) | 0 | 0 | 0 | 0 | 6 | 11 |
| <i>Leuctra nigra</i> (Olivier, 1811) | 12 | 2 | 133 | 23 | 27 | 350 |
| <i>Leuctra</i> sp. | 2 | 0 | 10 | 0 | 2 | 1 |
| <i>Nemoura</i> sp. | 373 | 94 | 4,064 | 2 | 3 | 3 |
| <i>Perla marginata</i> (Panzer, 1799) | 0 | 1 | 2 | 0 | 21 | 0 |
| <i>Protonemura</i> sp. | 107 | 0 | 731 | 0 | 58 | 0 |
| <i>Siphonoperla</i> sp. | 22 | 29 | 29 | 0 | 53 | 8 |
| <i>Adicella reducta</i> (McLachlan, 1865) | 0 | 0 | 5 | 0 | 0 | 0 |
| <i>Agapetus fuscipes</i> (Curtis, 1834) | 10 | 13 | 34 | 0 | 128 | 23 |
| <i>Anomalopterygella chauviniana</i> (Stein, 1874) | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>Beraea maurus</i> (Curtis, 1834) | 5 | 1 | 33 | 0 | 10 | 0 |
| <i>Beraea pullata</i> (Curtis, 1834) | 1 | 0 | 25 | 1 | 0 | 0 |

| Taxa | Side channel (n=9) | Downstream dam (n=9) | Dam (n=143) | Pond (n=9) | Riffle (n=9) | Pool (n=9) |
|--|-----------------------|-------------------------|-------------|------------|--------------|------------|
| <i>Beraeodes minutus</i> (Linnaeus, 1761) | 0 | 1 | 7 | 2 | 0 | 0 |
| Chaetopterygini/Stenophylacini Gen. sp. | 295 | 68 | 1,926 | 24 | 18 | 198 |
| <i>Chaetopteryx major</i> (McLachlan, 1876) | 6 | 2 | 78 | 0 | 60 | 0 |
| <i>Chaetopteryx villosa</i> (Fabricius, 1798) | 42 | 2 | 26 | 0 | 0 | 267 |
| <i>Crunoecia irrorata</i> (Curtis, 1834) | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>Cyrnus trimaculatus</i> (Curtis, 1834) | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Diplectronea felix</i> (McLachlan, 1878) | 1 | 0 | 17 | 0 | 2 | 0 |
| <i>Drusus annulatus</i> (Stephens, 1837) | 3 | 5 | 21 | 0 | 14 | 1 |
| <i>Ernodes articularis</i> (Pictet, 1834) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Glossosoma conformis</i> (Neboiss, 1963) | 0 | 2 | 0 | 0 | 17 | 0 |
| <i>Glyphotaenius pellucidus</i> (Retzius, 1783) | 1 | 0 | 3 | 0 | 0 | 0 |
| <i>Halesus digitatus/tesselatus</i> | 22 | 5 | 213 | 0 | 0 | 2 |
| <i>Halesus radiatus</i> (Curtis, 1834) | 40 | 5 | 642 | 10 | 1 | 72 |
| <i>Hydatophylax infumatus</i> (McLachlan, 1865) | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Hydropsyche angustipennis</i> (Curtis, 1834) | 23 | 0 | 1 | 0 | 0 | 0 |
| <i>Hydropsyche dinarica</i> (Marinkovic-Gospodnetic, 1979) | 0 | 0 | 7 | 0 | 0 | 0 |
| <i>Hydropsyche fulvipes</i> (Curtis, 1834) | 12 | 1 | 4 | 0 | 4 | 0 |
| <i>Hydropsyche instabilis</i> (Curtis, 1834) | 0 | 0 | 4 | 0 | 0 | 0 |
| <i>Hydropsyche saxonica</i> (McLachlan, 1884) | 28 | 56 | 55 | 2 | 0 | 0 |
| <i>Hydropsyche siltalai</i> (Doehler, 1963) | 0 | 1 | 96 | 0 | 7 | 0 |
| <i>Hydropsyche</i> sp. | 0 | 2 | 125 | 0 | 0 | 0 |
| <i>Lepidostoma basale</i> (Kolenati, 1848) | 0 | 0 | 4 | 0 | 0 | 1 |
| Limnephilini Gen. sp. | 9 | 20 | 728 | 0 | 2 | 0 |
| <i>Limnephilus lunatus</i> (Curtis, 1834) | 19 | 0 | 71 | 0 | 0 | 0 |
| <i>Limnephilus decipiens</i> (Kolenati, 1848) | 3 | 3 | 0 | 0 | 0 | 0 |
| <i>Limnephilus rhombicus</i> (Linnaeus, 1758) | 18 | 5 | 57 | 21 | 0 | 1 |
| <i>Lithax niger</i> (Hagen, 1859) | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Lype reducta</i> (Hagen, 1868) | 9 | 3 | 394 | 0 | 2 | 0 |
| <i>Micropterna lateralis/sequax</i> | 1 | 3 | 0 | 0 | 0 | 0 |

| Taxa | Side channel (n=9) | Downstream dam (n=9) | Dam (n=143) | Pond (n=9) | Riffle (n=9) | Pool (n=9) |
|---|-----------------------|-------------------------|-------------|------------|--------------|------------|
| <i>Notidobia ciliaris</i> (Linnaeus, 1761) | 0 | 0 | 1 | 1 | 0 | 5 |
| <i>Odontocerum albicorne</i> (Scopoli, 1763) | 1 | 28 | 9 | 4 | 24 | 30 |
| <i>Oecismus monedula</i> (Hagen, 1859) | 9 | 15 | 10 | 0 | 11 | 11 |
| <i>Philopotamus ludificatus</i> (McLachlan, 1878) | 0 | 0 | 19 | 0 | 68 | 0 |
| <i>Philopotamus montanus</i> (Donovan, 1813) | 54 | 1 | 452 | 0 | 15 | 0 |
| <i>Philopotamus variegatus</i> (Scopoli, 1763) | 0 | 0 | 13 | 0 | 0 | 0 |
| <i>Plectrocnemia conspersa</i> (Curtis, 1834) | 3 | 4 | 52 | 0 | 1 | 2 |
| <i>Plectrocnemia geniculata</i> (McLachlan, 1871) | 0 | 0 | 3 | 0 | 0 | 0 |
| <i>Potamophylax cingulatus</i> (Stephens, 1837) | 45 | 24 | 240 | 2 | 78 | 40 |
| <i>Potamophylax latipennis</i> (Curtis, 1834) | 0 | 0 | 5 | 0 | 1 | 0 |
| <i>Potamophylax luctuosus</i> (Piller & Mitterpacher, 1783) | 2 | 0 | 5 | 0 | 0 | 4 |
| <i>Rhyacophila sensu stricto</i> | 1 | 0 | 53 | 0 | 0 | 0 |
| <i>Rhyacophila laevis</i> (Pictet, 1834) | 0 | 0 | 3 | 0 | 0 | 0 |
| <i>Rhyacophila</i> sp. | 2 | 2 | 0 | 0 | 1 | 0 |
| <i>Rhyacophila praemorsa</i> (McLachlan, 1879) | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>Rhyacophila tristis</i> (Pictet, 1834) | 0 | 0 | 2 | 0 | 4 | 0 |
| <i>Sericostoma flavicorne/ personatum</i> | 23 | 19 | 107 | 20 | 54 | 193 |
| <i>Silo nigricornis</i> (Pictet, 1834) | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Silo pallipes</i> (Fabricius, 1781) | 1 | 13 | 2 | 0 | 4 | 0 |
| <i>Silo piceus</i> (Brauer, 1857) | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Stenophylax</i> sp. | 3 | 0 | 0 | 0 | 0 | 2 |
| <i>Wormaldia occipitalis</i> (Pictet, 1834) | 29 | 15 | 749 | 0 | 12 | 0 |
| <i>Dugesia</i> sp. | 48 | 65 | 894 | 0 | 122 | 1 |
| <i>Polycelis</i> sp. | 34 | 18 | 1,782 | 0 | 87 | 0 |

Table S2 Number of taxa (total and average) in the different habitats; number of Individuals per square metre (in total, without *Gammarus fossarum*, only *G. fossarum* Individuals)

| Habitat | Taxa total / average | Individuals total and m ² | Individuals m ² without <i>G. fossarum</i> | <i>G. fossarum</i> Individuals m ² |
|------------------------|----------------------|--------------------------------------|---|---|
| Dam (lotic) | 210 / 29 | 57,850 / 1,474 | 1,079 | 395 |
| Downstream dam (lotic) | 101 / 35 | 2,815 / 1,251 | 1,097 | 154 |
| Side channel (lotic) | 110 / 42 | 6,992 / 3,108 | 2,629 | 479 |
| Pond (lentic) | 64 / 19 | 3,165 / 1,407 | 1,404 | 3 |
| Riffle (lotic) | 91 / 40 | 4,108 / 1,826 | 1,227 | 599 |
| Pool (lentic) | 63 / 25 | 7,198 / 3,199 | 1,407 | 1,792 |

Table S3 Results iNEXT analysis, diversity estimates along with related statistics of beaver and non-beaver territories with the observed diversity (Observed), the asymptotic diversity estimate (Estimated), as well as standard error (s.e.) of the asymptotic estimate and the associated 95 % lower and upper confidence limits (LCL, UCL)

| Site | Diversity | Observed | Estimated | s.e. | LCL | UCL |
|----------------------|-------------------|----------|-----------|------|-----|-----|
| Beaver territory | Species richness | 250 | 340 | 30.4 | 298 | 422 |
| Beaver territory | Shannon diversity | 97 | 100 | 1.4 | 97 | 103 |
| Beaver territory | Simpson diversity | 66 | 67 | 0.9 | 66 | 69 |
| Non-beaver territory | Species richness | 113 | 128 | 8.1 | 118 | 153 |
| Non-beaver territory | Shannon diversity | 83 | 91 | 2.6 | 86 | 96 |
| Non-beaver territory | Simpson diversity | 67 | 72 | 2.3 | 67 | 76 |

Table S4 Taxa occurrence in beaver and non-beaver territories with water velocity preferences of the taxa. Information about aquatic taxa compiled by Schmidt-Kloiber & Hering (2015)

| Order | Family | Taxonname | Water velocity preference | Beaver territory | Non-beaver territory |
|------------|-------------|---|---------------------------|------------------|----------------------|
| Bivalvia | SPHAERIIDAE | <i>Pisidium sp.</i> | Indifferent | 636 | 79 |
| Coleoptera | CARABIDAE | <i>Acupalpus dubius Ad.</i> (Schilsky, 1888) | Semiaquatic | 1 | 0 |
| Coleoptera | DYTISCIDAE | <i>Agabus biguttatus Ad.</i> | Rheophile | 1 | 0 |
| Coleoptera | DYTISCIDAE | <i>Agabus paludosus Ad.</i> (Fabricius, 1801) | Rheo-Limnophile | 5 | 0 |
| Coleoptera | DYTISCIDAE | <i>Agabus sp. Lv.</i> | Limnophile | 1 | 0 |

| | | | | | |
|------------|---------------|---|-----------------|-------|----|
| Coleoptera | ELATERIDAE | <i>Agriotes obscurus</i> Ad. (Linnaeus, 1758) | Semiaquatic | 1 | 0 |
| Coleoptera | ELATERIDAE | <i>Agriotes</i> sp. Lv. | Semiaquatic | 1 | 0 |
| Coleoptera | HYDROPHILIDAE | <i>Anacaena globulus</i> Ad. (Paykull, 1798) | Rheo-Limnophile | 8 | 0 |
| Coleoptera | HYDROPHILIDAE | <i>Anacaena globulus</i> Lv. (Paykull, 1798) | Rheo-Limnophile | 2 | 0 |
| Coleoptera | CARABIDAE | <i>Bembidion guttula</i> Ad. (Fabricius, 1792) | Semiaquatic | 1 | 0 |
| Coleoptera | BYRRHIDAE | <i>Byrrhus</i> sp. Lv. | Semiaquatic | 1 | 0 |
| Coleoptera | CANTHARIDAE | <i>Cantharis</i> sp. Lv. | Semiaquatic | 1 | 0 |
| Coleoptera | HYDROPHILIDAE | <i>Cercyon analis</i> Ad. (Paykull, 1798) | Limnobiont | 1 | 0 |
| Coleoptera | HYDROPHILIDAE | <i>Cercyon ustulatus</i> Ad. (Preysslser, 1790) | Limno-rheophil | 2 | 0 |
| Coleoptera | SCIRTIDAE | <i>Cyphon</i> sp. Lv. | Limnophil | 1 | 0 |
| Coleoptera | CURCULIONIDAE | <i>Datonychus melanostictus</i> Ad. (Marsham, 1802) | Semiaquatic | 1 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Dianous coerulescens</i> Ad. (Gyllenhal, 1810) | Semiaquatic | 381 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Dianous coerulescens</i> Lv. (Gyllenhal, 1810) | Semiaquatic | 1 | 0 |
| Coleoptera | DRYOPIDAE | <i>Dryops ernesti</i> Ad. (Des Gozis, 1886) | Limnophile | 3 | 0 |
| Coleoptera | DRYOPIDAE | <i>Dryops luridus</i> Ad. (Erichson, 1847) | Limnophile | 37 | 0 |
| Coleoptera | DRYOPIDAE | <i>Dryops</i> sp. Ad. | Limnophile | 8 | 0 |
| Coleoptera | DRYOPIDAE | <i>Dryops</i> sp. Lv. | Limnophile | 15 | 0 |
| Coleoptera | DYTISCIDAE | <i>Dytiscidae</i> Gen. sp. | Limno-rheophil | 3 | 0 |
| Coleoptera | ELMIDAE | <i>Elmis aenea</i> Ad. (Müller, 1806) | Rheophile | 3 | 2 |
| Coleoptera | ELMIDAE | <i>Elmis aenea/mauguetii</i> Ad. | Rheophile | 34 | 0 |
| Coleoptera | ELMIDAE | <i>Elmis maugetii</i> Ad. (Latreille, 1802) | Rheophile | 69 | 0 |
| Coleoptera | ELMIDAE | <i>Elmis</i> sp. Ad. | Rheophile | 24 | 2 |
| Coleoptera | ELMIDAE | <i>Elmis</i> sp. Lv. | Rheophile | 86 | 5 |
| Coleoptera | SCIRTIDAE | <i>Elodes marginata</i> Lv. (Fabricius, 1798) | Rheophile | 5 | 35 |
| Coleoptera | SCIRTIDAE | <i>Elodes</i> sp. Lv. | Rheophile | 3,410 | 9 |
| Coleoptera | ELMIDAE | <i>Esolus angustatus</i> Ad. (Müller, 1821) | Rheobiont | 9 | 0 |
| Coleoptera | ELMIDAE | <i>Esolus parallelepipedus</i> Ad. (Müller, 1806) | Rheobiont | 1 | 0 |
| Coleoptera | ELMIDAE | <i>Esolus</i> sp. Lv. | Rheophile | 3 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Gabrius appendiculatus</i> Ad. (Sharp, 1910) | Semiaquatic | 1 | 0 |
| Coleoptera | GYRINIDAE | <i>Gyrinus substriatus</i> Ad. (Stephens, 1829) | Limno-rheophil | 1 | 0 |
| Coleoptera | HALIPLIDAE | <i>Haliplus ruficollis</i> Ad. (De Geer, 1774) | Limno-rheophil | 3 | 0 |
| Coleoptera | HALIPLIDAE | <i>Haliplus</i> sp. Lv. | Limnobiont | 17 | 0 |
| Coleoptera | HYDRAENIDAE | <i>Hydraena assimilis</i> Ad. (Rey, 1885) | Rheophile | 1 | 0 |
| Coleoptera | HYDRAENIDAE | <i>Hydraena gracilis</i> Ad. (Germar, 1823) | Rheophile | 48 | 17 |
| Coleoptera | HYDRAENIDAE | <i>Hydraena pygmaea</i> Ad. (Waterhouse, 1833) | Rheobiont | 9 | 1 |

| | | | | | |
|------------|-----------------|--|-----------------|--------|-------|
| Coleoptera | HYDROPHILIDAE | <i>Hydrobius subrotundus</i> Ad. (Stephens, 1829) | Limnophile | 1 | 0 |
| Coleoptera | HYDRAENIDAE | <i>Hydrochus angustatus</i> Ad. (Germar, 1823) | Not available | 1 | 0 |
| Coleoptera | HYDRAENIDAE | <i>Hydrochus elongatus</i> Ad. (Schaller, 1783) | Limnophile | 1 | 0 |
| Coleoptera | SCIRTIDAE | <i>Hydrocyphon deflexicollis</i> Lv. (Müller, 1821) | Rheophile | 35 | 37 |
| Coleoptera | DYTISCIDAE | <i>Hydroporus neglectus</i> Ad. (Schaum, 1845) | Limnobiont | 1 | 0 |
| Coleoptera | DYTISCIDAE | <i>Ilybius</i> sp. Lv. | Limnophile | 1 | 0 |
| Coleoptera | HYDROPHILIDAE | <i>Laccobius bipunctatus</i> Ad. (Fabricius, 1775) | Limnophile | 1 | 0 |
| Coleoptera | HYDROPHILIDAE | <i>Laccobius minutus</i> Ad. (Linnaeus, 1758) | Limno-Rheophile | 6 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Lesteva longolytrata</i> Ad. (Goeze, 1777) | Semiaquatic | 1 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Lesteva pubescens</i> Ad. (Mannerheim, 1830) | Semiaquatic | 3 | 0 |
| Coleoptera | HYDRAENIDAE | <i>Limnebius truncatellus</i> Ad. (Thunberg, 1794) | Rheo-limnophile | 1 | 0 |
| Coleoptera | ELMIDAE | <i>Limnius perrisi</i> Ad. (Dufour, 1843) | Rheobiont | 8 | 5 |
| Coleoptera | ELMIDAE | <i>Limnius perrisi</i> Lv. (Dufour, 1843) | Rheobiont | 4 | 27 |
| Coleoptera | ELMIDAE | <i>Limnius volckmari</i> Ad. (Panzer, 1793) | Rheophile | 41 | 9 |
| Coleoptera | ELMIDAE | <i>Limnius volckmari</i> Lv. (Panzer, 1793) | Rheophile | 23 | 9 |
| Coleoptera | CIIDAE | <i>Octotemnus glabriculus</i> Ad. (Gyllenhal, 1827) | Semiaquatic | 1 | 0 |
| Coleoptera | CARABIDAE | <i>Ocys tachysoides</i> Ad. (Antoine, 1933) | Semiaquatic | 1 | 0 |
| Coleoptera | GYRINIDAE | <i>Orectochilus villosus</i> Lv. (Müller, 1776) | Rheophile | 35 | 5 |
| Coleoptera | ELMIDAE | <i>Oulimnius</i> sp. Lv. | Rheo-limnophile | 1 | 0 |
| Coleoptera | ELMIDAE | <i>Oulimnius tuberculatus</i> Ad. (Müller, 1806) | Rheo-limnophile | 3 | 0 |
| Coleoptera | CHRYSOMELIDAE | <i>Phaedon armoraciae</i> Ad. (Linnaeus, 1758) | Semiaquatic | 2 | 0 |
| Coleoptera | CHRYSOMELIDAE | <i>Phyllotreta tetrastigma</i> Ad. (Comolli, 1837) | Semiaquatic | 2 | 0 |
| Coleoptera | DYTISCIDAE | <i>Platambus maculatus</i> Ad. (Linnaeus, 1758) | Rheo-limnophile | 1 | 0 |
| Coleoptera | DYTISCIDAE | <i>Platambus maculatus</i> Lv. (Linnaeus, 1758) | Rheo-limnophile | 9 | 0 |
| Coleoptera | CARABIDAE | <i>Pterostichus diligens</i> Ad. (Sturm, 1824) | Semiaquatic | 1 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Stenus clavicornis</i> Ad. (Scopoli, 1763) | Semiaquatic | 1 | 0 |
| Coleoptera | DYTISCIDAE | <i>Stictotarsus duodecimpustulatus</i> Ad. (Fabricius, 1792) | Rheo-limnophile | 1 | 0 |
| Coleoptera | CURCULIONIDAE | <i>Strophosoma melanogrammum</i> Ad. (Forster, 1771) | Semiaquatic | 1 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Quedius</i> sp. Ad. | Semiaquatic | 1 | 0 |
| Coleoptera | SCOLYTIDAE | <i>Xyleborus germanus</i> Ad. (Blandford, 1894) | Semiaquatic | 1 | 0 |
| Coleoptera | XYLOMIDAE | <i>Xylomidae</i> Gen. sp. | Semiaquatic | 1 | 0 |
| Crustacea | ASSELIDAE | <i>Asellus aquaticus</i> (Linnaeus, 1758) | Indifferent | 244 | 0 |
| Crustacea | GAMMARIDAE | <i>Gammarus fossarum</i> (Koch, 1836) | Rheophile | 16,685 | 5,378 |
| Diptera | ANISOPODIAE | <i>Mycetobia</i> sp. | Semiaquatic | 18 | 0 |
| Diptera | CERATOPOGONIDAE | <i>Ceratopogoninae</i> Gen. sp. | Indifferent | 242 | 53 |

| | | | | | |
|---------|----------------|--|-----------------|-------|-----|
| Diptera | CHIRONOMIDAE | <i>Chironomidae Gen. sp.</i> | Indifferent | 8,172 | 182 |
| Diptera | CHIRONOMIDAE | <i>Chironomus plumosus</i> | Indifferent | 2 | 0 |
| Diptera | CHIRONOMIDAE | <i>Chironomus riparius</i> | Not available | 48 | 0 |
| Diptera | CHIRONOMIDAE | <i>Orthoclaadiinae Gen. sp.</i> | Not available | 414 | 117 |
| Diptera | CHIRONOMIDAE | <i>Prodiamesa olivacea</i> (Meigen, 1818) | Rheo-Limnophile | 36 | 3 |
| Diptera | CHIRONOMIDAE | <i>Tanypodinae Gen. sp.</i> | Indifferent | 1,317 | 373 |
| Diptera | CHIRONOMIDAE | <i>Tanytarsini Gen. sp.</i> | Indifferent | 1,342 | 851 |
| Diptera | DIXIDAE | <i>Dixa sp.</i> | Rheo-Limnophile | 7 | 2 |
| Diptera | DOLICHOPODIDAE | <i>Dolichopodidae Gen. sp.</i> | Not available | 4 | 1 |
| Diptera | EHYDRIDAE | <i>Hydrellia sp.</i> | Not available | 1 | 0 |
| Diptera | EMPIDIDAE | <i>Chelifera sp.</i> | Not available | 19 | 9 |
| Diptera | EMPIDIDAE | <i>Clinocerinae Gen. sp.</i> | Rheophile | 18 | 0 |
| Diptera | EMPIDIDAE | <i>Empididae Gen. sp.</i> | Indifferent | 1 | 0 |
| Diptera | EMPIDIDAE | <i>Hemerodromia sp.</i> | Rheophile | 5 | 0 |
| Diptera | FANNIDAE | <i>Fanniidae Gen. sp.</i> | Not available | 2 | 0 |
| Diptera | LIMONIIDAE | <i>Austrolimnophila sp.</i> | Indifferent | 44 | 3 |
| Diptera | LIMONIIDAE | <i>Dicranomyia sp.</i> | Indifferent | 43 | 0 |
| Diptera | LIMONIIDAE | <i>Ellipteroides sp.</i> | Not available | 2 | 2 |
| Diptera | LIMONIIDAE | <i>Eloeophila sp.</i> | Rheo-Limnophile | 34 | 24 |
| Diptera | LIMONIIDAE | <i>Helius sp.</i> | Semiaquatic | 13 | 0 |
| Diptera | LIMONIIDAE | <i>Limonia sp.</i> | Not available | 2 | 0 |
| Diptera | LIMONIIDAE | <i>Limoniidae Gen. sp.</i> | Indifferent | 17 | 2 |
| Diptera | LIMONIIDAE | <i>Lipsothrix sp.</i> | Indifferent | 128 | 0 |
| Diptera | LIMONIIDAE | <i>Molophilus sp.</i> | Rheo-Limnophile | 9 | 1 |
| Diptera | LIMONIIDAE | <i>Neolimnomyia sp.</i> | Semiaquatic | 4 | 0 |
| Diptera | LIMONIIDAE | <i>Phylidorea sp.</i> | Not available | 2 | 0 |
| Diptera | LIMONIIDAE | <i>Pilaria sp.</i> | Indifferent | 13 | 1 |
| Diptera | LIMONIIDAE | <i>Pseudolimnophila sp.</i> | Limnophile | 25 | 0 |
| Diptera | LIMONIIDAE | <i>Rhypholophus sp.</i> | Indifferent | 5 | 2 |
| Diptera | LIMONIIDAE | <i>Scleroprocta sp.</i> | Not available | 1 | 1 |
| Diptera | LIMONIIDAE | <i>Thaumastoptera calceata</i> (Mik, 1866) | Semiaquatic | 18 | 0 |
| Diptera | MUSCIDAE | <i>Coenosinae Gen. sp.</i> | Not available | 1 | 0 |
| Diptera | MUSCIDAE | <i>Limnophora sp.</i> | Rheo-Limnophile | 13 | 0 |
| Diptera | MUSCIDAE | <i>Lispe sp.</i> | Not available | 67 | 1 |
| Diptera | MUSCIDAE | <i>Muscidae Gen. sp.</i> | Semiaquatic | 7 | 6 |

| | | | | | |
|---------------|----------------|---|-----------------|-------|-----|
| Diptera | PEDICIIDAE | <i>Dicranota sp.</i> | Rheo-Limnophile | 116 | 14 |
| Diptera | PEDICIIDAE | <i>Pedicia sp.</i> | Rheo-Limnophile | 1 | 1 |
| Diptera | PEDICIIDAE | <i>Tricyphona sp.</i> | Not available | 3 | 0 |
| Diptera | PSYCHODIDAE | <i>Bazarella/Berdeniella sp.</i> | Indifferent | 47 | 0 |
| Diptera | PSYCHODIDAE | <i>Psychodidae Gen. sp.</i> | Indifferent | 6 | 5 |
| Diptera | PTYCHOPTERIDAE | <i>Ptychoptera sp.</i> | Rheo-Limnophile | 15 | 72 |
| Diptera | RHAGIONIDAE | <i>Rhagionidae Gen. sp.</i> | Semiaquatic | 17 | 2 |
| Diptera | SCATOPHAGIDAE | <i>Scatophagidae Gen. sp.</i> | Not available | 2 | 0 |
| Diptera | SIMULIIDAE | <i>Prosimulium sp.</i> | Rheobiont | 4,268 | 489 |
| Diptera | SIMULIIDAE | <i>Prosimulium tomosvaryi</i> (Enderlein, 1921) | Rheophile | 581 | 6 |
| Diptera | SIMULIIDAE | <i>Simulium sp.</i> | Rheophile | 6,430 | 37 |
| Diptera | SIMULIIDAE | <i>Simulium venum-Gr.</i> | Rheophile | 243 | 0 |
| Diptera | STRATIOMYDAE | <i>Stratiomyidae Gen. sp.</i> | Not available | 1 | 0 |
| Diptera | SYRPHIDAE | <i>Melanogaster sp.</i> | Not available | 1 | 0 |
| Diptera | SYRPHIDAE | <i>Syrphidae Gen. sp.</i> | Not available | 3 | 0 |
| Diptera | TABANIDAE | <i>Chrysops sp.</i> | Limnophile | 8 | 0 |
| Diptera | TABANIDAE | <i>Tabanidae Gen. sp.</i> | Limnophile | 40 | 5 |
| Diptera | THAUMALEIDAE | <i>Androprosopa sp.</i> | Not available | 1 | 1 |
| Diptera | THAUMALEIDAE | <i>Thaumaleidae Gen. sp.</i> | Not available | 1 | 0 |
| Diptera | TIPULIDAE | <i>Tipula sp.</i> | Limnophile | 33 | 1 |
| Diptera | TRICHOCERIDAE | <i>Trichoceridae Gen. sp.</i> | Not available | 3 | 0 |
| Ephemeroptera | BAETIDAE | <i>Baetis alpinus</i> (Pictet 1843) | Rheophile | 0 | 94 |
| Ephemeroptera | BAETIDAE | <i>Baetis fuscatus</i> (Linnaeus, 1761) | Rheophile | 7 | 0 |
| Ephemeroptera | BAETIDAE | <i>Baetis muticus</i> (Linnaeus, 1758) | Rheophile | 665 | 63 |
| Ephemeroptera | BAETIDAE | <i>Baetis niger</i> (Linnaeus, 1761) | Rheophile | 245 | 0 |
| Ephemeroptera | BAETIDAE | <i>Baetis rhodani</i> (Pictet, 1843) | Rheophile | 992 | 10 |
| Ephemeroptera | BAETIDAE | <i>Baetis scambus</i> (Eaton, 1870) | Rheobiont | 2 | 0 |
| Ephemeroptera | BAETIDAE | <i>Baetis sp.</i> | Rheophile | 1,172 | 49 |
| Ephemeroptera | BAETIDAE | <i>Baetis vernus</i> (Curtis, 1834) | Rheophile | 3 | 0 |
| Ephemeroptera | BAETIDAE | <i>Centroptilum luteolum</i> (Müller, 1776) | Rheo-Limnophile | 23 | 0 |
| Ephemeroptera | BAETIDAE | <i>Cloeon dipterum</i> (Linnaeus, 1761) | Limno-Rheophile | 28 | 0 |
| Ephemeroptera | CAENIDAE | <i>Caenis sp.</i> | Indifferent | 1 | 0 |
| Ephemeroptera | EPHEMERIDAE | <i>Ephmera danica</i> (Müller, 1764) | Rheophile | 163 | 94 |
| Ephemeroptera | HEPTAGENIIDAE | <i>Ecdyonurus venosus-Gr.</i> | Rheobiont | 61 | 23 |
| Ephemeroptera | HEPTAGENIIDAE | <i>Epeorus assimilis</i> (Eaton, 1885) | Rheobiont | 9 | 23 |

| | | | | | |
|---------------|-------------------|---|-----------------|-------|-----|
| Ephemeroptera | HEPTAGENIIDAE | <i>Rhithrogena semicolorata-Gr.</i> | Rheobiont | 338 | 326 |
| Ephemeroptera | LEPTOPHLEBIIDAE | <i>Habroleptoides confusa</i> (Sartori & Jacob, 1986) | Rheophile | 1,957 | 135 |
| Ephemeroptera | LEPTOPHLEBIIDAE | <i>Habrophlebia lauta</i> (Eaton, 1884) | Rheo-Limnophile | 18 | 41 |
| Ephemeroptera | LEPTOPHLEBIIDAE | <i>Leptophlebia marginata</i> (Linnaeus, 1767) | Limno-Rheophile | 75 | 0 |
| Ephemeroptera | LEPTOPHLEBIIDAE | <i>Paraleptophlebia submarginata</i> (Stephens, 1835) | Rheophile | 858 | 85 |
| Gastropoda | PLANORBIDAE | <i>Ancylus fluviatilis</i> (Müller, 1774) | Rheobiont | 78 | 0 |
| Gastropoda | HYDROBIIDAE | <i>Bythinella dunkeri</i> (Frauenfeld, 1857) | Rheophile | 0 | 1 |
| Gastropoda | COCHLICOPIDAE | <i>Cochlicopa lubrica</i> (Müller, 1774) | Semiaquatic | 3 | 0 |
| Gastropoda | PATULIDAE | <i>Discus perspectivus</i> (Megerle von Mühlfeld, 1816) | Semiaquatic | 4 | 0 |
| Gastropoda | EUCLONIDAE | <i>Euconulus fulvus</i> (Müller, 1774) | Semiaquatic | 40 | 0 |
| Gastropoda | LYMNAEIDAE | <i>Galba truncatula</i> (Müller, 1774) | Semiaquatic | 93 | 0 |
| Gastropoda | PLANORBIDAE | <i>Gyraulus sp.</i> | Limno-Rheophile | 101 | 3 |
| Gastropoda | OXYCHILIDAE | <i>Oxychilidae sp.</i> | Semiaquatic | 33 | 0 |
| Gastropoda | PHYSIDAE | <i>Physa fontinalis</i> (Linnaeus, 1758) | Limno-Rheophile | 39 | 0 |
| Gastropoda | LYMNAEIDAE | <i>Radix balthica</i> (Linnaeus, 1758) | Indifferent | 112 | 1 |
| Gastropoda | HYGROMIIDAE | <i>Trochulus sp.</i> | Semiaquatic | 6 | 0 |
| Gastropoda | VERTIGINIDAE | <i>Vertigo antivertigo</i> (Draparnaud, 1801) | Not available | 4 | 0 |
| Gastropoda | PRISTILOMATIDAE | <i>Vitrea sp.</i> | Semiaquatic | 7 | 0 |
| Heteroptera | CYMIDAE | <i>Cymus clavivulus Ad.</i> (Fallen, 1807) | Terrestrisch | 1 | 0 |
| Heteroptera | GERRIDAE | <i>Gerridae Gen. sp.</i> | Not available | 2 | 0 |
| Heteroptera | NEPIDAE | <i>Nepa cinerea</i> (Linnaeus, 1758) | Limno-Rheophile | 4 | 0 |
| Hirudinea | GLOSSIPHONIIDAE | <i>Glossiphonia complanata</i> (Linnaeus, 1758) | Indifferent | 3 | 0 |
| Hydrachnidia | [Ph:Hydrachnidia] | <i>Hydrachnidia Gen. sp.</i> | Not available | 1 | 0 |
| Lepidoptera | PYRALIDAE | <i>Cataclysta lemnata</i> (Linnaeus, 1758) | Limnobiont | 3 | 0 |
| Lepidoptera | PYRALIDAE | <i>Elophila nymphaeata</i> (Linnaeus, 1758) | Limnophile | 1 | 0 |
| Megaloptera | SIALIDAE | <i>Sialis sp.</i> | Rheo-Limnophile | 106 | 44 |
| Neuroptera | OSMYLIDAE | <i>Osmylus fulvicephalus Lv.</i> (Scopoli, 1763) | Semiaquatic | 5 | 0 |
| Odonata | Aeshnidae | <i>Aeshna cyanea</i> (Müller, 1764) | Limnophile | 1 | 0 |
| Odonata | CALOPTERYGIDAE | <i>Calopteryx splendens</i> (Harris, 1780) | Rheo-Limnophile | 2 | 0 |
| Odonata | CALOPTERYGIDAE | <i>Calopteryx virgo</i> (Linnaeus, 1758) | Rheophile | 5 | 0 |
| Odonata | Cordulegastridae | <i>Cordulegaster boltonii</i> (Donovan, 1807) | Rheobiont | 22 | 3 |
| Odonata | LIBELLULIDAE | <i>Libellula depressa</i> (Linnaeus, 1758) | Limnophile | 2 | 0 |
| Odonata | COENAGRIONIDAE | <i>Pyrrhosoma nymphula</i> (Sulzer, 1776) | Limno-Rheophile | 7 | 0 |
| Oligochaeta | LUMBRICIDAE | <i>Eiseniella tetraedra</i> (Savigny, 1826) | Indifferent | 279 | 4 |
| Oligochaeta | LUMBRICULIDAE | <i>Lumbriculidae Gen. sp.</i> | Not available | 828 | 44 |

| | | | | | |
|-------------|-------------------|--|-----------------|-------|-----|
| Oligochaeta | [Kl:Oligochaeta] | <i>Naididae/Tubificidae Gen. sp.</i> | Not available | 302 | 37 |
| Oligochaeta | [Kl:Oligochaeta] | <i>Oligochaeta Gen. sp.</i> | Not available | 241 | 140 |
| Oligochaeta | LUMBRICIDAE | <i>Stygodrilus heringianus</i> (Claparède, 1862) | Rheo-Limnophile | 38 | 28 |
| Plecoptera | NEMOURIDAE | <i>Amphinemura sp.</i> | Rheophile | 1 | 0 |
| Plecoptera | TAENIOPTERYGIDAE | <i>Brachyptera risi</i> (Morton, 1896) | Rheophile | 4 | 2 |
| Plecoptera | TAENIOPTERYGIDAE | <i>Brachyptera seticornis</i> (Klapálek, 1902) | Rheobiont | 5 | 2 |
| Plecoptera | CHLOROPERLIDAE | <i>Chloroperla sp.</i> | Rheo-Limnophile | 1 | 2 |
| Plecoptera | PERLIDAE | <i>Dinocras cephalotes</i> (Curtis, 1827) | Rheophile | 1 | 4 |
| Plecoptera | CHLOROPERLIDAE | <i>Isoperla sp.</i> | Rheophile | 34 | 16 |
| Plecoptera | LEUCTRIDAE | <i>Leuctra braueri</i> (Kempny, 1898) | Not available | 0 | 17 |
| Plecoptera | LEUCTRIDAE | <i>Leuctra nigra</i> (Olivier, 1811) | Rheophile | 170 | 377 |
| Plecoptera | LEUCTRIDAE | <i>Leuctra sp.</i> | Rheophile | 12 | 3 |
| Plecoptera | NEMOURIDAE | <i>Nemoura sp.</i> | Not available | 4,533 | 6 |
| Plecoptera | PERLIDAE | <i>Perla marginata</i> (Panzer, 1799) | Rheophile | 3 | 21 |
| Plecoptera | NEMOURIDAE | <i>Protonemura sp.</i> | Not available | 838 | 58 |
| Plecoptera | CHLOROPERLIDAE | <i>Siphonoperla sp.</i> | Not available | 80 | 61 |
| Trichoptera | LEPTOCERIDAE | <i>Adicella reducta</i> (McLachlan, 1865) | Indifferent | 5 | 0 |
| Trichoptera | GLOSSOMATIDAE | <i>Agapetus fuscipes</i> (Curtis, 1834) | Rheophile | 57 | 151 |
| Trichoptera | LIMNEPHILIDAE | <i>Anomalopterygella chauviniana</i> (Stein, 1874) | Rheophile | 2 | 0 |
| Trichoptera | BERAEIDAE | <i>Beraea maurus</i> (Curtis, 1834) | Rheophile | 39 | 10 |
| Trichoptera | BERAEIDAE | <i>Beraea pullata</i> (Curtis, 1834) | Rheo-Limnophile | 27 | 0 |
| Trichoptera | BERAEODIDAE | <i>Beraeodes minutus</i> (Linnaeus, 1761) | Rheo-Limnophile | 10 | 0 |
| Trichoptera | LIMNEPHILIDAE | <i>Chaetopterygini/Stenophylacini Gen. sp.</i> | Not available | 2,313 | 216 |
| Trichoptera | LIMNEPHILIDAE | <i>Chaetopteryx major</i> (McLachlan, 1876) | Rheophile | 86 | 60 |
| Trichoptera | LIMNEPHILIDAE | <i>Chaetopteryx villosa</i> (Fabricius, 1798) | Rheo-Limnophile | 70 | 267 |
| Trichoptera | LEPIDOSTOMATIDAE | <i>Crunoecia irrorata</i> (Curtis, 1834) | Rheophile | 1 | 1 |
| Trichoptera | POLYCENTROPODIDAE | <i>Cyrnus trimaculatus</i> (Curtis, 1834) | Limno-Rheophile | 1 | 0 |
| Trichoptera | HYDROPSYCHIDAE | <i>Diplectronea felix</i> (McLachlan, 1878) | Not available | 18 | 2 |
| Trichoptera | LIMNEPHILIDAE | <i>Drusus annulatus</i> (Stephens, 1837) | Rheobiont | 29 | 15 |
| Trichoptera | BERAEIDAE | <i>Ernodes articularis</i> (Pictet, 1834) | Not available | 1 | 0 |
| Trichoptera | GLOSSOSOMATIDAE | <i>Glossosoma conformis</i> (Neboiss, 1963) | Rheophile | 2 | 17 |
| Trichoptera | LIMNEPHILIDAE | <i>Glyphotaelius pellucidus</i> (Retzius, 1783) | Limnophile | 4 | 0 |
| Trichoptera | LIMNEPHILIDAE | <i>Halesus digitatus/tesselatus</i> | Not available | 240 | 2 |
| Trichoptera | LIMNEPHILIDAE | <i>Halesus radiatus</i> (Curtis, 1834) | Rheo-Limnophile | 697 | 73 |
| Trichoptera | LIMNEPHILIDAE | <i>Hydatophylax infumatus</i> (McLachlan, 1865) | Rheo-Limnophile | 1 | 0 |

| | | | | | |
|-------------|-------------------|---|-----------------|-----|-----|
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche angustipennis</i> (Curtis, 1834) | Not available | 24 | 0 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche dinarica</i> (Marinkovic-Gospodnetic, 1979) | Nota available | 7 | 0 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche fulvipes</i> (Curtis, 1834) | Rheobiont | 17 | 4 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche instabilis</i> (Curtis, 1834) | Rheobiont | 4 | 0 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche saxonica</i> (McLachlan, 1884) | Rheophile | 141 | 0 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche siltalai</i> (Doehler, 1963) | Rheobiont | 97 | 7 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche</i> sp. | Rheophile | 127 | 0 |
| Trichoptera | LEPIDOSTOMATIDAE | <i>Lepidostoma basale</i> (Kolenati, 1848) | Rheophile | 4 | 1 |
| Trichoptera | LIMNEPHILIDAE | <i>Limnephilini</i> Gen. sp. | Not available | 757 | 2 |
| Trichoptera | LIMNEPHILIDAE | <i>Limnephilus lunatus</i> (Curtis, 1834) | Limno-Rheophile | 90 | 0 |
| Trichoptera | LIMNEPHILIDAE | <i>Limnephilus decipiens</i> (Kolenati, 1848) | Limno-Rheophile | 6 | 0 |
| Trichoptera | LIMNEPHILIDAE | <i>Limnephilus rhombicus</i> (Linnaeus, 1758) | Limno-Rheophile | 101 | 1 |
| Trichoptera | GOERIDAE | <i>Lithax niger</i> (Hagen, 1859) | Rheophile | 0 | 1 |
| Trichoptera | PSYCHOMYIIDAE | <i>Lype reducta</i> (Hagen, 1868) | Rheo-Limnophile | 406 | 2 |
| Trichoptera | LIMNEPHILIDAE | <i>Micropterna lateralis/sequax</i> | Rheophile | 4 | 0 |
| Trichoptera | SERICOSTOMATIDAE | <i>Notidobia ciliaris</i> (Linnaeus, 1761) | Rheophile | 2 | 5 |
| Trichoptera | ODONTOCERIDAE | <i>Odontocerum albicorne</i> (Scopoli, 1763) | Rheophile | 42 | 54 |
| Trichoptera | SERICOSTOMATIDAE | <i>Oecismus monedula</i> (Hagen, 1859) | Rheophile | 34 | 22 |
| Trichoptera | PHILOPOTAMIDAE | <i>Philopotamus ludificatus</i> (McLachlan, 1878) | Rheobiont | 19 | 68 |
| Trichoptera | PHILOPOTAMIDAE | <i>Philopotamus montanus</i> (Donovan, 1813) | Rheobiont | 507 | 15 |
| Trichoptera | PHILOPOTAMIDAE | <i>Philopotamus variegatus</i> (Scopoli, 1763) | Rheobiont | 13 | 0 |
| Trichoptera | POLYCENTROPODIDAE | <i>Plectrocnemia conspersa</i> (Curtis, 1834) | Rheophile | 59 | 3 |
| Trichoptera | POLYCENTROPODIDAE | <i>Plectrocnemia geniculata</i> (McLachlan, 1871) | Rheophile | 3 | 0 |
| Trichoptera | LIMNEPHILIDAE | <i>Potamophylax cingulatus</i> (Stephens, 1837) | Rheophile | 311 | 118 |
| Trichoptera | LIMNEPHILIDAE | <i>Potamophylax latipennis</i> (Curtis, 1834) | Rheo-Limnophile | 5 | 1 |
| Trichoptera | LIMNEPHILIDAE | <i>Potamophylax luctuosus</i> (Piller & Mitterpacher, 1783) | Rheophile | 7 | 4 |
| Trichoptera | RHYACOPHILIDAE | <i>Rhyacophila sensu stricto</i> | Rheophile | 54 | 0 |
| Trichoptera | RHYACOPHILIDAE | <i>Rhyacophila laevis</i> (Pictet, 1834) | Not available | 3 | 0 |
| Trichoptera | RHYACOPHILIDAE | <i>Rhyacophila</i> sp. | Rheobiont | 4 | 1 |
| Trichoptera | RHYACOPHILIDAE | <i>Rhyacophila praemorsa</i> (McLachlan, 1879) | Rheophile | 2 | 0 |
| Trichoptera | RHYACOPHILIDAE | <i>Rhyacophila tristis</i> (Pictet, 1834) | Rheophile | 2 | 4 |
| Trichoptera | SERICOSTOMATIDAE | <i>Sericostoma flavicorne/ personatum</i> | Not available | 169 | 247 |
| Trichoptera | GOERIDAE | <i>Silo nigricornis</i> (Pictet, 1834) | Rheophile | 1 | 0 |

| | | | | | |
|-------------|----------------|---|-----------------|-------|-----|
| Trichoptera | GOERIDAE | <i>Silo pallipes</i> (Fabricius, 1781) | Rheophile | 16 | 4 |
| Trichoptera | GOERIDAE | <i>Silo piceus</i> (Brauer, 1857) | Rheophile | 1 | 0 |
| Trichoptera | LIMNEPHILIDAE | <i>Stenophylax</i> sp. | Rheo-Limnophile | 3 | 2 |
| Trichoptera | PHILOPOTAMIDAE | <i>Wormaldia occipitalis</i> (Pictet, 1834) | Rheophile | 793 | 12 |
| Turbellaria | DUGESIIDAE | <i>Dugesia</i> sp. | Indifferent | 1,007 | 123 |
| Turbellaria | PLANARIIDAE | <i>Polycelis</i> sp. | Indifferent | 1,834 | 87 |

3.3 The macroinvertebrate fauna of maintained and abandoned beaver dams

Abstract

Beavers and their dams, once common in small streams throughout Eurasia and North America, are returning to their original range. Beaver dams are special habitats in the aquatic-terrestrial interface, but their macroinvertebrate fauna is hardly known. This study aims to qualify and quantify the invertebrate fauna of beaver dams, taking into account the maintenance status of the dams. Nine different areas covering the top, middle and base zones of eight maintained and eight abandoned beaver dams were sampled using a specially designed suction device. The invertebrate community of beaver dams proved to be diverse and predominantly rheophilic. Community composition reflects higher flow velocities in streamside habitats; this gradient is more pronounced in maintained than in abandoned dams. Shredders are the most abundant feeding type, but they are less frequent in streamside habitats, in particular in those of maintained dams, where passive filter feeders prevail. Terrestrial/Semiaquatic taxa colonising hygropetric areas were found in streamside habitats especially of abandoned dams. Our results underline that beaver dams provide a wide variety of environmental conditions and habitat types, which enhance biodiversity in small streams and their floodplains. Beaver dams in riverine landscapes should therefore be much more valued in floodplain conservation and management.

Introduction

Beaver dams are among the animal kingdom's architectural masterpieces, significantly modifying hydraulics, morphology and community composition of the streams where there are built (Müller-Schwarze, 2011). Beavers, *Castor canadensis* Kuhl, 1820 and *C. fiber* Linnaeus, 1758, construct dams exclusively in small streams up to 4th order to increase the water depth, thus enabling underwater access to their lodges (McDowell & Naiman 1986, Collen & Gibson 2001). River width, depth and slope, along with watershed area, floodplain morphology and vegetation cover, determine whether dams are built, their density, size and dimensions (Müller-Schwarze, 2011; Zavyalov, 2014). Due to individual site characteristics, the number of dams can vary between 0.1 dam/km (McComb et al., 1990) and 19 dams/km (Woo & Waddington, 1990).

Building materials for dams are mainly logs of varying lengths, stones, and mud (Müller-Schwarze, 2011; Rolauffs et al., 2001; Butler & Malanson 1995). The beaver skilfully integrates these materials into a tightly interwoven structure, adapted to channel morphology (Kroes & Bason, 2015) and flow velocity (Andersen & Shafroth, 2010). For stabilisation, beavers seal

the flow-facing side of the dams with mud (Müller-Schwarze, 2011); due to the reduced flow velocity, sediments accumulate in the ponds and the adjacent dam structure (Butler & Malanson, 1995; Kroes & Bason, 2015). Nevertheless, beaver dams retain their permeability, which is influenced by various environmental factors and the beavers' maintenance activities (Ronnquist & Westbrook, 2021). The sizes and shapes of beaver dams varies greatly, with the usual pattern being concave-upstream arches (Warren, 1932; Dugmore, 1914). The range of recorded dam heights varies between 0.3 m and 5 m (Müller, 2014), while the large majority is on average 1 m in height (Hafen et al., 2020). The length can measure 0.6 m in small canal dams (Townsend, 1953) up to several hundred metres (Thie, 2022), depending on the topography (Gurnell, 1998). Thereby, the construction activities of *Castor canadensis* and *Castor fiber* are very much the same, if both species are observed in the same areas with identical environments (Danilov et al., 2011). Danilov et. al (2011) demonstrate that the construction activity by beavers is exclusively determined by geomorphological and hydrographic settings in the habitat and that building behaviour has no species-specific features. Rolauffs et al. (2001) highlights the large internal surface area of beaver dams resulting in a network of interstitial spaces easily accessible to organisms. Furthermore, short-term flooding and drying within the dam causes rapid shifts between terrestrial and aquatic conditions (Rolauffs et al., 2001). Flow velocity within the dams can be very high and variable (Woo & Waddington, 1990), creating microhabitats with a lotic character in lowland streams, where otherwise lentic conditions prevail (Clifford et al., 1993). Beaver dams are constantly exposed to changing flow conditions and decomposition processes (Ronnquist & Westbrook, 2021; Woo & Waddington, 1990). Because of these dynamics, beavers repair and maintain their dams, and sometimes expand them to increase the size of the upstream pond (Richard, 1967; Wohl et al., 2019). These activities enhance habitat variability and flow diversity between the upper and lower parts of a dam (Rolauffs et al., 2001). Likewise, dams are regularly neglected or abandoned when they no longer serve any purpose or the beavers leave the area (Woo & Waddington, 1990; Bylak & Kukuła 2018). This reduces dam stability and increases dam permeability, as fine material is washed out and the water is flowing more rapidly through the remaining skeleton of branches, without allowing for much habitat variability from top to base (Woo & Waddington, 1990). The construction and maintenance of dams is an ongoing process, thus there is a large variance in the lifetime and maintenance states of the dams within a beaver territory (Johnston 2017). Thereby, single dams can withstand or be maintained from several months to decades (Johnston 2017). As beavers rapidly increase their range in Europe (Halley

et al., 2021; Wròbel, 2020), both maintained and abandoned beaver dams are increasingly common elements within the valleys of small streams.

From the perspective of macroinvertebrates, beaver dams, i.e., piles of dead wood in the aquatic-terrestrial interface, are very special habitats, but little is known on the communities colonising them. In general, beaver dams offer a wide variety of food sources to the invertebrate community: wood of different size (Barnes & Mallik, 1996; Bliersch & Kangas, 2014), from different trees species (Barnes & Mallik, 1996; Bliersch & Kangas, 2014), and in different decomposition stages (Woo & Waddington, 1990); tufts of grass, organic debris and accumulating leaves (Woo & Waddington, 1990; Bliersch & Kangas, 2014); and plankton that develops in the upstream beaver ponds (Czerniawski et al., 2017). So far, primarily beaver ponds have been studied to investigate the influence of beaver activities on invertebrate diversity (Harthun, 1998, 1999; Naiman et al., 1988; Willby et al., 2018). Additionally, studies that compare stream sections upstream and downstream of beaver territories are found quite frequently (Fuller & Peckarsky, 2011a, 2011b; Redin & Sjöberg, 2013; Smith et al., 1991). There are several studies on invertebrates in beaver created wetland complexes (e.g., Naiman et al. 1984; Nummi, 1989; Hood & Larsen, 2014, 2015; Bush et al., 2016, 2019; Nummi et al., 2021), including studies focusing on fish communities (e.g., Hägglund & Sjöberg, 1999; Bylak & Kukuła, 2014, 2018; Renik & Hafs, 2020; Fritz & Gangloff, 2022). Thereby, beaver dams are generally not considered as movement barriers for fish species, especially for native species (Lokteff & Roper, 2016; Cutting et al., 2018; Pollock et al., 2022). It has been shown that physical dam features such as height, upstream location and the presence of side channels (Lokteff et al., 2013), as well as breach status (maintenance condition) and hydrological links (Cutting et al., 2018) determine the passability of beaver dams for fish species.

However, macroinvertebrates within beaver dams have only been studied by Clifford et al. (1993) and Rolauffs et al. (2001). Clifford et al. (1993) sampled the dams qualitatively using pond nets (500 and 150 µm), either by thoroughly disturbing the substrates so that organisms drifted into the net, or by removing individual parts of the dam and rinsing them off. A first quantitative study of beaver dams was carried out by Rolauffs et al. (2001), in which the beaver dams were sampled with emergence traps. In both studies, an invertebrate fauna typical for fast-flowing streams was detected. Reflecting habitat variability, the heterogeneity of species composition, abundance and biomass were significantly higher in beaver dams compared to free-flowing stream sections and beaver ponds (Rolauffs et al., 2001). The composition of functional feeding types of the free-flowing stream segments and beaver dams was very similar

and included filter feeders, shredders, gatherers, grazers and predators (Clifford et al., 1993). The available studies, however, did not lead to generalisable patterns of benthic invertebrate communities in beaver dams. Rolauffs et al. (2001) focussed on insect emergence and thus did not consider hololimnic organisms. Rolauffs et al. (2001) and Clifford et al., (1993) investigated beaver dams without distinguishing the states of maintenance (maintained vs. abandoned).

Here, we comparatively studied maintained and abandoned beaver dams (Fig. 1) with the aim to comprehensively characterise their macroinvertebrate fauna in different zones (Fig. 2). Individually, we expected:

Hypothesis 1: The fauna of maintained dams is spatially more variable than those of abandoned dams. If still in use, beavers maintain dam stability by adding and arranging branches, stones and mud, thus increasing habitat variability and flow diversity. In abandoned beaver dams, these differences dissolve, as fine sediment is washed out and therefore the variability from top to base diminishes (Woo & Waddington, 1990).

Hypothesis 2: Consequently, we consider the fauna of abandoned beaver dams to be composed of more rheophilic species in all parts of the dam.

Hypothesis 3: Following the descriptions of Rolauffs et al. (2001), we assume a flow gradient from the upper to the lower areas, so that the proportion of rheophilic species reaches its maximum at the base of a dam, where flow velocity is highest. Limnophilic or indifferent species are more likely to reside in the upper areas, especially of maintained dams, characterised by minimal flow velocities.

Hypothesis 4: Concerning feeding types, the percentage of grazers and shredders is expected to be highest in the top area of a dam. Food for shredders (woody substrate, leaves, and wads of grass) is actively introduced by beavers or accumulates upstream of a dam, and biofilms (i.e., food for grazers) develop on the branches that are exposed to sunlight. Passive filter feeders are found exclusively in middle and lower areas of maintained dams, as a result of high flow velocity and high throughput of drifting food particles.

Hypothesis 5: Terrestrial/semiaquatic species are found, occasionally, in the upper and marginal areas of beaver dams, especially if dams are still maintained. The marginal parts are in direct contact to the shore, and the upper parts of maintained dams are only infrequently overflowed, making these areas readily accessible to terrestrial or semiaquatic species.

Material and methods

Study area and study streams

The studied streams of 1st to 3rd order (Strahler, 1954) are part of the Inde-Rur-Maas catchment area (<https://www.elwasweb.nrw.de>) and inlets of a water reservoir (Wehebachtalsperre) in the Hürtgenwald (50°44`N, 6°20`E). This is a 120 km² state forest (<https://www.wald-und-holz.nrw.de>, 2022) in the western part of Germany and the federal state of North Rhine-Westphalia, adjacent to the Netherlands and Belgium, which belongs to the Rhenish Massif. The area, at an elevation of 240-450 m a.s.l., has a moderate atlantic climate with cool summers and mild winters. The average temperature in this area is 8.5 °C (<https://cdc.dwd.de/portal>) and the annual precipitation is 1062 mm (<https://www.elwasweb.nrw.de>). The area is characterised by a steep relief that facilitates the formation of a finely branched and dense network of streams (Sommerhäuser & Pottgiesser, 2002). Due to a reintroduction project from 1981 to 1989, the European beaver (*C. fiber*) has returned to this area (Naumann, 1991). In the subsequent decades, the beaver population increased and populated the wider surrounding. Overall population size in the federal state of North Rhine-Westphalia, of which the population originating from the Hürtgenwald is the main part, is estimated about >1200 individuals or 0.2 beavers/km² (Dalbeck, 2021). In the study area, the estimated average density is 4 dams/km (Dalbeck et al., 2014).

In winter 2017/2018, three streams with similar characteristics in terms of altitude, stream size and slope were selected and the dams within these streams were mapped. On this basis, 48 beaver dams in three territories were surveyed and classified into maintained and abandoned dams (Fig. 1). We characterised maintained beaver dams by freshly processed and installed branches, as well as an intact mud layer on the crest, which are both lacking in abandoned dams. We randomly selected in total eight maintained and eight abandoned dams for further examination (Fig. 1). The age of these dams ranged between two and eight years. In our observations, even dams with the same age may vary in terms of morphology, substrate density, permeability and thus taxa composition. Therefore, we used a simple definition to distinguish two types of dams (regardless of the age) to generalise the effects of abandoned vs. maintained dams. All dams were intact (not breached) and were still impounding the stream with an upstream pond. The arrangement of the dams corresponds to a disjunct series (Kroes & Bason, 2015), which means that there was always a free-flowing section below the dams (≤ 2 m), so that no silt accumulated on this dam side. All territories are located in the middle reaches (rhithral) of the studied streams.

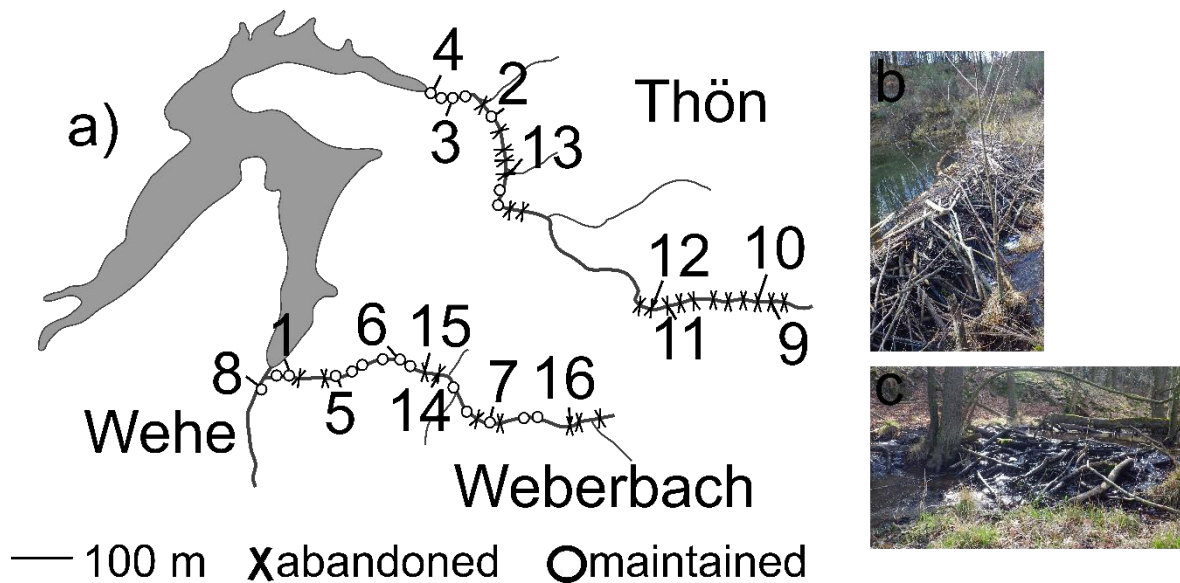


Figure 1 a) Study area with the distribution of 48 mapped beaver dams, including the investigated dams (1-16). In the stream Thön there are two territories, one near the mouth of the water reservoir (dams 4, 3, 2, 13); next further upstream (dams 12, 11, 10, 9). One territory is in the stream Weberbach (dams 1, 5, 6, 14, 15, 7, 16) and extends into the confluence of the Weiße Wehe stream (dam 8). Maintained dams are marked with a white circle and black outline, abandoned with a black cross. **b)** Picture of a maintained beaver dam, spring 2018 in the stream Weberbach. **c)** Picture of an Abandoned beaver dam, spring 2018 in the stream Thön.

Study design

We measured height, width (Fig. 2a) and length of the 16 dams with a 50 m long tape measure. We measured the total length of the dam, separating the “aquatic part” with contact to the watercourse and the “terrestrial part” connecting the dam with the shore. The terrestrial part becomes larger when the dam is abandoned and the impounding effect decreases.

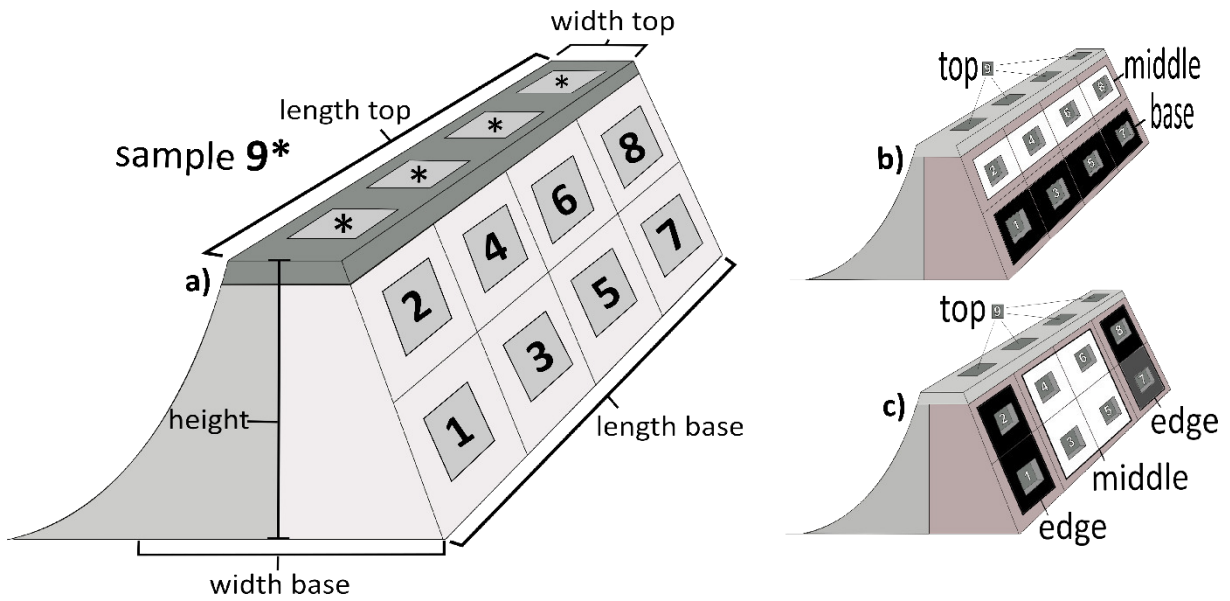


Figure 2 a) Sample point distribution on a dam, showing sample number 1-8 (0.25m^2 each) at the streamside and sample number 9 consisting of four single samples that were pooled (1m^2) and measured dam dimensions, including the width and length of the top and the base of a dam and its height. b) Sample combination for analysis, Combination 1, comparing top, middle and base areas of a dam, c) sample Combination 2, comparing top, edge and middle areas of a dam

Nine areas of each individual beaver dam (Fig. 2a) were sampled once in spring (March-April) 2018. The areas included the top of the dam adjacent to the pondside, as well as eight areas on the upper and lower sections on the streamside. We further refer to the samples as pondside or streamside samples, depending on their location of the dam, in reference to Rolauuffs' (1999) designation. Sampling was conducted with a vacuum sampler, which was specifically designed for this purpose (Schloemer & Hoffmann, 2018). Sampling was standardised by area and time. Each sampling area was vacuumed for three minutes, while the area sampled differed between pondside and streamside samples. Only at the streamside, the dam has a clear three-dimensional structure with bulks and spikes, the cavities between which were vacuumed, while at the pondside, the dam has a smooth surface without cavities and was thus vacuumed only at the surface (Fig. 2a). Accordingly, we chose a smaller area per sample at the streamside as compared to the pondside samples. Each streamside sample accounted for 0.25m^2 ($0.5\text{m} * 0.5\text{m}$), while the single pondside sample accounted for 1m^2 (four individual areas of $0.25\text{m} *$

0.25 m at the top of a dam that were pooled together). Due to the highly variable morphology and surface of a dam, the dimensions of the sample areas were approximated.

Prior to sampling, depth, substrates, and gaps in the streamside sampling areas were examined by palpation. During the sampling time, all these gaps were sampled as deep as possible; if stones (≥ 10 cm) were detected and were loose enough, we removed and vacuumed them and put them back inside. The crest was vacuumed in a swabbing motion, and larger branches were removed, vacuumed and returned to prevent sampling pond substrate. The prime target of our sampling were aquatic taxa. Therefore, only gaps and parts with contact to water were sampled, with a focus on the inner structure of the beaver dams. However, the entire dam is in the transition zone of aquatic and terrestrial habitats, thus also offering habitats for terrestrial and semiaquatic organisms.

In total, 144 samples were taken (nine sampling areas on 16 dams). Every sample was filtered through a 500 μm sieve in the field and screened for species other than benthic invertebrates (e.g., fish). These were released back into the dam, while the rest of the sample was transferred into a container and preserved in 96% ethanol for further processing. In the laboratory, each sample was rinsed with water through a 2 mm mesh following the method of Meier et al. (2006) for macrozoobenthos collection and analyses, before the sample was divided into small amounts, which were ultimately transferred into a tray for sorting. Identification was on species level, except for most Diptera that were identified to genus or family level.

Data preparation and analysis

In a single sample originating from the streamside of a maintained dam, no specimens were detected. This we traced back to technical reasons and excluded the sample from the dataset. Accordingly, the total population of samples contained 71 samples for maintained dams (8 = pondside, 63 = streamside) and 72 samples for abandoned dams (8 = pondside, 64 = streamside). With the resulting table of the number of individuals per taxon and sample (ind./m^2), we performed a taxonomic adjustment according to AQEM Consortium (2002) to ensure that taxonomic identification was consistent across instars. Furthermore, we removed all taxa that occurred just in one or two samples. To make sure we sampled invertebrate taxa adequately in each dam structure, we ran a species accumulation curve using the `specaccum` function of the `vegan` package (Oksanen et al., 2020) in Rstudio (R Core Team, 2021). The number of species and individuals in the different beaver dam areas and maintenance states was tested for significant differences with the Kruskal-Wallis test followed by the Dunn test (Holm

corrected) with the `ggbetweenstats` function of the package `ggstatsplot` (Patil, 2021) in Rstudio (R Core Team, 2021). With the same function, the mean values of the measured dam dimensions of abandoned and maintained dams were tested for significant differences with Welch's t-test.

We tested Hypothesis 1 (spatial variability of benthic invertebrate communities in maintained and abandoned dams) with the `betadisper` function of the `vegan` package (Oksanen et al., 2020) in Rstudio (R Core Team, 2021). The data was Hellinger transformed, and a Bray-Curtis dissimilarity matrix was created. In order to test the variability within the different dam habitats/categories, we performed a PCoA (`betadisper`) on the dissimilarity matrix. Since the samples had unequal sample size, we used the default adjustment option of the `vegan` package (Oksanen et al., 2020). The results of the PCoA were subjected to an ANOVA, calculating the between-group distance by the distances from the centroids, and were displayed with the effect-size Eta-squared. The means of the groups were compared with the TukeyHSD-test ("Honest Significant Difference" method) and confidence intervals at 95%. These calculations were also performed with the `vegan` package (Oksanen et al., 2020). The results are displayed in a biplot, showing the variability of the data and between each group. The distance between the centroids within each different group, is displayed in boxplots with jittered points. Our null hypothesis is that there is no difference between the invertebrate communities of the dam categories. We used different sets of sample combinations for analysis: Combination 1 compared the top, the middle and the base of the dams (Fig. 2b)), Combination 1+m.s. (+m.s.= including maintenance state) compared the same areas like Combination 1, but also regarding the maintenance state (maintained top, middle, base; abandoned top, middle, base).

Combination 2 compared the side/edge and the middle areas of the dams (Fig. 2c), Combination 2+m.s. compared also side/edge and middle areas regarding the maintenance state (maintained edge, middle; abandoned edge, middle). Combination 3 compared the streamside to the pondside area (Combination 3+m.s.: maintained stream-, pondside; abandoned stream-, pondside). Finally, we compared all samples of maintained with all samples from abandoned beaver dams (Combination 4).

To test Hypothesis 2 (rheophilic species are more abundant in abandoned dams), Hypothesis 3 (rheophilic species are more abundant at the dam's basis) and Hypothesis 5 (terrestrial/semiaquatic species are more abundant in maintained dams), we calculated the percentages of species with different water velocity preferences (named current preferences in Schmidt-Kloiber & Hering, 2015) for the communities of the different dam areas. We used the tool "Perlodes Online" (<http://www.gewaesser-bewertung-berechnung.de>) that is based on trait

information compiled by Schmidt-Kloiber & Hering (2015); water velocity preferences were originally assembled by Schmedtje & Colling (1996). Hereby, a specific water velocity preference is assigned to every taxon and indicated by a numeric value. Terrestrial and semiaquatic taxa not included in Perlodes Online were assigned to the additional category “terrestrial/semiaquatic”. We applied the same formula, which is implemented in “Perlodes-Online”, and conducted the calculation in Excel to include the attribute “terrestrial/semiaquatic”. The formula is: $P_{VP} = \frac{\sum_i n_i}{N} * 100$ (n_i = number of individuals of i^{th} taxon with specific water velocity preference (P_{VP}), N = total abundance).

To test Hypothesis 4 (feeding types), we calculated the percentage of feeding types of the individual samples’ communities. Here, we also used the same method as the online tool “Perlodes-Online” but re-calculated in Excel to include the terrestrial/semiaquatic taxa. The formula is: $P_{ft} = \frac{\sum_i ft * n_i}{N} * \frac{100}{10}$ (ft = point value of the i^{th} taxon of specific feeding type (P_{ft}), n_i = number of individuals of i^{th} taxon with specific feeding type, N = total abundance). For each taxon, 10 points are distributed between feeding types corresponding to the taxon’s preferred diet. For the terrestrial/semiaquatic taxa, we added feeding types according to additional literature (Gepp, 2003; Speiser, 2001; van Stuivenberg, 1997). The percentage of feeding types and water velocity preferences in the different beaver dam areas and maintenance states was also tested for significant differences with the Kruskal-Wallis test followed by the Dunn test (Holm corrected) with the `ggbetweenstats` function in Rstudio (Patil, 2021).

To calculate the preference of a taxon towards a specific dam category (Hypotheses 1-5), we computed the indicator value Index “IndVal” (Dufrêne & Legendre, 1997) using the `multipatt` function of the R package “`indicpecies`” (DeCáceres, 2020). The IndVal-Index is based on the mean abundance of a taxon as well as on its occurrence, and it is independent of the relative abundance of other taxa (Dufrêne & Legendre, 1997). The IndVal-Index ranges between 0 and 100 % and reaches its maximum when all individuals of a species are found in a single group of sites, and when the species occurs in all sites of that group (Dufrêne & Legendre, 1997). Results are expressed in value A – “specificity” (species occurrence within the different dam categories), and value B – “fidelity” (species occurrence within a specific dam category). The statistical significance of the association of a species with a certain dam category was tested with a permutation test, which is already default in the `multipatt` function (DeCáceres, 2020).

Results

Overview

On average, the studied beaver territories represented a pond cascade of 400 m length and consisted of 16 dams per colony (Fig. 1). Due to one territory that was completely abandoned (Fig. 1), 40 % of the dams were in a “maintained” and 60 % in an “abandoned” state, at the time of the study. On average, the distance between dams is 30 m (range: 10–36 m).

Beaver dam dimensions differ between the maintenance states (Tab. 1). The height, the length with contact to the water body (p-value= <0.01) and the length of the dam base (p-value= <0.01) was on average greater for maintained dams, while dam width (top and base: p-value= 0.02) and total length was on average greater for abandoned dams (Tab. 1).

Table 1 Average dimensions of maintained and abandoned beaver dams (m). Including mean values, min and max values in brackets, Standard Error (SE) and p-values as result of pairwise Welch’s t-test.

| Dimension (m) | Maintained dams (n= 8) | | Abandoned dams (n=8) | | Welch’s test |
|-------------------------------|---------------------------|-----------|-------------------------|-----------|----------------|
| | <i>Mean</i> (min-max) | <i>SE</i> | <i>mean</i> (min-max) | <i>SE</i> | <i>p-value</i> |
| Height | 1.1 (0.6 - 1.6) | 0.13 | 0.9 (0.6 - 1.2) | 0.09 | 0.2 |
| Length dam top - aquatic part | 10.3 (5.3 - 14) | 1.24 | 5.5 (2.5 - 9) | 0.73 | <0.01 |
| Length dam top - total | 13.4 (5.3 - 21) | 1.99 | 13.7 (7 - 30.7) | 2.84 | 0.9 |
| Length dam base | 8.4 (3.3 - 12.2) | 1.21 | 3.7 (2 - 6.3) | 0.43 | <0.01 |
| Width - dam top | 0.5 (0.3-0.9) | 0.07 | 0.7 (0.2-1.7) | 0.17 | 0.5 |
| Width - dam base | 1.3 (0.6-2) | 0.18 | 1.9 (1.3-2.4) | 0.12 | 0.02 |

We identified 57,716 individuals assigned to 130 taxa (Tab. S1) that were present in at least three sample sites. Additional 84 taxa with altogether 155 individuals (Tab. S1) were recorded in just one or two samples. The latter taxa were used to derive species numbers in abandoned and maintained dams, but excluded from the other analyses. 47 taxa exclusively occurred in abandoned dams, while 40 taxa exclusively occupied maintained dams (Tab. S1). In total, we detected an almost similar taxa richness in abandoned (174 taxa) and maintained beaver dams (167 taxa), while the overall number of individuals was higher in abandoned (33,417 individuals) than in maintained dams (24,454 individuals). The latter finding is related to the high abundance of the amphipod *Gammarus fossarum* (Koch, 1835) in abandoned dams. The slope of species accumulation curves (Fig. S1) is approaching zero, indicating a sufficient sampling effort.

The median number of taxa differs between the pondside and streamside habitats of maintained and abandoned dams (Fig. S2a; Kruskal-Wallis test: 22.35, p -value = <0.001). In abandoned dams, the numbers are higher (pondside = 28.5; streamside = 33) than in maintained beaver dams (pondside = 23.5; streamside = 24). When considering maintenance status and habitats, the numbers only differ significantly between the categories “streamside-abandoned” and “streamside-maintained” (Dunn test, Holm-corrected: p -value = 0.007) and between the categories “streamside-abandoned” and “pondside-maintained” (Dunn test, Holm-corrected: p -value <0.001). The median abundance (ind./m²) of all four categories differ significantly (Fig. S2b; Kruskal-Wallis test: 33.03, p -value = <0.001), and ranged between 387 ind./m² (pondside-maintained) and 1584 ind./m² (streamside-abandoned). Abundance differs most strongly between abandoned streamside areas and the pondside of maintained and abandoned dams (Dunn test, Holm corrected: p -value = <0.001).

Community Analysis

Variance and diversity of the invertebrate community of the different habitats were further specified by a PCoA (betadisper), and an ANOVA (Tab. 2), alongside with the TukeyHSD-test (Tab. S2). The PCoA (Fig. 3a) shows the variability of the invertebrate communities of pondside and streamside samples of abandoned and maintained dams. The communities of each habitat are separate (Eta-squared= 0.08; p-value= <0.009). Furthermore, the boxplot shows (Fig. 3b), that communities of maintained beaver dams are more diverse than those of abandoned beaver dams.

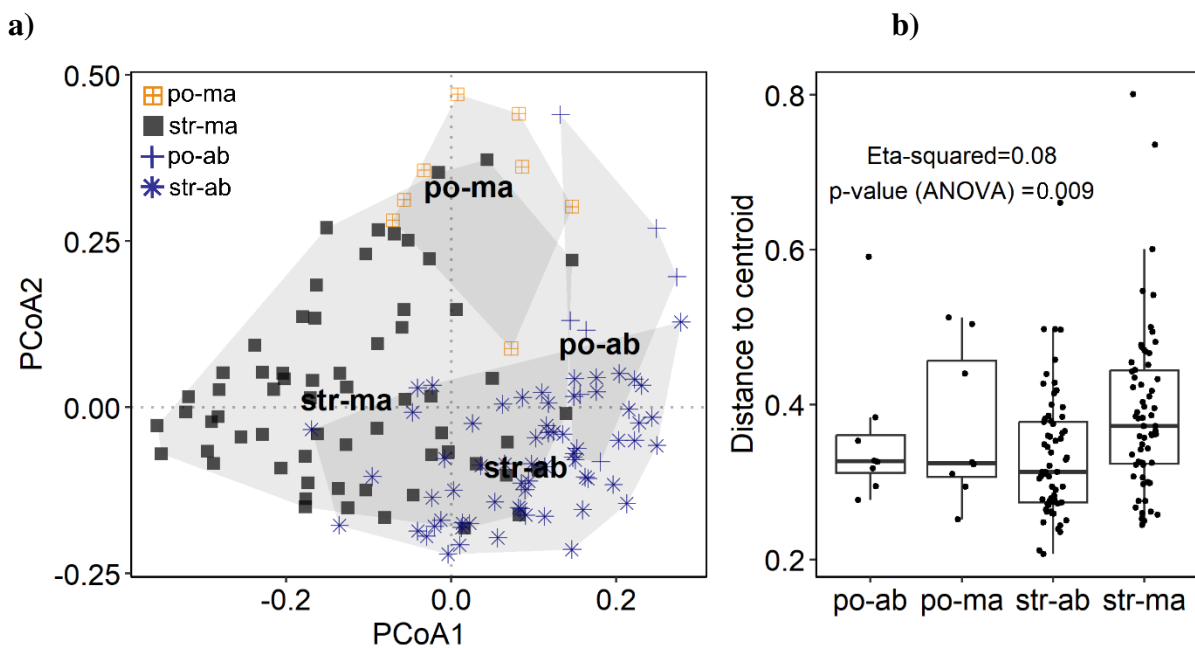


Figure 3 a) PCoA shows the variability within and between each group of the pondside and streamside of abandoned and maintained dams “side and state” (Combination 3+m.s.). b) Boxplot with jittered points showing the distance between the centroids, within each different group, of the pondside and streamside of abandoned and maintained dams. po= pondside, str= streamside, ma= maintained, ab= abandoned. Illustration created with Rstudio (R core Team, 2021)

The maintenance state (Fig. S3a) most strongly impacts the diversity of the invertebrate community (Eta-squared= 0.09; p-value= <0.001). The mean difference between the groups with the confidence intervals at 95% (TukeyHSD-test) is 0.087 for abandoned and maintained dams. Figures for all sample site combinations, next to “side and state” (Combination 3+m.s., Fig. 3), are given in the supplementary material (Fig. S3a-f), as well as all results of the TukeyHSD-test (Tab. S2).

Table 2 Results of the Eta-square and p-Value of ANOVA for each sample site combination. +m.s.= including maintenance state; e.g., 1+m.s.: top, middle, base of maintained dams; top, middle, base of abandoned dams

| Sample site combination | Eta-square (η^2) | p-value |
|---|-------------------------|--------------|
| Combination 1 / 1+m.s.: dam top, middle, base areas | 0 / 0.08 | 0.88 / 0.037 |
| Combination 2 / 2+m.s.: dam edge, middle areas | 0 / 0.08 | 0.86 / 0.035 |
| Combination 3 / 3+m.s.: pondside, streamside areas | 0 / 0.08 | 0.64 / 0.009 |
| Combination 4: maintained, abandoned dams | 0.09 | <0.001 |

Water velocity preference

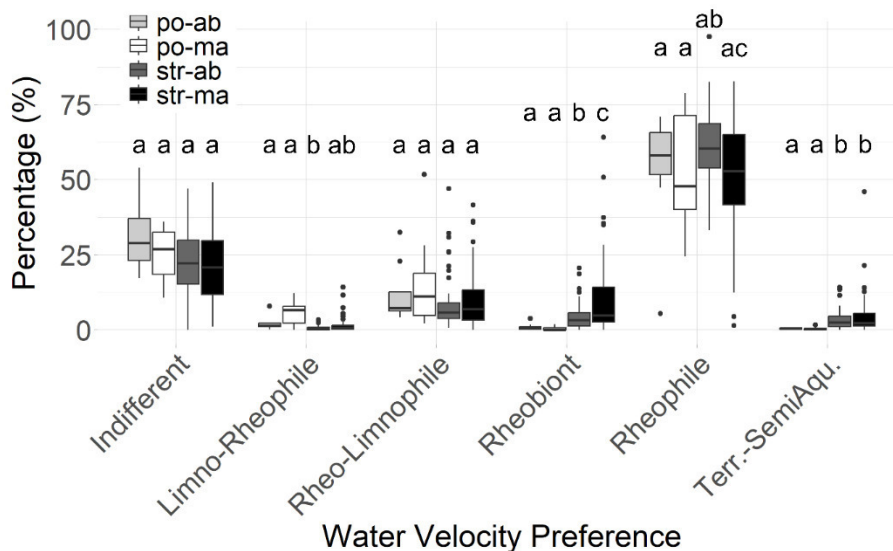


Figure 4 Percentage (%) of water velocity preferences of the community in the dam areas “side and state” (Combination 3+m.s.). po= pondside, str= streamside, ma= maintained, ab= abandoned. Terr.-SemiAqu.= Terrestrial/Semiaquatic. Values below 1% were excluded; this concerns the preferences “limnophile” and “limnobiont”. Significant differences between categories are indicated with different letters. Boxplots show the median (middle line), quartiles (boxes), 1.5x the interquartile range (whiskers) and extreme values (dots). Illustration created with Rstudio (R core Team, 2021).

Rheophilic taxa represent the highest proportion of the community in all dam categories (Fig. 4) and range between a median of 48 % (pondside-maintained) and 60 % (streamside-abandoned). While the percentages differ between the four dam categories (Kruskal-Wallis test: $X^2= 8.52$, p-value= 0.04), the pairwise comparison resulted only in significant difference of the streamside of maintained and abandoned dams (p-value= 0.03). The second and third group with the highest percentage (Fig. 4) are indifferent taxa (Kruskal-Wallis test: $X^2=5.0$, p-value= 0.17) and rheo-limnophilic (preferring slow water velocity) taxa (Kruskal-Wallis test: $X^2= 3.77$, p-value= 0.29). Despite these similarities, there are obvious differences between dam categories: The median percentages of rheobiont taxa, i.e., those only occurring in strong water velocity, differ the most between the four dam categories (Kruskal-Wallis test: $X^2= 32.54$, p-value= <0.001). Rheobiont taxa occur almost exclusively in streamside habitats and have a higher percentage in maintained (5 %) than in abandoned (3 %) dams (Dunn test, Holm corrected: p-value = 0.02). In addition, taxa preferring low water velocities i.e., limno-rheophile taxa, barely occur (<2 %) with exception of the pondside of maintained dams (7 %) (Kruskal-Wallis test: $X^2= 17.80$, p-value= <0.001). Thus, pond- and streamside areas of maintained dams show the highest differences in water velocity preferences, from very low flow on top to very high flow in the middle and base areas of a dam (Fig. 4).

Terrestrial/semiaquatic taxa occur almost exclusively in streamside habitats with an equally high median percentage in abandoned (2.5 %) and maintained (2.2 %) dams (Kruskal-Wallis test: $X^2= 32.31$, p-value= <0.001). The differences between the streamside and the pondside categories are all significant (Dunn test, Holm corrected: p-value= <0.001). Occurring terrestrial or semiaquatic taxa include the beetle *Dianous coerulescens* (Gyllenhal, 1810) of the

family Staphylinidae, the snail *Vertigo antivertigo* (Draparnaud, 1801) of the family Vertiginidae and the larvae of the Neuroptera *Osmylus fulvicephalus* (Scopoli, 1763) of the family Osmylidae (Tab. S1). Table S3 in the supplementary material contains detailed information on the water velocity preferences of the individual taxa.

Feeding types

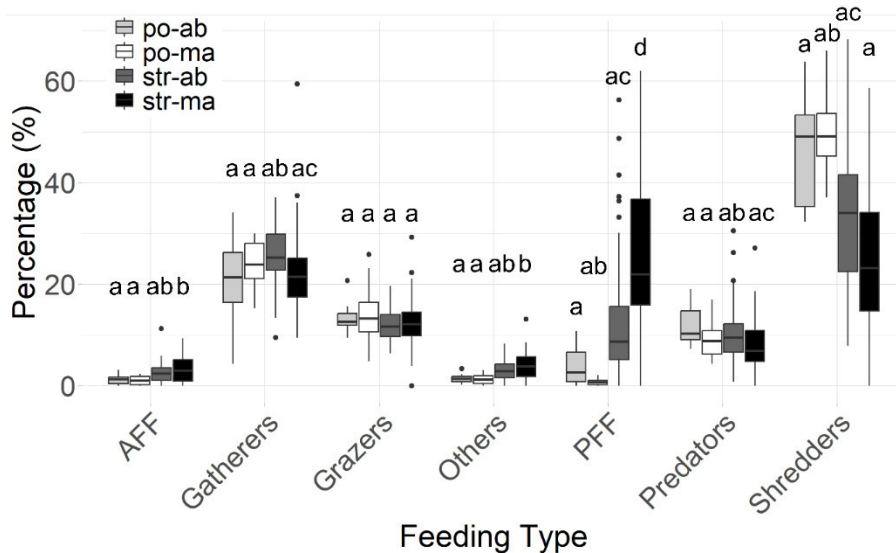


Figure 5 Percentage (%) of feeding types of the community in the dam areas “side and state” (Combination 3+m.s.). po= pondside, str= streamside, ma= maintained, ab= abandoned. AFF= Active-Filter Feeders; PFF= Passive-Filter-Feeders. The type “Others” combines xylophagous taxa, miners, parasites, other feeding types and not determined taxa. Significant differences between categories are indicated with different letters. Boxplots show the median (middle line), quartiles (boxes), 1.5x the interquartile range (whiskers) and extreme values (dots). Illustration created with Rstudio (R core Team, 2021).

Shredders are most abundant in all four dam categories (Fig. 5), but they are generally less frequently occurring in streamside habitats, in particular in those of maintained beaver dams (Kruskal-Wallis test: $X^2= 33.07$, p-value= <0.001). Here, significant differences are detected between the streamside of maintained dams with every other category (Dunn test, Holm corrected: streamside-abandoned p-value= 0.003; pondsides p-value= <0.001). Passive filter feeders, which extract drifting material from the running water, prevail in the streamside of maintained dams (Fig. 5). Additionally, significant differences are detected between the streamside of maintained dams with every other category (Dunn test, Holm corrected: p-value= <0.001). In the streamside habitats of abandoned beaver dams, passive filter feeders are much less abundant, and they are almost absent in the pondside habitats of both maintained and abandoned beaver dams (Fig. 5). Overall, maintained streamside habitats seem to provide the most variable food sources leading to a balanced distribution of feeding type categories (Fig. 5). The significant differences of the median proportions of most feeding types clearly highlight the different nature of maintained-streamside habitats compared to the other three dam categories (Fig. 5). In contrast, there are no significant differences between the median proportions of feeding types between the pondside of maintained and abandoned dams (Fig. 5). Table S3 in the supplementary material contains detailed information of the feeding types of the individual taxa.

Indicator species

In total, 22 taxa were identified as indicators for the different dam categories (Tab. S4), which further characterise the respective habitat conditions. Indicators for the dam category abandoned-pondside (Tab. S4) include shredders like the Trichoptera *Potamophylax cingulatus* (Stephens, 1837) of the family Limnephilidae (IndVal=82 %, p-value=0.001) and the mud-dwelling predator *Sialis lutaria* (Linnaeus, 1758) (*Sialidae*, Megaloptera) (IndVal= 46 %, p-value= 0.044). Species characterising abandoned-streamside habitats include the two net-building Trichoptera larvae of the family Philopotamidae, *Philopotamus montanus* (Donovan, 1813) (IndVal= 68 %, p-value= 0.01) and *Wormaldia occipitalis* (Pictet, 1834) (IndVal= 78 %, p-value= 0.001), but also the wood-mining genus *Lipsothrix* (IndVal= 57 %, p-value= 0.001) of the family Limoniidae (Diptera) and the riparian rove beetle *Dianous coeruleus* (Gyllenhal, 1810) (IndVal= 67 %, p-value= 0.007). Maintained-pondside species include typical pond-dwellers, like the Gastropoda *Radix balthica* (Linnaeus, 1758) (IndVal= 58%, p-value= 0.022) of the family Limnaeidae and *Physa fontinalis* (Linnaeus, 1758) (IndVal= 47 %, p-value= 0.031) of the family Physidae that graze on biofilms available on branches, but also shredders like various Trichoptera taxa (Tab. S4). Finally, taxa characterising the category

maintained-streamside exclusively include passive filter-feeders preferring medium to strong flow velocities like Simuliidae larvae (e.g., *Prosimulium* sp.; IndVal= 77 %, p-value= 0.004) and the Trichoptera *Hydropsyche saxonica* (McLachlan), 1884 of the family Hydropsychidae (IndVal= 49%, p-value= 0.034).

Discussion

The invertebrate fauna of the studied beaver dams, regardless of the dam category, is typical for small streams of lower mountain areas. It is species-rich, with a high proportion of amphipods, Ephemeroptera and Trichoptera taxa, which prefer cool, well-oxygenated water. This confirms the findings of Rolauffs et al. (2001) and Clifford et al. (1993), who characterised beaver dams as lotic habitats with a rheophilic species community. Similar to the study of Rolauffs (1999), we discovered characteristic species of the headwater region (crenal) e.g., larvae of the caddisfly family Philopotamidae and Hydropsychidae (e.g., *H. saxonica*, *Diplectrona felix* McLachlan, 1878) were dominant. We even found rare and specialised headwater species, like the case bearing Tipulidae (Diptera) larvae *Thaumastoptera calceata* (Mik, 1866), who is described as one of the most typical inhabitants of cold springs (Lenz, 1920) and the dragonfly larvae *Cordulegaster boltonii* Donovan, 1807 (Sternberg et al., 2000). This rheophilic community is common within the dams throughout the beaver territories, contrasting the communities typical of beaver ponds (Harthun, 1998, 1999; Naiman et al., 1988). Nevertheless, beaver dam communities have many peculiarities, which discriminate them from the general fauna of small mountain brooks. In particular, the high proportion of passive filter-feeders is striking and most likely depending on the plankton community developing in the upstream beaver ponds in combination with the high flow velocities, especially in the streamside habitats. Clifford et al. (1993) also emphasised the high amount of passive filter feeders in beaver dams and characterised especially Simuliidae larvae as a typical fauna element of this habitat. Additionally, the high spatial discrimination of invertebrate communities renders the beaver dam a unique habitat within the framework of small mountain brooks.

Our results differ to those obtained by Rolauffs et al. (2001) and Clifford et al. (1993) in some regards, which is mainly rooted in the sampling methods applied. Rolauffs et al. (2001), who investigated one of the streams also addressed in our study, used emergence traps and thus missed hololimic taxa such as *Gammarus*, which is the most abundant taxon in the beaver dams. On the other hand, we may have missed several of the smaller Diptera taxa (larvae < 2 mm), which were dominant in the two other studies. This is particularly true for midge larvae

(Chironomidae), who mainly emerged in summer according to Rolauuffs et al. (2001) and might just have been too small when the sampling for the current study took place. Therefore, our sampling does not represent a full inventory of the dam fauna, but a spot check of the organisms ≥ 2 mm colonising the dam in spring, before emergence, at times when larval size of most merolimnic species is maximal.

Community analysis (Hypothesis 1)

The first hypothesis that the fauna of maintained dams is spatially more variable than that of abandoned dams, has been confirmed. The PCoA and ANOVA alongside the TukeyHSD-test clearly reveal the larger variability of the fauna of maintained dams, especially of streamside habitats (but regard that sample size was lower in pondside habitats). The analysis also confirms that the maintenance state is the greatest influencing factor on community composition. In addition, the distribution of water flow preferences and feeding types supports the conjecture that the habitat conditions are more variable in maintained dams, most likely due to the maintenance activity of beavers. Maintenance activities are required to prevent the flow from washing away dam material and weaken the whole structure (Woo & Waddington, 1990). Abandoned dams therefore become more permeable, allowing water to pass readily through the entire structure (Woo & Waddington, 1990); as a consequence, the extremes of both lentic and lotic habitats get lost. The effects on invertebrate communities are obvious, already on the level of coarse taxonomic entities. For example, one difference between maintained and abandoned dams is the high proportion of amphipods (consisting almost exclusively of the species *G. fossarum*). This highly mobile species accumulates primarily in dams with a species-specific food supply, e.g., rotting wood. We sampled in spring, at times when the availability of leaves in the stream is minimal – this might be an additional reason why *G. fossarum* accumulates in beaver dams. Abandoned dams are obviously more accessible to the species, as the number of gaps is higher, and more wood becomes available. Also, other hololimnic species are more abundant in the abandoned dams e.g., the less mobile snail *Ancylus fluviatilis* (Müller, 1774). It feeds on algal layers on stones and wood in fast-running streams (Arens, 1990) and was frequently observed on stones inside the dams (Tab. S3).

Water velocity preference (Hypotheses 2 and 3)

According to Hypothesis 2, we expected the fauna of abandoned beaver dams to be more rheophilic, as these dams are no longer repaired, and the water can flow more rapidly through the remaining structure. However, this was not the case. Regardless of the maintenance state, taxa depending on lotic conditions account for at least two-thirds of the invertebrate community

in all dam categories. In the streamside of maintained dams, the percentage of taxa depending on high flow velocities is even greater than in abandoned dams. Also, the indicators for the category maintained-streamside are exclusively specialists for fast-flowing conditions (Simuliidae, Hydropsychidae). In particular, the high abundance of Simuliidae characterise the streamside of maintained dams as fast flowing-area. According to Harrod (1965), the larvae of *Simulium ornatum* (Meigen, 1818) requires a velocity of > 0.19 m/s to hold the cephalic fans open in the water. Feeding of *Simulium* larvae almost entirely depends on their cephalic fans (Zahar, 1951). In addition, Zahar (1951) states that the filtration efficiency of *Simulium* larvae increases with flow velocity, as more water can be filtered within a given period of time, while at the same time losses due to sinking of drifting material is prevented. In addition to flow velocity and food conditions, beaver dams provide excellent attachment substrates. In lotic systems, many sedentary or sessile filter-feeders rely on solid substrates in local hydraulic environments, which guarantee a sufficient delivery of suspended materials (Hoffmann & Hering, 2000). The indicator species *H. saxonica* most likely needs similar conditions, which are provided by the streamside of maintained dams. Furthermore, *Hydropsyche* larvae bite out large depressions in wood structure, into which they construct the retreat portion of their shelter (Hoffmann & Hering, 2000). In the category “streamside-abandoned”, the indicator taxa mentioned before are replaced by the net-spinning caddis larvae *W. occipitalis* and *P. montanus*. These species also use coarse woody debris for net attachment and retreat building (Hoffmann & Hering, 2000); however, the nets of Philopotamid larvae are long tubular bags made out of very fine rectangular meshwork (Edington, 1968). These nets are common in places where water is percolating through piles of boulders or woody structures and where nets are hanging in a thin film of waters, in order to filter diatoms and fine detritus particles (Edington, 1968). Such trickle areas must therefore frequently exist in the streamside of abandoned dams. We assume that Philopotamid nets are generally occurring in less strong current than those of *Hydropsyche* and *Simulium* larvae and thus the conditions in abandoned dams are preferable. Also, the predacious beetle *D. coerulescens*, another indicator taxon of streamside-abandoned, requires trickle or hygropetric areas. There is little information about the hydraulic conditions in a beaver dam; experimental investigations, by Hart et al. (2020) could show that the discharge increases with porosity, which is congruent with our Hypothesis. The studied dams are made of wood, a few stones and little sediment, this material composition leads to a comparatively high permeability (Ronnquist & Westbrook, 2021) regardless of the maintenance state. The diameter and the number of the pores/gaps are smaller and rarer in maintained dams, in the manner of our observations. According to the equation of continuity (“small diameter – faster

flow velocity”), this would result in higher flow velocities within maintained dams. Referring to the work of Müller and Watling (2016), the hydraulic condition in a beaver dam is best described by Darcy’s law, where flow velocity is a linear function of head difference. For a 5 cm increase in head, the flow velocity increases by 0.05m/s (Müller & Watling, 2016). In our study, maintained dams are on average 0.2 m higher than the abandoned ones, so assuming the relationship suggested by Müller and Watling (2015) flow velocity would on average increase by 0.2 m/s. Beaver dams primarily create lentic water bodies (beaver ponds), but are themselves a lotic water habitat supporting a lotic fauna. Our results revealed that the maintenance state has a direct influence on flow velocity. In combination with dam area, this results in a complex water flow pattern, that leads to a variable dam colonisation with invertebrates.

According to Hypothesis 3, we expected a higher proportion of rheophilic species in the streamside of dams, where flow velocity is assumed to be highest, while limnophilic or indifferent species were expected to prefer the pondside, especially of maintained dams, which is characterised by minimal flow velocities. This hypothesis was supported. Community composition reveals that flow velocity increases from the pondside to the streamside. This gradient is most pronounced in maintained dams and dissipates in abandoned ones. Similar results were obtained by Rolauuffs et al. (2001), whose measurements showed that flow velocity was lowest in the pondside (max. 0.2 m/s) and highest in the streamside area (on average: 0.4 m/s; max. 1.0 m/s). Accordingly, indicator taxa for the pondside include several lentic taxa e.g., caddisflies of the family Limnephilidae like *Limnephilus lunatus* (Curtis, 1834), but also lotic taxa such as *Halesus radiatus* (Curtis, 1834), *H. digitatus/tesselatus* and *Potamophylax cingulatus* (Stephens, 1837).

Feeding types (Hypothesis 4)

With Hypothesis 4, we expected the proportion of grazers and shredders to be highest in the upper areas of a dam, where food supply and flow velocity is consistent with their needs. This hypothesis was supported. Almost half of the invertebrate fauna of the category maintained-pondside is composed of shredders, with grazers comprising an additional 13%. The share of shredders and grazers in the other dam categories are lower. Furthermore, the indicator taxa of the category maintained-pondside include the snails *R. balthica* and *P. fontinalis* as well as the mayfly *Baetis rhodani* (Pictet 1843) of the family Baetidae that all feed on biofilms (Arens, 1920). Similar to Blersch & Kangas (2014), we have observed that the top of maintained dams is passively extended by washed up remains of the beavers’ gnawing activities or branches that have fallen into the stream. The former lead to the accumulation of smaller and debarked

branches, whose smooth surface is often covered with an epixylic biofilm, which may be several millimetres thick. The crest of the beaver dam is usually fully exposed to the sun and the water of the beaver ponds is most likely nutrient-rich; therefore, the conditions for biofilm growth are ideal. In addition, the beavers repair the crest with muds of grass, floating leaves accumulate along the crest and of course the crest is also composed of woody structures; all these provide food to shredders. Accordingly, several of the indicator taxa are shredding species e.g., representatives of the tribes Chaetopterygini and Stenophylacini and *P. cingulatus*. In general, shredders and gatherers were the main feeding types in beaver dams, with an exceptionally high proportion of passive filter-feeders in the streamside, as mentioned earlier.

Terrestrial/semiaquatic taxa (Hypothesis 5)

Finally, we expected terrestrial or semiaquatic species predominantly in the upper and marginal areas of beaver dams, especially if dams are still maintained (Hypothesis 5). However, the contrary was the case, as the observed terrestrial/semiaquatic species predominantly occur in the streamside of the dams, especially of abandoned dams. As already outlined for Hypothesis 2, abandoned dams provide thin layers of water on woody structures, a habitat, which may enable the persistence of species using atmospheric oxygen, as the water depth is minimal. At the same time, prey availability is huge and mobile species, such as the beetle *D. coerulea*, can access large parts of the dam, which is characterised by holes and gaps, when searching for prey. *D. coerulea* is a typical species of the fauna hygropetrica which is linked to the splash zone of waterfalls and banks of fast flowing streams with overflowed mosses and other vegetation (Koch, 1989; van Stuijvenberg, 1997). The species was already recorded in a beaver dam in Bavaria (Schloemer & Hoffmann, 2018). *V. antivertigo* is described as a typical swamp inhabitant, living at the shore of waterbodies and in marshy meadows (Wiese, 2016). The larvae of *O. fulvicephalus* is another element of the riparian fauna that also likes to reside under water part-time (Moog, 2019). For such species living between aquatic and terrestrial conditions, beaver dams can provide ideal conditions.

Conclusions

Beaver dams provide a wide variety of environmental conditions and habitat types. Within a very small area, conditions can reach from lentic to lotic situations and microhabitats are available for species with all types of flow preferences and feeding types. Beaver dams undergo a distinct succession, especially when they are abandoned, which further enhance the variability of habitat types of a dam. Beaver dams in their various maintenance and decay states provide valuable habitats for a wide variety of organisms in small floodplains. Our results clearly outline that beaver dams are an important component of the numerous habitats created by beavers that increase invertebrate diversity in streams and adjacent floodplains. Therefore, the impact of beaver activities on biodiversity is underestimated, if the fauna of beaver dams is not taken into account.

References

- Andersen, D. C. & P. B. Shafroth, 2010. Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona. *Ecohydrology* 3: 325–338. <https://doi.org/10.1002/eco.113>
- AQEM Consortium, 2002. Manual for the application of the AQEM system: A comprehensive method to assess European streams using benthic macroinvertebrates, developed for the purpose of the Water Framework Directive (No. Version 1.0). <http://www.aqem.de>
- Arens, W., 1990. Wear and tear of mouthparts: a critical problem in stream animals feeding on epilithic algae. *Canadian Journal of Zoology* 68: 1896–1914. <https://doi.org/10.1139/z90-269>
- Barnes, D. M. & A. U. Mallik, 1996. Use of woody plants in construction of beaver dams in northern Ontario. *Canadian Journal of Zoology* 9: 1781–1786. <https://doi.org/10.1139/z96-197>
- Blersch, D. M. & P. C. Kangas, 2014. Signatures of self-assembly in size distributions of wood members in dam structures of *Castor canadensis*. *Global Ecology and Conservation* 2: 204–213. <https://doi.org/10.1016/j.gecco.2014.08.011>
- Bush, B. & S. Wissinger, 2016. Invertebrates in Beaver-Created Wetlands and Ponds. *Invertebrates in Freshwater Wetlands*. Springer, Cham., 129: 411–449. https://doi.org/10.1007/978-3-24978-0_12

- Bush, B., C. Stenert, L. Maltchik & D. Batzer, 2019. Beaver-created successional gradients increase β -diversity of invertebrates by turnover in stream-wetland complexes. *Freshwater Biology* 64: 1265-1274. <https://doi.org/10.1111/fwb.13302>
- Butler, D. R. & G. P. Malanson, 1995. Sedimentation rates and patterns in beaver ponds in a mountain environment. *Geomorphology* 13: 255-269. [https://doi.org/10.1016/0169-555X\(95\)00031-Y](https://doi.org/10.1016/0169-555X(95)00031-Y)
- Bylak, A., K. Kukuła & J. Mitka, 2014. Beaver impact on stream fish life histories: the role of landscape and local attributes. *Canadian Journal of Fisheries and Aquatic Sciences* 71: 1603-1615. <https://doi.org/10.1139/cjfas-2014-0105>
- Bylak, A. & K. Kukuła, 2018. Living with an engineer: fish metacommunities in dynamic patchy environments. *Marine and Freshwater* 69: 883-893. <https://doi.org/10.1071/MF17255>
- Collen, P. & R. J. Gibson, 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects. *Reviews in Fish Biology and Fisheries* 10: 439-461
- Clifford, H. F., G. M. Wiley & R. J. Casey, 1993. Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. *Canadian Journal of Zoology* 71: 1439–1447. <https://doi.org/10.1139/z93-199>
- Cutting, K., J. Ferguson, M. Anderson, K. Cook, S. Davis & R. Levine, 2018. Linking beaver dam affected flow dynamics to upstream passage of Arctic grayling. *Ecology and Evolution* 8: 12905-12917. <https://doi.org/10.1002/ece3.4728>
- Czerniawski, R., L. Sługocki & M. Kowalska-Górska, 2017. Effects of beaver dams on the zooplankton assemblages in four temperate lowland streams (NW Poland). *Biologia* 4: 417-430. <https://doi.org/10.1515/biolog-2017-0047>
- Dalbeck, L., 2021. Bestandsentwicklung des Bibers am Beispiel des Kreises Düren. In *Wald und Holz NRW (Ed.), 40 Jahre Biber-Wiederansiedlung in Nordrhein-Westfalen*: 14–17. Retrived from <http://www.wald-und-holz.nrw.de/>.
- Dalbeck, L., J. Janssen & L. S. Völsger, 2014. Beavers (*Castor fiber*) increase habitat availability, heterogeneity and connectivity for common frogs (*Rana temporaria*). *Amphibia-Reptilia* 35: 321–329. <https://doi.org/10.1163/15685381-00002956>
- Danilov, P., V. Kanshiev & F. Fyodorov, 2011. Characteristics of North American and Eurasian beaver ecology in Karelia. In: Sjöberg, G. & J.P. Ball, 2011. *Restoring the*

- European beaver 2011: 50 years of experience. Section 2 – Biology of two beaver species in Europe. Chapter 6: 55-72. Sofia. Pensoft
- DeCáceres, M., 2020. Package 'indicspecies'. Retrieved from <http://cran.r-project.org/web/packages/indicspecies/vignettes/indicspecies>
- Dufrêne, M. & P. Legendre, 1997. Species Assemblages and Indicator Species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.
- Dugmore, A. R., 1914. The romance of the beaver: being the history of the beaver in the Western Hemisphere. JB Lippincott.
- Edington, J. M., 1968. Habitat Preferences in Net-Spinning Caddis Larvae with Special Reference to the Influence of Water Velocity. *The Journal of Animal Ecology* 37: 1-675. <https://doi.org/10.2307/3081>
- Fritz, S. & M. Gangloff, 2022. The effects of beaver impoundments on montane stream fish communities. *Aquatic Conservation: Marine and Freshwater Ecosystems* 32: 1618-1633. <https://doi.org/10.1002/aqu.3876>
- Fuller, M. R. & B. L. Peckarsky, 2011a. Does the morphology of beaver ponds alter downstream ecosystems? *Hydrobiologia* 1: 35-48. <https://doi.org/10.1007/s10750-011-0611-x>
- Fuller, M. R. & B. L. Peckarsky, 2011b. Ecosystem engineering by beavers affects mayfly life histories. *Freshwater Biology* 5: 969-979. <https://doi.org/10.1111/j.1365-2427.2010.02548.x>
- Gepp, J., 2003. Der Bachhaft *Osmylus fulvicephalus* - 240 Jahre nach seiner Beschreibung durch Johannes Antonius Scopoli - Österreichs Insekt des Jahres (Osmylidae, Neuroptera). *Carinthia II* 193/113: 325–334.
- Gurnell, A. M., 1998. The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography* 22: 167–189. <https://doi.org/10.1177/030913339802200202>
- Hafen, K. C., J. M. Wheaton, B. B. Roper, P. Bailey & N. Bouwes, 2020. Influence of topographic, geomorphic, and hydrologic variables on beaver dam height and persistence in the intermountain western United States. *Earth Surf. Process. Landforms (Earth Surface Processes and Landforms)* 11: 2664–2674. <https://doi.org/10.1002/esp.4921>

- Halley, D. J., A. P. Saveljev, F. Rosell, 2021: Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia. *Mammal Review* 51, 1: 1-24.
<https://doi.org/10.1111/mam.12216>
- Harrod, J. J., 1965. Effect of current speed on the cephalic fans of the larva of *Simulium ornatum* var. *nitidifrons* Edwards (Diptera: Simuliidae). *Hydrobiologia* 26: 8–12.
<https://doi.org/10.1007/BF00142248>
- Hart, J., M. Rubinato & T. Lavers, 2020: An Experimental Investigation of the Hydraulics and Pollutant Dispersion Characteristics of a Model Beaver dam. *Water* 9: 1-22.
<https://doi.org/10.3390/w12092320>
- Harthun, M., 1998. Biber als Landschaftsgestalter - Einfluß des Bibers (*Castor fiber albicus* Matschie, 1907) auf die Lebensgemeinschaft von Mittelgebirgsbächen. 1-199.
 Schriftenreihe der Horst-Rohde-Stiftung. Maecenata. München
- Harthun, M., 1999. Der Einfluss des Bibers (*Castor fiber albicus*) auf die Fauna (Odonata, Mollusca, Trichoptera, Ephemeroptera, Diptera) von Mittelgebirgsbächen in Hessen (Deutschland). *Limnologica* 29: 449-464. [https://doi.org/10.1016/S0075-9511\(99\)80052-8](https://doi.org/10.1016/S0075-9511(99)80052-8)
- Hägglund, A. & G. Sjöberg, 1999. Effects of beaver dams on the fish fauna of forest streams. *Forest Ecology and Management* 115:259-266. [https://doi.org/10.1016/S0378-1127\(98\)00404-6](https://doi.org/10.1016/S0378-1127(98)00404-6)
- Hood, G. A. & D. G. Larson, 2014. Beaver-Created Habitat Heterogeneity Influences Aquatic Invertebrate Assemblages in Boreal Canada. *Wetlands* 34: 19-29.
<https://doi.org/10.1007/s13157-013-0476-z>
- Hoffmann, A. & D. Hering, 2000. Wood-Associated Macroinvertebrate Fauna in Central European Streams. *International Review Hydrobiology* 85: 25–48.
[https://doi.org/10.1002/\(SICI\)1522-2632\(200003\)85:1<25::AID-IROH25>3.0.CO;2-R](https://doi.org/10.1002/(SICI)1522-2632(200003)85:1<25::AID-IROH25>3.0.CO;2-R)
- Johnston, C., 2017. *Beavers: Boreal Ecosystem Engineers*. Springer International Publishing: 1-272. Cham. <https://doi.org/10.1007/978-3-319-61533-2>
- Koch, K., 1989. *Die Käfer Mitteleuropas*. Krefeld: Goecke & Evers.
- Kroes, D. E. & C. W. Bason, 2015. Sediment-trapping by Beaver Ponds in Streams of the Mid-Atlantic Piedmont and Coastal Plain, USA. *Southeastern Naturalist* 14: 577–595.
- Lenz, F., 1920. *Thaumastoptera calceata* Mik. Eine gehäusetragende Tipulidenlarve. *Archiv für Naturgeschichte* 85: 114-136

- Lokteff, R., B. Roper & J. Wheaton, 2013. Do Beaver Dams Impede the Movement of Trout? *Transactions of the American Fisheries Society* 142: 1114-1125.
<https://doi.org/10.1080/00028487.2013.797497>
- Meier, C., P. Haase, P. Rolauffs, K. Schindehütte, F. Schöll, A. Sundermann & D. Hering, 2006. Methodisches Handbuch Fließgewässerbewertung zur Untersuchung und Bewertung von Fließgewässern auf der Basis des Makrozoobenthos vor dem Hintergrund der EG-Wasserrahmenrichtlinie. <http://www.fliessgewaesserbewertung.de>
- McComb, W. C., J. R. Sedell & T. D. Buchholz, 1990. Dam-Site selection by beavers in an eastern Oregon basin. *Great Basin Naturalist* 50: 273–281.
- McDowell, D. M. & R. J. Naiman, 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia* 68: 481-489
- Moog, O., 2019. Der Europäische Bachhaft - ein Ufer-Insekt mit Höhlenaffinität? *Osmylus fulvicephalus* - a shore insect with cave affinity? *Höhlenkundliche Mitteilungen des Landesvereins Für Höhlenkunde in Wien und Niederösterreich*. (5-6): 94–95.
- Müller, G., 2014. Ingenieurtechnische Aspekte der Biberdämme. *KW Korrespondenz Wasserwirtschaft* 7: 158–163.
- Müller, G. & J. Watling, 2016. The engineering in beaver dams. In Constantinescu, G., M. Garcia & D. Hanes (Eds.), *A Balkema book, River flow 2016: Proceedings of the International Conference on Fluvial Hydraulics (River Flow 2016)*. St. Louis, USA. 11-14 July 2016 (pp. 2094–2099). Boca Raton: CRC Press.
<https://doi.org/10.1201/9781315644479-326>
- Müller-Schwarze, D., 2011. *The beaver: Its life and impact* (2nd ed.). Cornell University Press, p. 216
- Naiman, R. J., C. A. Johnston & J. C. Kelley, 1988. Alteration of North American Streams by Beaver. *BioScience* 11: 753-762. <https://doi.org/10.2307/1310784>
- Naiman, R. J., D. M. McDowell & B. Farr, 1984. The influence of beaver (*Castor canadensis*) on the production dynamics of aquatic insects. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* 22: 1801-1810.
<https://doi.org/10.1080/03680770.1983.11897578>
- Naumann, G., 1991. Aussetzen von Bibern in der Eifel - Ein Beispiel für die Problematik von Wiedereinbürgerungen. *Naturschutz Im Rheinland, Rheinischer Verein für Denkmalpflege und Landschaftsschutz, Jahrbuch 1989-1991*: 137–150.

- Nummi, P., 1989. Simulated effects of the beaver on vegetation, invertebrates and ducks. *Annales Zoologici Fennici* 26: 43-52.
- Nummi, P., W. Liao, J. van der Schoor, J. Loehr, 2021. Beaver creates early successional hotspots for water beetles. *Biodiversity and Conservation* 30: 2655-2670.
<https://doi.org/10.1007/s10531-021-02213-8>
- Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlenn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. Stevens, E. Szoecs & H. Wagner, 2020. Package 'vegan'. *Community Ecology Package*. (Version R package version 2.5-7.)
Cran.R-project.org: Cran.R-project.org. <https://CRAN.R-project.org/package=vegan>
- Patil, I., 2021. Visualizations with statistical details: The ggstatsplot approach. *Journal of Open Source Software*, 6(61), 3167. <https://doi.org/10.21105/joss.03167>
- Pollock, M., S. Witmore & E. Yokel, 2022. Field experiments to assess passage of juvenile salmonids across beaver dams during low flow conditions in a tributary to the Klamath River, California, USA. *PloS one* 17: 1-24. <https://doi.org/10.1371/journal.pone.0268088>
- R Core Team, 2021. R: A language and environment for statistical computing. Freeware. R Foundation for statistical computing, Vienna, Austria. <http://www.R-project.org/>
- Redin, A. & G. Sjöberg, 2013. Effects of Beaver Dams on Invertebrate Drift in Forest Streams. *Sumarski list* 11-12: 597-607
- Renik, K. M. & A. W. Hafs, 2020. Effect of Beaver on Brook Trout Habitat in North Shore, Lake Superior, Streams. *North American Journal of Fisheries Management* 40: 427-445.
<https://doi.org/10.1002/nafm.10422>
- Richard, P. B., 1967. Le déterminisme de la construction des barrages chez le Castor du Rhône. *Revue D'Ecologie, Terre Et Vie, Société Nationale De Protection De La Nature*: 339-470.
- Rolauffs, P., 1999. Untersuchungen zur Besiedlung von Biberdämmen durch Insekten unter besonderer Berücksichtigung der Emergenz. Diploma Thesis: 1-160. Faculty of Biology, University Essen.
- Rolauffs, P., D. Hering & S. Lohse, 2001. Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. *Hydrobiologia* 459: 201-212.
- Ronnquist, A. L. & C. J. Westbrook, 2021. Beaver dams: How structure, flow state, and landscape setting regulate water storage and release. *The Science of the Total Environment* 785: 1-12. <https://doi.org/10.1016/j.scitotenv.2021.147333>

- Schloemer, S. & A. Hoffmann, 2018. The Beaver Dam Vacuum Sampler - a new sampling method to investigate the invertebrate fauna in beaver dams. *Lauterbornia* 85: 117–121.
- Schmedtje, U. & M. Colling, 1996. Ökologische Typisierung der aquatischen Makrofauna (Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft No. 4). München. https://www.gewaesserbewertung-berechnung.de/files/downloads/perlodes/PerlodesOnline_Dokumentation_Teil_III_Beschreibung_Indizes.pdf
- Schmidt-Kloiber, A. & D. Hering, 2015. www.freshwaterecology.info – An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators* 53: 271-282. <https://doi.org/10.1016/j.ecolind.2015.02.007>
- Smith, M. E., C. T. Driscoll, B. J. Wyskoski, C. M. Brooks & C. C. Cosentini, 1991. Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Canadian Journal of Zoology* 69: 55-61. <https://doi.org/10.1139/z91-009>
- Sommerhäuser, M. & T. Pottgiesser, 2002. Fließgewässertypenatlas Nordrhein-Westfalens (Merkblätter Nr. 36). Essen.
- Speiser, B., 2001. Food and Feeding Behaviour. In G. M. Barker (Ed.), *The biology of terrestrial molluscs*: 259–288. Wallingford, Oxon, UK, New York, NY, USA: CABI Pub.
- Sternberg, K., R. Buchwald & U. Stephan, 2000. *Cordulegaster boltonii*. In: Sternberg, K. & R. Buchwald, 2000. *Die Libellen Baden-Württembergs – Band 2: Großlibellen (Anisoptera)*: 191-208. Verlag Eugen Ulmer
- Strahler, A. N., 1954. Statistical Analysis in Geomorphic Research. *The Journal of Geology* 62: 1–25. <https://doi.org/10.1086/626131>
- Thie, J., 2022. Exploring Beaver Habitat in Canada: The Longest Beaver Dam in the World. https://www.geostrategis.com/p_beaver-longestdam.htm
- Townsend, J. E., 1953. Beaver Ecology in Western Montana with Special Reference to Movements. *Journal of Mammalogy* 34: 459. <https://doi.org/10.2307/1375861>
- Van Stuivenberg, F., 1997. Tabel en verspreidingsatlas van de Nederlandse Steninae (Coleoptera: Staphylinidae). *Nederlandse Faunistische Mededelingen* 6: 3–60.
- Warren, E. R., 1932. Position of wood in beaver dams. *Science (New York, N.Y.)* 75, 1937: 194-195. <https://doi.org/10.1126/science.75.1937.194-b>

- Wiese, V., 2016. Die Landschnecken Deutschlands: Finden - erkennen - bestimmen (2., durchgesehene Auflage). Quelle & Meyer Bestimmungsbücher. Wiebelsheim: Quelle & Meyer Verlag
- Willby, N. J., A. Law, O. Levanoni, G. Foster & F. Ecke, 2018. Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. *Philosophical transactions of the Royal Society, Series B, Biological Sciences* 373: 1-8. <https://doi.org/10.1098/rstb.2017.0444>
- Wohl, E., D. N. Scott & S. E. Yochum, 2019. Managing for large wood and Beaver dams in stream corridors. General Technical Report-Rocky Mountain Research Station. USDA Forest Service, (RMRS-GTR-404):136
- Woo, M.-K. & J. M. Waddington, 1990. Effects of Beaver Dams on Subarctic Wetland Hydrology. *Arctic* 43: 223–230.
- Wróbel, M., 2020. Population of Eurasian beaver (*Castor fiber*) in Europe. *Global Ecology and Conservation* 23: 1-4. <https://doi.org/10.1016/j.gecco.2020.e01046>
- Zahar, A. R., 1951. The Ecology and Distribution of Black-Flies (Simuliidae) in South-East Scotland. *The Journal of Animal Ecology* 20: 33. <https://doi.org/10.2307/1643>
- Zavyalov, N. A., 2014. Beavers (*Castor fiber* and *Castor canadensis*), the founders of habitats and phytophages. *Biology Bulletin Reviews* 4: 157–180. <https://doi.org/10.1134/S207908641402008X>

Appendix - Supplementary material

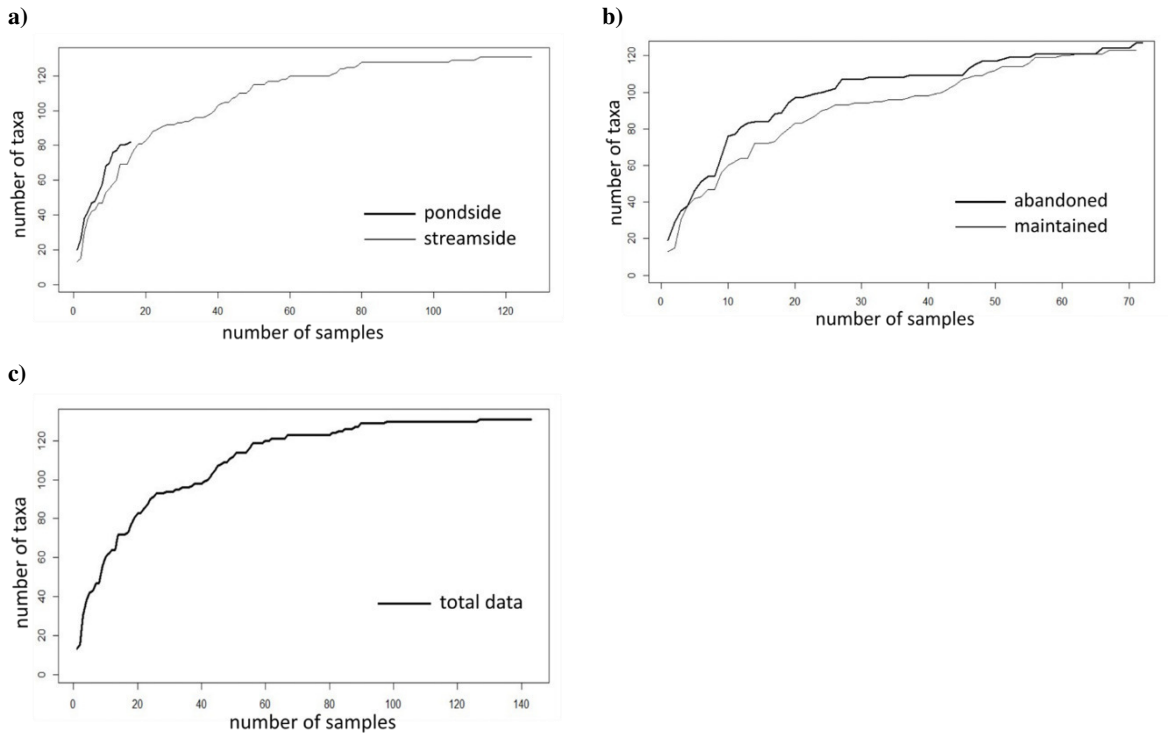


Fig. S1 Species accumulation curve, **a)** showing number of taxa in pond- and streamside samples, **b)** showing number of taxa in abandoned and maintained dam samples, **c)** showing number of taxa of all dam samples. Illustration created in Rstudio (R core Team, 2021).

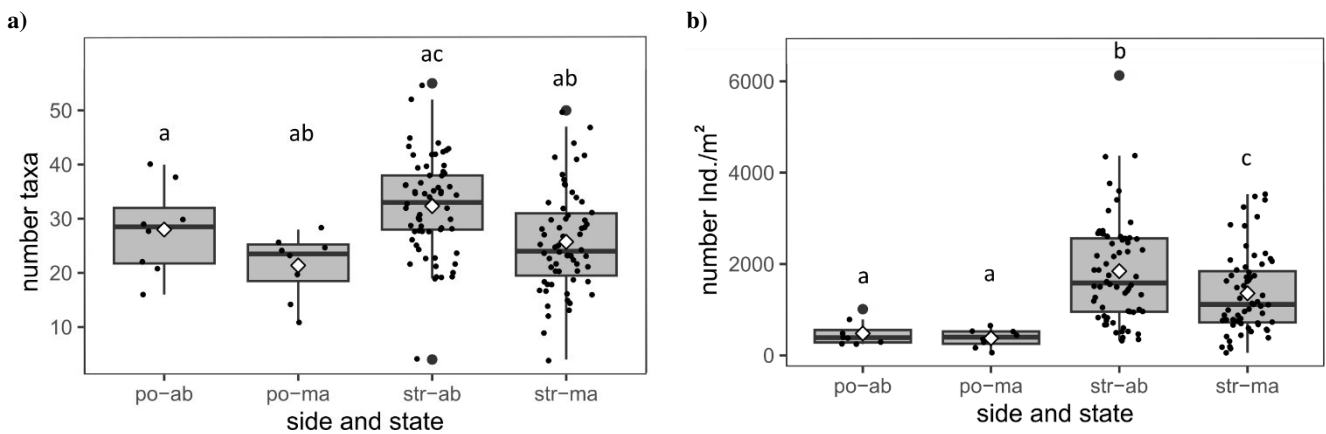
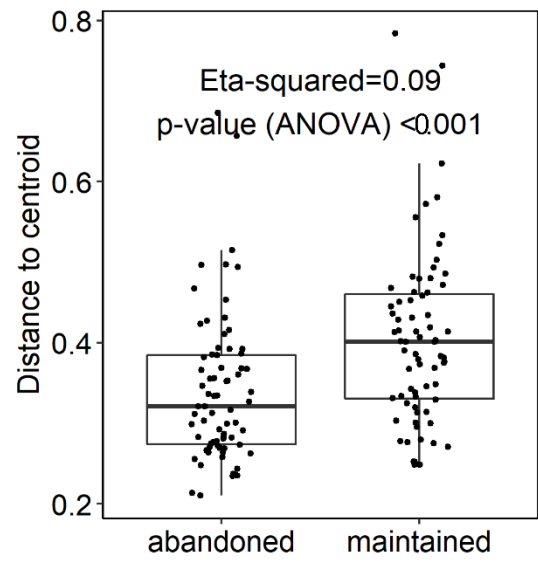
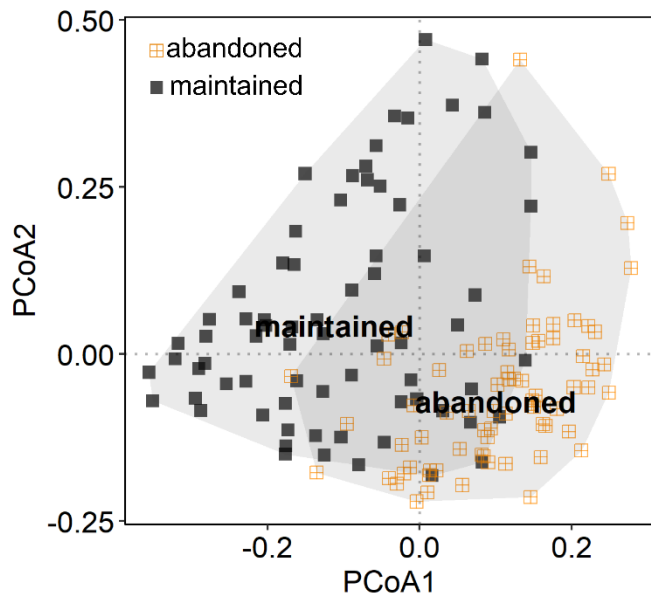
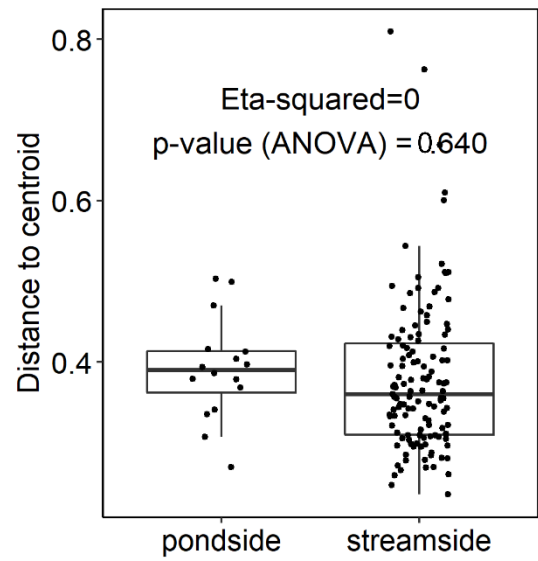
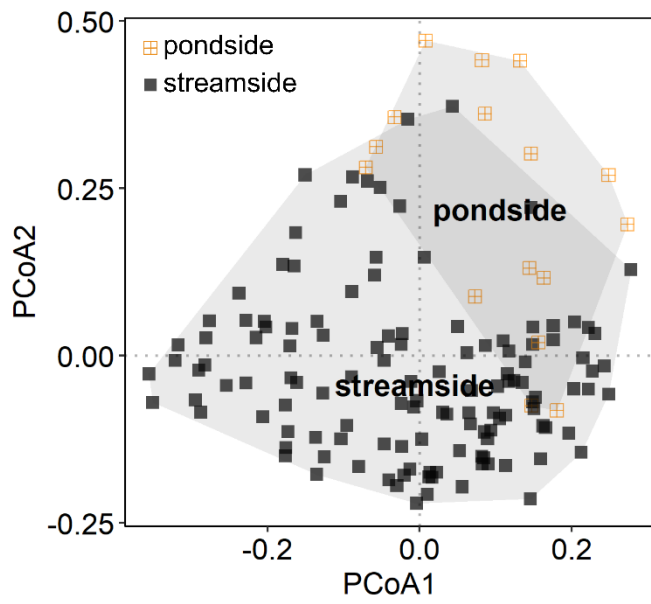


Fig. S2 a) number of taxa in the different dam areas, **b)** number of individuals per m^2 (Ind./ m^2) in the different dam areas; po-ab= pondside abandoned, po-ma= pondside maintained, str-ab= streamside abandoned, str-ma= streamside maintained. Significant differences between categories are indicated with different letters. Boxplots show the median (middle line), quartiles (boxes), 1.5x the interquartile range (whiskers) and dots all values. Diamond shape show the mean value Illustration created with Rstudio (R core Team, 2021).

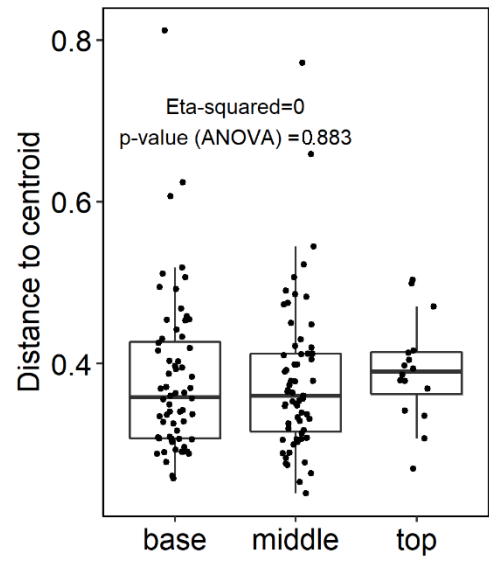
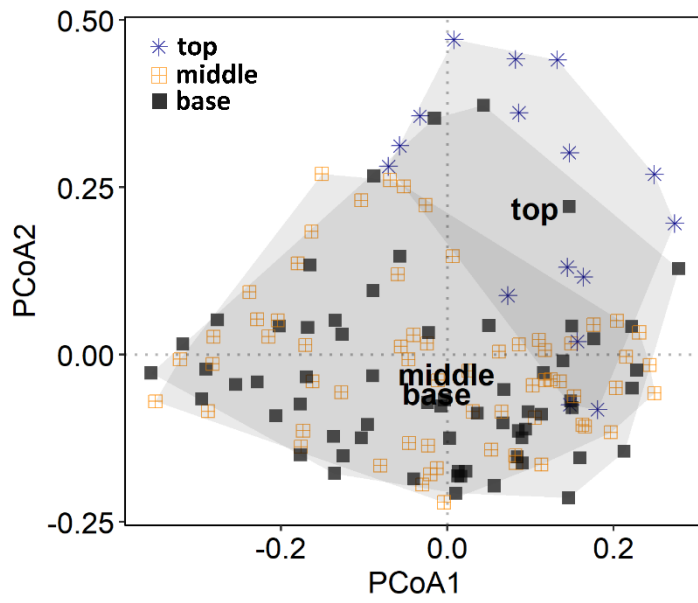
a)



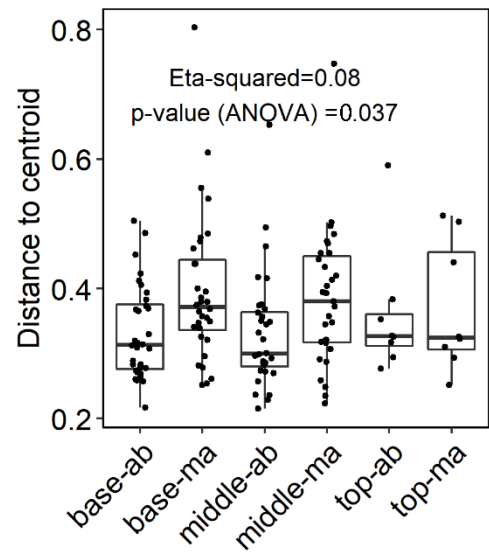
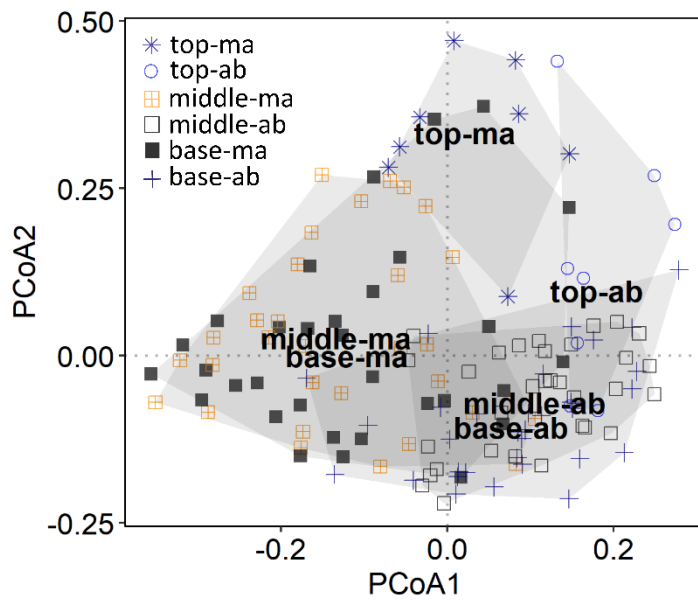
b)



c)



d)



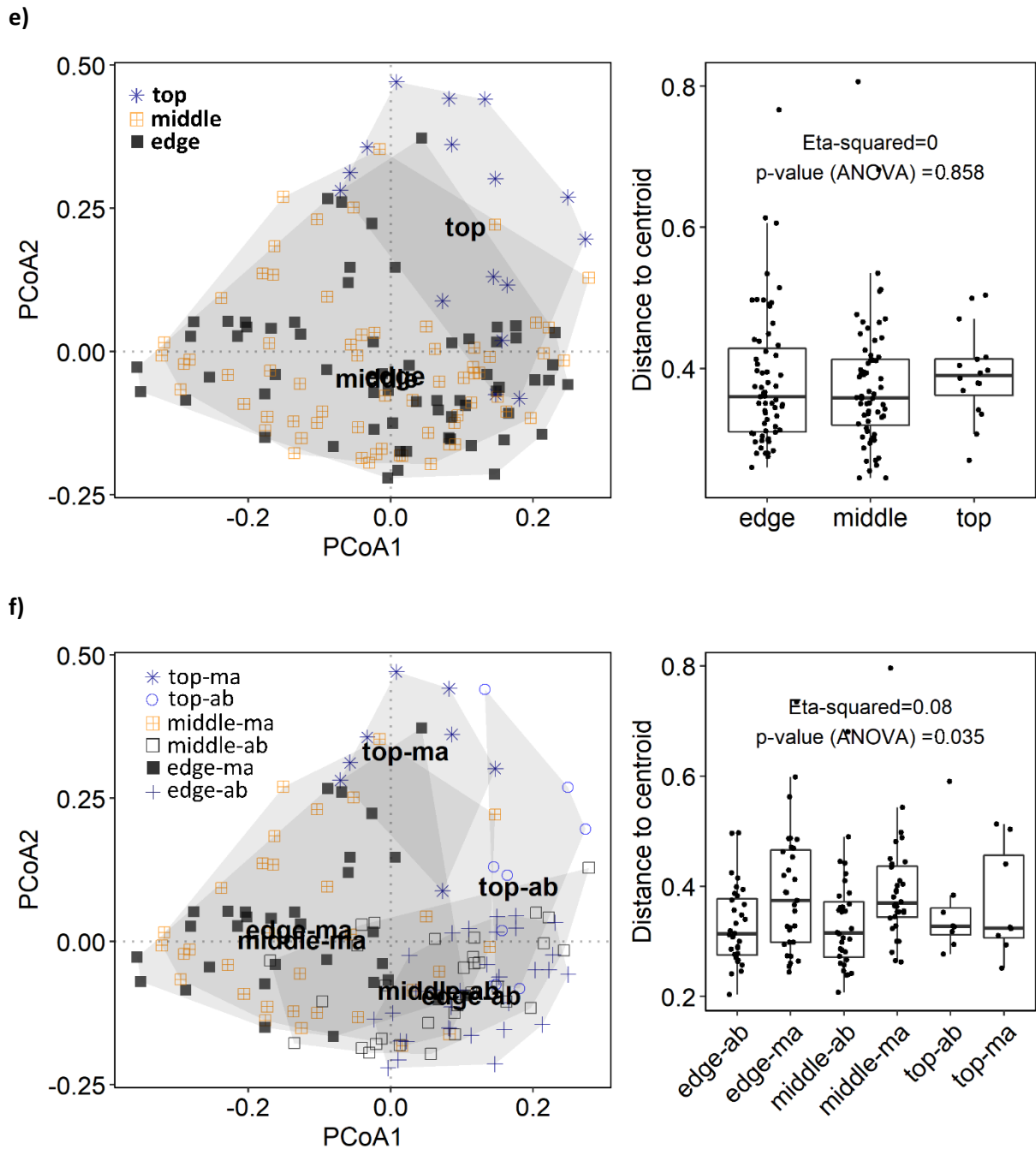


Fig. S3 PCoA **a)** shows the variability within and between each group of abandoned and maintained dams “maintenance state” (Combination 4), **b)** shows the variability within and between each group of the stream- and pondside of dams (Combination 3), **c)** shows the variability within and between each group of the top, middle and base parts of the dams (Combination 1), **d)** shows the variability within and between each group of the top, middle and base areas of the dams including the maintenance state (Combination 1+m.s.), **e)** shows the variability within and between each group of the edge and middle areas of the dams (Combination 2), **f)** shows the variability within and between each group of the edge and middle areas of the dams including the maintenance state (Combination 2+m.s.). Boxplots with jittered points showing the distance between the centroids, within each different group. ab= abandoned, ma= maintained. Illustration created with Rstudio (R core Team, 2021).

Table S1: Complete taxa list with numbers of individuals (m²) in the pondside (maintained & abandoned) and streamside (maintained & abandoned) of the 16 studied beaver dams with indication of the life stage (larvae=Lv., adult= Ad.) of the Coleoptera and Neuroptera.

| Order | Family | Taxa | Life stage | pondside-abandoned | pondside-maintained | streamside-abandoned | streamside-maintained |
|------------|---------------|---|------------|--------------------|---------------------|----------------------|-----------------------|
| Bivalvia | SPHAERIIDAE | <i>Pisidium sp.</i> | | 2 | 0 | 272 | 204 |
| Coleoptera | DRYOPIDAE | <i>Dryops luridus</i> (Erichson, 1847) | Ad. | 8 | 11 | 16 | 56 |
| Coleoptera | DRYOPIDAE | <i>Dryops sp.</i> | Lv. | 0 | 0 | 8 | 8 |
| Coleoptera | DYTISIDAE | <i>Agabus paludosus</i> (Fabricius, 1801) | Ad. | 0 | 0 | 20 | 0 |
| Coleoptera | ELMIDAE | <i>Elmis sp.</i> | Lv. | 2 | 0 | 228 | 20 |
| Coleoptera | ELMIDAE | <i>Elmis aenea</i> (Müller, 1806) | Ad. | 1 | 0 | 8 | 0 |
| Coleoptera | ELMIDAE | <i>Elmis maugetii</i> (Latreille, 1802) | Ad. | 0 | 0 | 156 | 80 |
| Coleoptera | ELMIDAE | <i>Limnius volckmari</i> (Panzer, 1793) | Lv. | 0 | 0 | 20 | 12 |
| Coleoptera | ELMIDAE | <i>Limnius volckmari</i> (Panzer, 1793) | Ad. | 0 | 0 | 24 | 0 |
| Coleoptera | GYRINIDAE | <i>Orectochilus villosus</i> (Müller, 1776) | Lv. | 0 | 2 | 52 | 44 |
| Coleoptera | HALIPLIDAE | <i>Haliphus sp.</i> | Lv. | 0 | 0 | 60 | 4 |
| Coleoptera | HYDRAENIDAE | <i>Hydraena gracilis</i> (Germar, 1823) | Ad. | 0 | 0 | 68 | 12 |
| Coleoptera | HYDRAENIDAE | <i>Hydraena pygmaea</i> (Waterhouse, 1833) | Ad. | 0 | 0 | 32 | 4 |
| Coleoptera | HYDROPHILIDAE | <i>Anacaena globulus</i> (Paykull, 1798) | Ad. | 0 | 0 | 16 | 16 |
| Coleoptera | HYDROPHILIDAE | <i>Laccobius minutus</i> (Linnaeus, 1758) | Ad. | 2 | 1 | 8 | 4 |
| Coleoptera | SCIRTIDAE | <i>Elodes sp.</i> | Lv. | 128 | 97 | 5424 | 5740 |
| Coleoptera | STAPHYLINIDAE | <i>Dianous coeruleus</i> (Gyllenhal, 1810) | Ad. | 2 | 0 | 956 | 560 |
| Coleoptera | STAPHYLINIDAE | <i>Lesteva pubescens</i> (Mannerheim, 1830) | Ad. | 0 | 0 | 8 | 4 |
| Crustacea | ASSELIDAE | <i>Asellus aquaticus</i> (Linnaeus, 1758) | | 21 | 0 | 892 | 0 |

| Order | Family | Taxa | Life stage | pondside-abandoned | pondside-maintained | streamside-abandoned | streamside-maintained |
|-----------|-----------------|---|------------|--------------------|---------------------|----------------------|-----------------------|
| Crustacea | GAMMARIDAE | <i>Gammarus fossarum</i> (Koch, 1836) | | 1210 | 326 | 41008 | 13876 |
| Diptera | CERATOPOGONIDAE | <i>Ceratopogoninae Gen. sp.</i> | | 4 | 0 | 196 | 168 |
| Diptera | CHIRONOMIDAE | <i>Chironomidae Gen. sp.</i> | | 160 | 129 | 12772 | 13332 |
| Diptera | CHIRONOMIDAE | <i>Prodiamesa olivacea</i> (Meigen, 1818) | | 0 | 0 | 12 | 4 |
| Diptera | CHIRONOMIDAE | <i>Tanypodinae Gen. sp.</i> | | 23 | 32 | 644 | 588 |
| Diptera | CHIRONOMIDAE | <i>Tanytarsini Gen. sp.</i> | | 49 | 9 | 1708 | 996 |
| Diptera | DIXIDAE | <i>Dixa sp.</i> | | 1 | 1 | 12 | 0 |
| Diptera | EMPIDIDAE | <i>Clinocerinae Gen. sp.</i> | | 0 | 0 | 40 | 32 |
| Diptera | EMPIDIDAE | <i>Hemerodromia sp.</i> | | 0 | 0 | 8 | 12 |
| Diptera | LIMONIIDAE | <i>Austrolimnophila sp.</i> | | 0 | 1 | 116 | 52 |
| Diptera | LIMONIIDAE | <i>Dicranomyia sp.</i> | | 0 | 0 | 104 | 64 |
| Diptera | LIMONIIDAE | <i>Eloeophila sp.</i> | | 1 | 4 | 40 | 24 |
| Diptera | LIMONIIDAE | <i>Helius sp.</i> | | 0 | 1 | 8 | 32 |
| Diptera | LIMONIIDAE | <i>Lipsothrix sp.</i> | | 3 | 1 | 412 | 144 |
| Diptera | LIMONIIDAE | <i>Molophilus sp.</i> | | 0 | 0 | 12 | 8 |
| Diptera | LIMONIIDAE | <i>Neolimnomyia sp.</i> | | 0 | 0 | 16 | 0 |
| Diptera | LIMONIIDAE | <i>Pilaria sp.</i> | | 1 | 0 | 4 | 4 |
| Diptera | LIMONIIDAE | <i>Pseudolimnophila sp.</i> | | 1 | 4 | 8 | 40 |
| Diptera | LIMONIIDAE | <i>Rhypholophus sp.</i> | | 0 | 3 | 4 | 4 |
| Diptera | LIMONIIDAE | <i>Thaumastoptera calceata</i> (Mik, 1866) | | 0 | 0 | 48 | 24 |
| Diptera | MUSCIDAE | <i>Muscidae Gen. sp.</i> | | 1 | 1 | 40 | 272 |
| Diptera | PEDICIIDAE | <i>Dicranota sp.</i> | | 1 | 1 | 236 | 128 |
| Diptera | PSYCHODIDAE | <i>Bazarella/Berdeniella sp.</i> | | 0 | 0 | 28 | 160 |
| Diptera | PTYCHOPTERIDAE | <i>Ptychoptera sp.</i> | | 0 | 0 | 12 | 4 |
| Diptera | RHAGIONIDAE | <i>Rhagionidae Gen. sp.</i> | | 0 | 0 | 52 | 4 |
| Diptera | SIMULIIDAE | <i>Prosimulium sp.</i> | | 11 | 3 | 2716 | 8012 |
| Diptera | SIMULIIDAE | <i>Prosimulium tomosvaryi</i> (Enderlein, 1921) | pupae | 1 | 0 | 260 | 872 |
| Diptera | SIMULIIDAE | <i>Simulium morsitans</i> (Edwards, 1915) | pupae | 0 | 0 | 0 | 56 |
| Diptera | SIMULIIDAE | <i>Simulium sp.</i> | | 118 | 22 | 7484 | 15180 |
| Diptera | SIMULIIDAE | <i>Simulium venum</i> Gr. | pupae | 1 | 0 | 356 | 500 |
| Diptera | TABANIDAE | <i>Tabanidae Gen. sp.</i> | | 1 | 1 | 16 | 28 |

| Order | Family | Taxa | Life stage | pondside- abandoned | pondside- maintained | streamside- abandoned | streamside- maintained |
|---------------|---------------------------|---|------------|------------------------|-------------------------|--------------------------|---------------------------|
| Diptera | TIPULIDAE | <i>Tipula sp.</i> | | 0 | 1 | 64 | 44 |
| Diptera | ANISOPODIAE/MYCETOBIIIDAE | <i>Mycetobia sp.</i> | | 0 | 0 | 52 | 20 |
| Ephemeroptera | BAETIDAE | <i>Baetis sp.</i> | | 88 | 145 | 1700 | 1420 |
| Ephemeroptera | BAETIDAE | <i>Baetis buceratus</i> (Eaton, 1870) | | 0 | 1 | 12 | 24 |
| Ephemeroptera | BAETIDAE | <i>Baetis fuscatus</i> (Linnaeus, 1761) | | 2 | 2 | 0 | 12 |
| Ephemeroptera | BAETIDAE | <i>Baetis muticus</i> (Linnaeus, 1758) | | 50 | 10 | 1284 | 272 |
| Ephemeroptera | BAETIDAE | <i>Baetis niger</i> (Linnaeus, 1761) | | 17 | 101 | 188 | 180 |
| Ephemeroptera | BAETIDAE | <i>Baetis rhodani</i> (Pictet, 1843) | | 30 | 177 | 708 | 1120 |
| Ephemeroptera | BAETIDAE | <i>Centropilum luteolum</i> (Müller, 1776) | | 8 | 9 | 8 | 4 |
| Ephemeroptera | EPHEMERIDAE | <i>Ephemera danica</i> (Müller, 1764) | | 1 | 1 | 60 | 108 |
| Ephemeroptera | HEPTAGENIIDAE | <i>Ecdyonurus venosus</i> Gr. | | 4 | 11 | 116 | 20 |
| Ephemeroptera | HEPTAGENIIDAE | <i>Rhithrogena semicolorata</i> Gr. | | 7 | 0 | 224 | 112 |
| Ephemeroptera | LEPTOPHLEBIIDAE | <i>Habroleptoides confusa</i> (Sartori & Jacob, 1986) | | 185 | 12 | 6036 | 740 |
| Ephemeroptera | LEPTOPHLEBIIDAE | <i>Habrophlebia lauta</i> (Eaton, 1884) | | 4 | 0 | 16 | 4 |
| Ephemeroptera | LEPTOPHLEBIIDAE | <i>Leptophlebia marginata</i> (Linnaeus, 1767) | | 0 | 5 | 56 | 80 |
| Ephemeroptera | LEPTOPHLEBIIDAE | <i>Paraleptophlebia submarginata</i> (Stephens, 1835) | | 30 | 7 | 2624 | 308 |
| Gastropoda | EUCLONIDAE | <i>Euconulus fulvus</i> (Müller, 1774) | | 0 | 0 | 48 | 112 |
| Gastropoda | HYGROMIIDAE | <i>Trochulus sp.</i> | | 0 | 0 | 8 | 16 |
| Gastropoda | LYMNAEIDAE | <i>Galba truncatula</i> (Müller, 1774) | | 21 | 14 | 96 | 136 |
| Gastropoda | LYMNAEIDAE | <i>Radix balthica</i> (Linnaeus, 1758) | | 0 | 13 | 88 | 260 |
| Gastropoda | OXYCHILIDAE | <i>Oxychilidae sp.</i> | | 0 | 0 | 52 | 80 |
| Gastropoda | PATULIDAE | <i>Discus perspectivus</i> (Megerle von Mühlfeld, 1816) | | 0 | 0 | 16 | 0 |
| Gastropoda | PHYSIDAE | <i>Physa fontinalis</i> (Linnaeus, 1758) | | 0 | 18 | 4 | 80 |
| Gastropoda | PLANORBIDAE | <i>Ancylus fluviatilis</i> (Müller, 1774) | | 3 | 1 | 172 | 68 |
| Gastropoda | PLANORBIDAE | <i>Gyraulus sp.</i> | | 0 | 5 | 44 | 324 |
| Gastropoda | PRISTILOMATIDAE | <i>Vitrea sp.</i> | | 0 | 0 | 24 | 4 |
| Gastropoda | VERTIGINIDAE | <i>Vertigo antivertigo</i> (Draparnaud, 1801) | | 0 | 0 | 4 | 12 |
| Heteroptera | NEPIDAE | <i>Nepa cinerea</i> (Linnaeus, 1758) | | 2 | 0 | 4 | 4 |

| Order | Family | Taxa | Life stage | pondside-abandoned | pondside-maintained | streamside-abandoned | streamside-maintained |
|-------------|-------------------|--|------------|--------------------|---------------------|----------------------|-----------------------|
| Megaloptera | SIALIDAE | <i>Sialis sp.</i> | | 3 | 0 | 48 | 28 |
| Neuroptera | OSMYLIDAE | <i>Osmylus fulvicephalus</i> (Scopoli, 1763) | Lv. | 0 | 0 | 20 | 0 |
| Odonata | CALOPTERYGIDAE | <i>Calopteryx virgo</i> (Linnaeus, 1758) | | 0 | 0 | 16 | 4 |
| Odonata | Cordulegastriidae | <i>Cordulegaster boltonii</i> (Donovan, 1807) | | 0 | 0 | 52 | 4 |
| Oligochaeta | [Kl:Oligochaeta] | <i>Naididae Tubificidae Gen. sp.</i> | | 0 | 1 | 44 | 36 |
| Oligochaeta | LUMBRICIDAE | <i>Eiseniella tetraedra</i> (Savigny, 1826) | | 17 | 6 | 644 | 328 |
| Oligochaeta | LUMBRICIDAE | <i>Stylodrilus heringianus</i> (Claparède, 1862) | | 0 | 0 | 36 | 20 |
| Oligochaeta | LUMBRICULIDAE | <i>Lumbriculidae Gen. sp.</i> | | 14 | 0 | 1508 | 1236 |
| Plecoptera | CHLOROPERLIDAE | <i>Isoperla sp.</i> | | 1 | 0 | 60 | 36 |
| Plecoptera | CHLOROPERLIDAE | <i>Siphonoperla sp.</i> | | 3 | 2 | 52 | 44 |
| Plecoptera | LEUCTRIDAE | <i>Leuctra nigra</i> (Olivier, 1811) | | 14 | 0 | 440 | 36 |
| Plecoptera | LEUCTRIDAE | <i>Leuctra sp.</i> | | 0 | 0 | 16 | 24 |
| Plecoptera | NEMOURIDAE | <i>Nemoura sp.</i> | | 302 | 759 | 3916 | 8096 |
| Plecoptera | NEMOURIDAE | <i>Protonemura sp.</i> | | 12 | 0 | 1404 | 1472 |
| Trichoptera | BERAEIDAE | <i>Beraea maurus</i> (Curtis, 1834) | | 0 | 0 | 124 | 8 |
| Trichoptera | BERAEIDAE | <i>Beraea pullata</i> (Curtis, 1834) | | 0 | 0 | 12 | 88 |
| Trichoptera | BERAEODIDAE | <i>Beraeodes minutus</i> (Linnaeus, 1761) | | 1 | 0 | 8 | 16 |
| Trichoptera | GLOSSOMATIDAE | <i>Agapetus fuscipes</i> (Curtis, 1834) | | 3 | 0 | 116 | 8 |
| Trichoptera | HYDROPSYCHIDAE | <i>Diplectrona felix</i> (McLachlan, 1878) | | 0 | 0 | 64 | 4 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche dinarica</i> (Marinkovic-Gospodnetic, 1979) | | 0 | 0 | 4 | 24 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche fulvipes</i> (Curtis, 1834) | | 0 | 0 | 0 | 16 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche instabilis</i> (Curtis, 1834) | | 0 | 0 | 8 | 8 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche saxonica</i> (McLachlan, 1884) | | 0 | 0 | 28 | 192 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche siltalai</i> (Doehler, 1963) | | 0 | 0 | 60 | 324 |

| Order | Family | Taxa | Life stage | pondside- abandoned | pondside- maintained | streamside- abandoned | streamside- maintained |
|-------------|------------------|---|------------|------------------------|-------------------------|--------------------------|---------------------------|
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche sp.</i> | | 2 | 4 | 104 | 372 |
| Trichoptera | LEPIDOSTOMATIDAE | <i>Lepidostoma basale</i> (Kolenati, 1848) | | 0 | 0 | 0 | 16 |
| Trichoptera | LEPTOCERIDAE | <i>Adicella reducta</i> (McLachlan, 1865) | | 0 | 0 | 8 | 12 |
| Trichoptera | LIMNEPHILIDAE | <i>Chaetopteryx villosa</i> (Fabricius, 1798) | | 2 | 2 | 84 | 4 |
| Trichoptera | LIMNEPHILIDAE | <i>Chaetopteryx major</i> (McLachlan, 1876) | | 22 | 8 | 172 | 20 |
| Trichoptera | LIMNEPHILIDAE | <i>Drusus annulatus</i> (Stephens, 1837) | | 0 | 0 | 56 | 28 |
| Trichoptera | LIMNEPHILIDAE | <i>Glyphotaelius pellucidus</i> (Retzius, 1783) | | 1 | 0 | 8 | 0 |
| Trichoptera | LIMNEPHILIDAE | <i>Halesus digitatus/tesselatus</i> | | 36 | 86 | 100 | 264 |
| Trichoptera | LIMNEPHILIDAE | <i>Halesus radiatus</i> (Curtis, 1834) | | 174 | 295 | 316 | 376 |
| Trichoptera | LIMNEPHILIDAE | <i>Chaetopterygini/Stenophylacini Gen. sp.</i> | | 565 | 290 | 3088 | 1196 |
| Trichoptera | LIMNEPHILIDAE | <i>Limnephilini Gen. sp.</i> | | 123 | 277 | 668 | 668 |
| Trichoptera | LIMNEPHILIDAE | <i>Limnephilus lunatus</i> (Curtis, 1834) | | 1 | 57 | 0 | 40 |
| Trichoptera | LIMNEPHILIDAE | <i>Limnephilus rhombicus</i> (Linnaeus, 1758) | | 6 | 11 | 32 | 112 |
| Trichoptera | LIMNEPHILIDAE | <i>Potamophylax cingulatus</i> (Stephens, 1837) | | 57 | 6 | 616 | 92 |
| Trichoptera | LIMNEPHILIDAE | <i>Potamophylax latipennis</i> (Curtis, 1834) | | 2 | 1 | 4 | 4 |
| Trichoptera | LIMNEPHILIDAE | <i>Potamophylax luctuosus</i> (Piller & Mitterpacher, 1783) | | 1 | 1 | 12 | 0 |
| Trichoptera | ODONTOCERIDAE | <i>Odontocerum albicorne</i> (Scopoli, 1763) | | 0 | 0 | 32 | 4 |
| Trichoptera | PHILOPOTAMIDAE | <i>Philopotamus ludificatus</i> (McLachlan, 1878) | | 0 | 0 | 60 | 16 |
| Trichoptera | PHILOPOTAMIDAE | <i>Philopotamus montanus</i> (Donovan, 1813) | | 7 | 0 | 1220 | 560 |
| Trichoptera | PHILOPOTAMIDAE | <i>Philopotamus variegatus</i> (Scopoli, 1763) | | 0 | 0 | 0 | 52 |

| Order | Family | Taxa | Life stage | pondside-abandoned | pondside-maintained | streamside-abandoned | streamside-maintained |
|---|-------------------|--|------------|--------------------|---------------------|----------------------|-----------------------|
| Trichoptera | PHILOPOTAMIDAE | <i>Wormaldia occipitalis</i> (Pictet, 1834) | | 12 | 0 | 2424 | 524 |
| Trichoptera | POLYCENTROPODIDAE | <i>Plectrocnemia conspersa</i> (Curtis, 1834) | | 6 | 0 | 156 | 28 |
| Trichoptera | PSYCHOMYIIDAE | <i>Lype reducta</i> (Hagen, 1868) | | 23 | 1 | 800 | 680 |
| Trichoptera | RHYACOPHILIDAE | <i>Rhyacophila sensu stricto</i> | | 0 | 0 | 104 | 108 |
| Trichoptera | SERICOSTOMATIDAE | <i>Oecismus monedula</i> (Hagen, 1859) | | 2 | 1 | 28 | 0 |
| Trichoptera | SERICOSTOMATIDAE | <i>Sericostoma flavicorne/personatum</i> | | 9 | 0 | 340 | 52 |
| Turbellaria | DUGESIIDAE | <i>Dugesia sp.</i> | | 91 | 4 | 2812 | 384 |
| Turbellaria | PLANARIIDAE | <i>Polycelis sp.</i> | | 118 | 6 | 5692 | 940 |
| Taxa that were only detected in one or two samples and therefore excluded from the data analysis | | | | | | | |
| Order | Family | Taxa | | pondside-abandoned | pondside-maintained | streamside-abandoned | streamside-maintained |
| Coleoptera | BYRRHIDAE | <i>Byrrhus sp.</i> | Lv. | 0 | 0 | 4 | 0 |
| Coleoptera | CANTHARIDAE | <i>Cantharis sp.</i> | Lv. | 0 | 0 | 4 | 0 |
| Coleoptera | CARABIDAE | <i>Acupalpus dubius</i> (Schilsky, 1888) | Ad. | 0 | 0 | 0 | 4 |
| Coleoptera | CARABIDAE | <i>Ocys tachysoides</i> (Antoine, 1933) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | CARABIDAE | <i>Bembidion guttata</i> (Fabricius, 1792) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | CHRYSOMELIDAE | <i>Phyllotreta tetrastigma</i> (Comolli, 1837) | Ad. | 0 | 0 | 8 | 0 |
| Coleoptera | CHRYSOMELIDAE | <i>Phaedon armoraciae</i> (Linnaeus, 1758) | Ad. | 0 | 0 | 8 | 0 |
| Coleoptera | CIIDAE | <i>Octotemnus glabriculus</i> (Gyllenhal, 1827) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | CURCULIONIDAE | <i>Strophosoma melanogrammum</i> (Forster, 1771) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | CURCULIONIDAE | <i>Datonychus melanostictus</i> (Marsham, 1802) | Ad. | 0 | 0 | 0 | 4 |
| Coleoptera | DYTISIDAE | <i>Agabus biguttatus</i> (Olivier, 1795) | Ad. | 0 | 0 | 0 | 4 |
| Coleoptera | DYTISIDAE | <i>Ilybius sp.</i> | Lv. | 0 | 0 | 0 | 4 |

| Order | Family | Taxa | Life stage | pondside-abandoned | pondside-maintained | streamside-abandoned | streamside-maintained |
|------------|---------------|--|------------|--------------------|---------------------|----------------------|-----------------------|
| Coleoptera | DYTISIDAE | <i>Hydroporus neglectus</i> (Schaum, 1845) | Ad. | 0 | 1 | 0 | 0 |
| Coleoptera | DYTISIDAE | <i>Stictotarsus duodecimpustulatus</i> (Fabricius, 1792) | Ad. | 1 | 0 | 0 | 0 |
| Coleoptera | DYTISIDAE | <i>Platambus maculatus</i> (Linnaeus, 1758) | Ad. | 0 | 0 | 0 | 4 |
| Coleoptera | ELATERIDAE | <i>Agriotes obscurus</i> Ad. (Linnaeus, 1758) | Ad. | 0 | 0 | 0 | 4 |
| Coleoptera | ELATERIDAE | <i>Agriotes</i> sp. | Lv. | 0 | 0 | 0 | 4 |
| Coleoptera | ELMIDAE | <i>Elmis aenea/mauguetii</i> | Lv. | 0 | 0 | 132 | 0 |
| Coleoptera | ELMIDAE | <i>Oulimnius tuberculatus</i> (Müller, 1806) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | ELMIDAE | <i>Esolus angustatus</i> (Müller, 1821) | Ad. | 0 | 0 | 4 | 4 |
| Coleoptera | HALIPLIDAE | <i>Haliphus ruficollis</i> (De Geer, 1774) | Ad. | 0 | 0 | 4 | 4 |
| Coleoptera | HYDRAENIDAE | <i>Limnebius truncatellus</i> (Thunberg, 1794) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | HYDRAENIDAE | <i>Hydraena assimilis</i> (Rey, 1885) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | HYDROCHIDAE | <i>Hydrochus angustatus</i> (Germar, 1823) | Ad. | 0 | 1 | 0 | 0 |
| Coleoptera | HYDROPHILIDAE | <i>Anacaena globulus</i> (Paykull, 1798) | Lv. | 0 | 0 | 8 | 0 |
| Coleoptera | HYDROPHILIDAE | <i>Cercyon analis</i> (Paykull, 1798) | Ad. | 0 | 0 | 0 | 4 |
| Coleoptera | HYDROPHILIDAE | <i>Cercyon ustulatus</i> (Preyssler, 1790) | Ad. | 0 | 0 | 4 | 4 |
| Coleoptera | HYDROPHILIDAE | <i>Hydrobius subrotundus</i> (Stephens, 1829) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | SCIRTIDAE | <i>Cyphon</i> sp. | Lv. | 0 | 0 | 4 | 0 |
| Coleoptera | SCOLITIDAE | <i>Xyleborus germanus</i> (Blandford, 1894) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Dianous coerulescens</i> (Gyllenhal, 1810) | Lv. | 0 | 0 | 4 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Lesteva longoelytrata</i> (Goeze, 1777) | Ad. | 0 | 0 | 4 | 0 |
| Coleoptera | STAPHYLINIDAE | <i>Gabrius appendiculatus</i> (Sharp, 1910) | Ad. | 0 | 0 | 4 | 0 |

| Order | Family | Taxa | Life stage | pondside-abandoned | pondside-maintained | streamside-abandoned | streamside-maintained |
|---------------|----------------|---|------------|--------------------|---------------------|----------------------|-----------------------|
| Coleoptera | STAPHYLINIDAE | <i>Stenus clavicornis</i> (Scopoli, 1763) | Ad. | 0 | 0 | 0 | 4 |
| Diptera | EMPIDIDAE | <i>Empididae Gen. sp.</i> | | 0 | 0 | 4 | 0 |
| Diptera | EPHYDRIDAE | <i>Hydrellia sp.</i> | | 0 | 0 | 0 | 4 |
| Diptera | FANNIIDAE | <i>Fannia sp.</i> | | 0 | 0 | 0 | 4 |
| Diptera | LIMONIIDAE | <i>Elliptera sp.</i> | | 0 | 0 | 4 | 4 |
| Diptera | LIMONIIDAE | <i>Limonia sp.</i> | | 0 | 0 | 0 | 8 |
| Diptera | LIMONIIDAE | <i>Phylidorea sp.</i> | | 0 | 0 | 4 | 4 |
| Diptera | LIMONIIDAE | <i>Scleroprocta sp.</i> | | 0 | 0 | 4 | 0 |
| Diptera | MUSCIDAE | <i>Coenosiinae Gen. sp.</i> | | 0 | 0 | 0 | 4 |
| Diptera | MUSCIDAE | <i>Muscidae Gen. sp.</i> | | 1 | 0 | 0 | 0 |
| Diptera | SCATOPHAGIDAE | <i>Scatophagidae Gen. sp.</i> | | 0 | 0 | 0 | 8 |
| Diptera | SIMULIIDAE | <i>Prosimulium rufipes</i> (Meigen, 1830) | pupae | 0 | 0 | 0 | 4 |
| Diptera | SIMULIIDAE | <i>Simulium monticola</i> (Friederichs, 1920) | pupae | 0 | 0 | 0 | 8 |
| Diptera | SIMULIIDAE | <i>Simulium variegatum</i> (Meigen, 1818) | pupae | 1 | 0 | 0 | 0 |
| Diptera | Stratiomyidae | <i>Stratiomyidae Gen. sp.</i> | | 1 | 0 | 0 | 0 |
| Diptera | SYRPHIDAE | <i>Melanogaster sp.</i> | | 0 | 0 | 0 | 4 |
| Diptera | SYRPHIDAE | <i>Syrphidae Gen. sp.</i> | | 0 | 0 | 4 | 8 |
| Diptera | TABANIDAE | <i>Haematopota sp.</i> | | 1 | 0 | 0 | 0 |
| Diptera | THAUMALEIDAE | <i>Androprosopa sp.</i> | | 0 | 0 | 0 | 4 |
| Diptera | THAUMALEIDAE | <i>Thaumaleidae Gen. sp.</i> | | 0 | 0 | 4 | 0 |
| Diptera | TIPULIDAE | <i>Tipula maxima-Gr.</i> | | 0 | 0 | 8 | 0 |
| Diptera | TIPULIDAE | <i>Tipula vittata</i> | | 0 | 1 | 0 | 0 |
| Diptera | TRICHO CERIDAE | <i>Trichoceridae sp.</i> | | 0 | 0 | 4 | 0 |
| Diptera | XYLOMYIDAE | <i>Xylomidae Gen. sp.</i> | | 0 | 0 | 0 | 4 |
| Ephemeroptera | BAETIDAE | <i>Baetis scambus</i> (Eaton, 1870) | | 0 | 1 | 0 | 0 |
| Ephemeroptera | BAETIDAE | <i>Baetis vernus</i> (Curtis, 1834) | | 0 | 0 | 0 | 12 |
| Ephemeroptera | BAETIDAE | <i>Cloeon dipterum</i> (Linnaeus, 1761) | | 0 | 5 | 0 | 0 |
| Ephemeroptera | CAENIDAE | <i>Caenis sp.</i> | | 1 | 0 | 0 | 0 |
| Ephemeroptera | HEPTAGENIIDAE | <i>Ecdyonurus torrentis</i> (Kimmins, 1942) | | 0 | 0 | 12 | 0 |
| Ephemeroptera | HEPTAGENIIDAE | <i>Epeorus assimilis</i> (Eaton, 1865) | | 0 | 0 | 4 | 0 |

| Order | Family | Taxa | Life stage | pondside- abandoned | pondside- maintained | streamside- abandoned | streamside- maintained |
|----------------|-------------------|--|------------|------------------------|-------------------------|--------------------------|---------------------------|
| Gastropoda | COCHLICOPIDAE | <i>Cochlicopa lubrica</i> (Müller, 1774) | | 0 | 0 | 0 | 12 |
| Heteroptera | GERRIDAE | <i>Gerridae Gen. sp.</i> | | 0 | 0 | 0 | 8 |
| Hirudinea | GLOSSIPHONIIDAE | <i>Glossiphonia complanata</i> (Linnaeus, 1758) | | 0 | 0 | 4 | 0 |
| Lepidoptera | PYRALIDAE | <i>Cataclysta lemnata</i> (Linnaeus, 1758) | | 0 | 0 | 8 | 0 |
| Odonata | AESHNIDAE | <i>Aeshna cyanea</i> (Müller, 1764) | | 0 | 1 | 0 | 0 |
| Odonata | COENAGRIONIDAE | <i>Pyrrhosoma nymphula</i> (Sulzer, 1776) | | 0 | 2 | 0 | 0 |
| Odonata | CALOPTERYGIDAE | <i>Calopteryx splendens</i> (Harris, 1780) | | 0 | 0 | 0 | 8 |
| Plecoptera | PERLIDAE | <i>Perla marginata</i> (Panzer, 1799) | | 0 | 0 | 4 | 4 |
| Plecoptera | TAENIOPTERYGIDAE | <i>Brachyptera risi</i> (Morton, 1896) | | 0 | 1 | 0 | 4 |
| Plecoptera | TAENIOPTERYGIDAE | <i>Brachyptera seticornis</i> (Klapálek, 1902) | | 0 | 0 | 0 | 12 |
| Trichoptera | BERAEIDAE | <i>Ernodes articularis</i> (Pictet, 1834) | | 0 | 0 | 0 | 4 |
| Trichoptera | GOERIDAE | <i>Silo pallipes</i> (Fabricius, 1781) | | 1 | 0 | 4 | 0 |
| Trichoptera | HYDROPSYCHIDAE | <i>Hydropsyche angustipennis</i> (Curtis, 1834) | | 0 | 0 | 0 | 4 |
| Trichoptera | LEPIDOSTOMATIDAE | <i>Crunoecia irrorata</i> (Curtis, 1834) | | 0 | 0 | 4 | 0 |
| Trichoptera | LIMNEPHILIDAE | <i>Anomalopterygella chauviniana</i> (Stein, 1874) | | 0 | 0 | 8 | 0 |
| Trichoptera | LIMNEPHILIDAE | <i>Hydatophylax infumatus</i> (McLachlan, 1865) | | 0 | 0 | 4 | 0 |
| Trichoptera | POLYCENTROPODIDAE | <i>Plectrocnemia geniculata</i> (McLachlan, 1871) | | 1 | 0 | 0 | 8 |
| Trichoptera | RHYACOPHILIDAE | <i>Rhyacophila laevis</i> (Pictet, 1834) | | 0 | 0 | 12 | 0 |
| Trichoptera | RHYACOPHILIDAE | <i>Rhyacophila tristis</i> (Pictet, 1834) | | 0 | 0 | 4 | 4 |
| Trichoptera | SERICOSTOMATIDAE | <i>Notidobia ciliaris</i> (Linnaeus, 1761) | | 0 | 0 | 0 | 4 |
| Trombidiformes | HYDRACHNOIDEA | <i>Hydrachnidia Gen. sp.</i> | | 0 | 0 | 0 | 4 |

Table S2: Tukey multiple comparison of means (95% family-wise confidence level) of all beaver dam sample combinations.

| Group | diff | lwr | upr | p adj |
|--|--------------|--------------|------------|-----------|
| Maintained-abandoned | 0.08743113 | 0.04876998 | 0.1260923 | 1.59e-05 |
| Streamside-pondside | -0.008883659 | -0.06780486 | 0.05003754 | 0.7660918 |
| pondside maintained-pondside abandoned | 0.06352212 | -0.08347600 | 0.21052024 | 0.6755627 |
| streamside abandoned-pondside abandoned | 0.00789604 | -0.10235255 | 0.11814463 | 0.9976980 |
| streamside maintained-pondside abandoned | 0.08450188 | -0.02584389 | 0.19484765 | 0.1962065 |
| streamside abandoned-pondside maintained | -0.05562608 | -0.16587467 | 0.05462251 | 0.5568600 |
| streamside maintained-pondside maintained | 0.02097976 | -0.08936601 | 0.13132553 | 0.9602208 |
| streamside maintained-streamside abandoned | 0.07660584 | 0.02442833 | 0.12878336 | 0.0011471 |
| middle-edge | 0.003777553 | -0.04356385 | 0.05111896 | 0.9804979 |
| top-edge | 0.012252993 | -0.06242331 | 0.08692930 | 0.9201490 |
| top-middle | 0.008475440 | -0.06608261 | 0.08303349 | 0.9608257 |
| edge maintained-edge abandoned | 0.08540932 | 0.003551984 | 0.16726665 | 0.0354136 |
| middle abandoned-edge abandoned | 0.02745508 | -0.053749996 | 0.10866015 | 0.9244408 |
| middle maintained-edge abandoned | 0.09788403 | 0.016678960 | 0.17908911 | 0.0085277 |
| top abandoned-edge abandoned | 0.00907602 | -0.119320476 | 0.13747252 | 0.9999500 |
| top maintained-edge abandoned | 0.07259814 | -0.055798357 | 0.20099464 | 0.5773953 |
| middle abandoned-edge maintained | -0.05795424 | -0.139811574 | 0.02390309 | 0.3219076 |
| middle maintained-edge maintained | 0.01247472 | -0.069382618 | 0.09433205 | 0.9978643 |
| top abandoned-edge maintained | -0.07633330 | -0.205143311 | 0.05247671 | 0.5257024 |
| top maintained-edge maintained | -0.01281118 | -0.141621191 | 0.11599883 | 0.9997306 |
| middle maintained-middle abandoned | 0.07042896 | -0.010776119 | 0.15163403 | 0.1292837 |
| top abandoned-middle abandoned | -0.01837906 | -0.146775555 | 0.11001744 | 0.9984182 |
| top maintained-middle abandoned | 0.04514306 | -0.083253435 | 0.17353956 | 0.9118216 |
| top abandoned-middle maintained | -0.08880801 | -0.217204511 | 0.03958848 | 0.3481381 |
| top maintained-middle maintained | -0.02528589 | -0.153682391 | 0.10311060 | 0.9928473 |
| top maintained-top abandoned | 0.06352212 | -0.098888029 | 0.22593227 | 0.8678776 |
| Middle-base | -0.009878117 | -0.05778497 | 0.03802873 | 0.8769108 |
| Top-base | 0.006167929 | -0.06928064 | 0.08161650 | 0.9795402 |
| Top-middle | 0.016046047 | -0.05952219 | 0.09161428 | 0.8699822 |
| abandoned crown-abandoned base | -0.018052730 | -0.147950211 | 0.11184475 | 0.9986277 |
| abandoned middle-abandoned base | -0.027645516 | -0.109799896 | 0.05450886 | 0.925846 |
| maintained base-abandoned base | 0.071176642 | -0.010977738 | 0.15333102 | 0.1300633 |
| maintained crown-abandoned base | 0.045469389 | -0.084428091 | 0.17536687 | 0.9133331 |
| maintained middle-abandoned base | 0.056650783 | -0.026163482 | 0.13946505 | 0.3607123 |
| abandoned middle-abandoned crown | -0.009592786 | -0.139490266 | 0.12030469 | 0.9999379 |
| maintained base-abandoned crown | 0.089229372 | -0.040668108 | 0.21912685 | 0.3559690 |
| maintained crown-abandoned crown | 0.063522120 | -0.100786641 | 0.22783088 | 0.8734236 |
| maintained middle-abandoned crown | 0.074703513 | -0.055612318 | 0.20501934 | 0.5624896 |
| maintained base-abandoned middle | 0.098822158 | 0.016667778 | 0.18097654 | 0.0087313 |
| maintained crown-abandoned middle | 0.073114905 | -0.056782575 | 0.20301239 | 0.5822585 |
| maintained middle-abandoned middle | 0.084296299 | 0.001482034 | 0.16711056 | 0.0434553 |
| maintained crown-maintained base | -0.025707253 | -0.155604733 | 0.10419023 | 0.9926829 |
| maintained middle-maintained base | -0.014525859 | -0.097340124 | 0.06828841 | 0.9958372 |
| maintained middle-maintained crown | 0.011181394 | -0.119134437 | 0.14149722 | 0.9998697 |

Table S3: Feeding types and water velocity preferences of the taxa relevant for analysis. Information about aquatic taxa compiled by Schmidt-Kloiber & Hering (2015), we added feeding types for terrestrial/semiaquatic taxa according to additional literature (Gepp, 2003; Speiser, 2001; van Stuivenberg, 1997). For each taxon, 10 points are distributed between feeding types corresponding to the taxon's preferred diet, same method as the online tool "Perlodes-Online"

| Order | Taxa | Water Velocity Preference | Shredders | Gatherers | Grazers | Active Filter Feeders | Passive Filter Feeders | Predators | Others |
|------------|---|---------------------------|-----------|-----------|---------|-----------------------|------------------------|-----------|--------|
| Bivalvia | <i>Pisidium sp.</i> | Indifferent | 0 | 0 | 0 | 10 | 0 | 0 | 0 |
| Coleoptera | <i>Dryops luridus</i> Ad. (Erichson, 1847) | Limnophile | 0 | 2 | 8 | 0 | 0 | 0 | 0 |
| Coleoptera | <i>Dryops sp.</i> Lv. | Limnophile | 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| Coleoptera | <i>Agabus paludosus</i> Ad. (Fabricius, 1801) | Rheo-Limnophile | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Coleoptera | <i>Elmis sp.</i> Lv. | Rheophile | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| Coleoptera | <i>Elmis aenea</i> Ad. (Müller, 1806) | Rheophile | 0 | 1 | 9 | 0 | 0 | 0 | 0 |
| Coleoptera | <i>Elmis maugetii</i> Ad. (Latreille, 1802) | Rheophile | 0 | 1 | 9 | 0 | 0 | 0 | 0 |
| Coleoptera | <i>Limnius volckmari</i> Ad. (Panzer, 1793) | Rheophile | 1 | 1 | 8 | 0 | 0 | 0 | 0 |
| Coleoptera | <i>Limnius volckmari</i> Lv. (Panzer, 1793) | Rheophile | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| Coleoptera | <i>Orectochilus villosus</i> Lv. (Müller, 1776) | Rheophile | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Coleoptera | <i>Haliphus sp.</i> Lv. | Limnobiont | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| Coleoptera | <i>Hydraena gracilis</i> Ad. (Germar, 1823) | Rheophile | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| Coleoptera | <i>Hydraena pygmaea</i> Ad. (Waterhouse, 1833) | Rheobiont | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| Coleoptera | <i>Anacaena globulus</i> Ad. (Paykull, 1798) | Rheo-Limnophile | 2 | 3 | 3 | 0 | 0 | 2 | 0 |
| Coleoptera | <i>Laccobius minutus</i> Ad. (Linnaeus, 1758) | Limno-Rheophile | 1 | 3 | 3 | 0 | 0 | 3 | 0 |
| Coleoptera | <i>Elodes sp.</i> Lv. | Rheophile | 2 | 5 | 2 | 0 | 0 | 1 | 0 |
| Coleoptera | <i>Dianous coeruleus</i> Ad. (Gyllenhal, 1810) | Terrestrial/Semiaquatic | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Coleoptera | <i>Lesteva pubescens</i> Ad. (Mannerheim, 1830) | Terrestrial/Semiaquatic | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| Crustacea | <i>Asellus aquaticus</i> (Linnaeus, 1758) | Indifferent | 3 | 4 | 3 | 0 | 0 | 0 | 0 |
| Crustacea | <i>Gammarus fossarum</i> (Koch, 1836) | Rheophile | 7 | 2 | 1 | 0 | 0 | 0 | 0 |

| Order | Taxa | Water Velocity Preference | Shredders | Gatherers | Grazers | Active Filter Feeders | Passive Filter Feeders | Predators | Others |
|---------------|---|---------------------------|-----------|-----------|---------|-----------------------|------------------------|-----------|--------|
| Diptera | <i>Ceratopogoninae Gen. sp.</i> | Indifferent | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Diptera | <i>Chironomidae Gen. sp.</i> | Indifferent | 0 | 3 | 2 | 2 | 0 | 1 | 2 |
| Diptera | <i>Prodiamesa olivacea</i> (Meigen, 1818) | Rheo-Limnophile | 0 | 7 | 0 | 3 | 0 | 0 | 0 |
| Diptera | <i>Tanypodinae Gen. sp.</i> | Indifferent | 0 | 6 | 0 | 0 | 0 | 4 | 0 |
| Diptera | <i>Tanytarsini Gen. sp.</i> | Indifferent | 0 | 3 | 2 | 2 | 0 | 1 | 2 |
| Diptera | <i>Dixa sp.</i> | Rheo-Limnophile | 0 | 3 | 0 | 7 | 0 | 0 | 0 |
| Diptera | <i>Clinocerinae Gen. sp.</i> | Rheophile | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Diptera | <i>Hemerodromia sp.</i> | Rheophile | 0 | 5 | 0 | 0 | 0 | 5 | 0 |
| Diptera | <i>Austrolimnophila sp.</i> | Indifferent | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Dicranomyia sp.</i> | Indifferent | 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Eloeophila sp.</i> | Rheo-Limnophile | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Heliopsis sp.</i> | Terrestrial/Semiaquatic | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Lipsothrix sp.</i> | Indifferent | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| Diptera | <i>Molophilus sp.</i> | Rheo-Limnophile | 7 | 3 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Neolimnomyia sp.</i> | Terrestrial/Semiaquatic | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Pilaria sp.</i> | Indifferent | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Pseudolimnophila sp.</i> | Limnophile | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Rhypholophus sp.</i> | Indifferent | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Thaumastopectera calceata</i> (Mik, 1866) | Terrestrial/Semiaquatic | 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Muscidae Gen. sp.</i> | Terrestrial/Semiaquatic | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Diptera | <i>Dicranota sp.</i> | Rheo-Limnophile | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Diptera | <i>Bazarella/Berdeniella sp.</i> | Indifferent | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| Diptera | <i>Ptychoptera sp.</i> | Rheo-Limnophile | 5 | 5 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Rhagionidae Gen. sp.</i> | Terrestrial/Semiaquatic | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Diptera | <i>Prosimulium sp.</i> | Rheobiont | 0 | 0 | 1 | 0 | 9 | 0 | 0 |
| Diptera | <i>Prosimulium tomosvaryi</i> (Enderlein, 1921) | Rheophile | 0 | 0 | 1 | 0 | 9 | 0 | 0 |
| Diptera | <i>Simulium morsitans</i> (Edwards, 1915) | Rheophile | 0 | 0 | 0 | 0 | 10 | 0 | 0 |
| Diptera | <i>Simulium sp.</i> | Rheophile | 0 | 0 | 0 | 0 | 10 | 0 | 0 |
| Diptera | <i>Simulium vernum Gr.</i> | Rheophile | 0 | 0 | 0 | 0 | 10 | 0 | 0 |
| Diptera | <i>Tabanidae Gen. sp.</i> | Limnophile | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Diptera | <i>Tipula sp.</i> | Limnophile | 6 | 4 | 0 | 0 | 0 | 0 | 0 |
| Diptera | <i>Mycetobia sp.</i> | Terrestrial/Semiaquatic | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| Ephemeroptera | <i>Baetis sp.</i> | Rheophile | 0 | 5 | 5 | 0 | 0 | 0 | 0 |

| Order | Taxa | Water Velocity Preference | Shredders | Gatherers | Grazers | Active Filter Feeders | Passive Filter Feeders | Predators | Others |
|---------------|--|---------------------------|-----------|-----------|---------|-----------------------|------------------------|-----------|--------|
| Ephemeroptera | <i>Baetis buceratus</i> (Eaton, 1870) | Rheophile | 0 | 5 | 5 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Baetis fuscatus</i> (Linnaeus, 1761) | Rheophile | 0 | 5 | 5 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Baetis muticus</i> (Linnaeus, 1758) | Rheophile | 0 | 5 | 5 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Baetis niger</i> (Linnaeus, 1761) | Rheophile | 0 | 5 | 5 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Baetis rhodani</i> (Pictet, 1843) | Rheophile | 0 | 5 | 5 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Centroptilum luteolum</i> (Müller, 1776) | Rheo-Limnophile | 0 | 3 | 7 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Ephemera danica</i> (Müller, 1764) | Rheophile | 0 | 3 | 0 | 7 | 0 | 0 | 0 |
| Ephemeroptera | <i>Ecdyonurus venosus</i> Gr. | Rheobiont | 0 | 5 | 5 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Rhithrogena</i> <i>semicolorata</i> Gr. | Rheobiont | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Habroleptoides confusa</i> (Sartori & Jacob, 1986) | Rheophile | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Habrophlebia lauta</i> (Eaton, 1884) | Rheo-Limnophile | 0 | 8 | 2 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Leptophlebia marginata</i> (Linnaeus, 1767) | Limno-Rheophile | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Ephemeroptera | <i>Paraleptophlebia</i> <i>submarginata</i> (Stephens, 1835) | Rheophile | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda | <i>Euconulus fulvus</i> (Müller, 1774) | Terrestrial/Semiaquatic | 3 | 2 | 3 | 0 | 0 | 0 | 2 |
| Gastropoda | <i>Trochulus sp.</i> | Terrestrial/Semiaquatic | 3 | 2 | 3 | 0 | 0 | 0 | 2 |
| Gastropoda | <i>Galba truncatula</i> (Müller, 1774) | Limno-Rheophile | 3 | 2 | 3 | 0 | 0 | 0 | 2 |
| Gastropoda | <i>Radix balthica</i> (Linnaeus, 1758) | Indifferent | 2 | 3 | 3 | 0 | 0 | 0 | 2 |
| Gastropoda | <i>Oxychilidae sp.</i> | Terrestrial/Semiaquatic | 3 | 2 | 3 | 0 | 0 | 0 | 2 |
| Gastropoda | <i>Discus perspectivus</i> (Megerle von Mühlfeld, 1816) | Terrestrial/Semiaquatic | 3 | 2 | 3 | 0 | 0 | 0 | 2 |
| Gastropoda | <i>Physa fontinalis</i> (Linnaeus, 1758) | Limno-Rheophile | 2 | 0 | 6 | 0 | 0 | 0 | 2 |

| Order | Taxa | Water Velocity Preference | Shredders | Gatherers | Grazers | Active Filter Feeders | Passive Filter Feeders | Predators | Others |
|-------------|---|---------------------------|-----------|-----------|---------|-----------------------|------------------------|-----------|--------|
| Gastropoda | <i>Ancylus fluviatilis</i> (Müller, 1774) | Rheobiont | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| Gastropoda | <i>Gyraulus</i> sp. | Limno-Rheophile | 2 | 0 | 6 | 0 | 0 | 0 | 2 |
| Gastropoda | <i>Vitrea</i> sp. | Terrestrial/Semiaquatic | 3 | 2 | 3 | 0 | 0 | 0 | 2 |
| Gastropoda | <i>Vertigo antivertigo</i> (Draparnaud, 1801) | Terrestrial/Semiaquatic | 3 | 2 | 3 | 0 | 0 | 0 | 2 |
| Heteroptera | <i>Nepa cinerea</i> (Linnaeus, 1758) | Limno-Rheophile | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Megaloptera | <i>Sialis</i> sp. | Rheo-Limnophile | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Neuroptera | <i>Osmylus fulvicephalus</i> Lv. (Scopoli, 1763) | Terrestrial/Semiaquatic | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Odonata | <i>Calopteryx virgo</i> (Linnaeus, 1758) | Rheophile | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Odonata | <i>Cordulegaster boltonii</i> (Donovan, 1807) | Rheobiont | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Oligochaeta | <i>Naididae Tubificidae</i> Gen. sp. | Terrestrial/Semiaquatic | 0 | 8 | 2 | 0 | 0 | 0 | 0 |
| Oligochaeta | <i>Eiseniella tetraedra</i> (Savigny, 1826) | Indifferent | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Oligochaeta | <i>Stylodrilus heringianus</i> (Claparède, 1862) | Rheo-Limnophile | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Oligochaeta | <i>Lumbriculidae</i> Gen. sp. | Terrestrial/Semiaquatic | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| Plecoptera | <i>Isoperla</i> sp. | Rheophile | 1 | 1 | 1 | 0 | 0 | 7 | 0 |
| Plecoptera | <i>Siphonoperla</i> sp. | Rheophile | 1 | 2 | 1 | 0 | 0 | 6 | 0 |
| Plecoptera | <i>Leuctra nigra</i> (Olivier, 1811) | Rheophile | 3 | 4 | 3 | 0 | 0 | 0 | 0 |
| Plecoptera | <i>Leuctra</i> sp. | Rheophile | 3 | 4 | 3 | 0 | 0 | 0 | 0 |
| Plecoptera | <i>Nemoura</i> sp. | Rheophile | 7 | 3 | 0 | 0 | 0 | 0 | 0 |
| Plecoptera | <i>Protonemura</i> sp. | Rheophile | 5 | 2 | 3 | 0 | 0 | 0 | 0 |
| Trichoptera | <i>Beraea maurus</i> (Curtis, 1834) | Rheophile | 7 | 0 | 3 | 0 | 0 | 0 | 0 |
| Trichoptera | <i>Beraea pullata</i> (Curtis, 1834) | Rheo-Limnophile | 2 | 6 | 2 | 0 | 0 | 0 | 0 |
| Trichoptera | <i>Beraeodes minutus</i> (Linnaeus, 1761) | Rheo-Limnophile | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| Trichoptera | <i>Agapetus fuscipes</i> (Curtis, 1834) | Rheophile | 0 | 2 | 8 | 0 | 0 | 0 | 0 |
| Trichoptera | <i>Diplectrona felix</i> (McLachlan, 1878) | Rheophile | 0 | 0 | 2 | 0 | 5 | 3 | 0 |

| Order | Taxa | Water Velocity Preference | Shredders | Gatherers | Grazers | Active Filter Feeders | Passive Filter Feeders | Predators | Others |
|-------------|---|---------------------------|-----------|-----------|---------|-----------------------|------------------------|-----------|--------|
| Trichoptera | <i>Hydropsyche dinarica</i> (Marinkovic-Gospodnetic, 1979) | Rheophile | 0 | 0 | 2 | 0 | 5 | 3 | 0 |
| Trichoptera | <i>Hydropsyche fulvipes</i> (Curtis, 1834) | Rheobiont | 0 | 0 | 2 | 0 | 5 | 3 | 0 |
| Trichoptera | <i>Hydropsyche instabilis</i> (Curtis, 1834) | Rheobiont | 0 | 0 | 2 | 0 | 5 | 3 | 0 |
| Trichoptera | <i>Hydropsyche saxonica</i> (McLachlan, 1884) | Rheophile | 0 | 0 | 2 | 0 | 5 | 3 | 0 |
| Trichoptera | <i>Hydropsyche siltalai</i> (Doehler, 1963) | Rheobiont | 0 | 0 | 2 | 0 | 5 | 3 | 0 |
| Trichoptera | <i>Hydropsyche sp.</i> | Rheophile | 0 | 0 | 2 | 0 | 5 | 3 | 0 |
| Trichoptera | <i>Lepidostoma basale</i> (Kolenati, 1848) | Rheophile | 2 | 0 | 5 | 0 | 0 | 0 | 3 |
| Trichoptera | <i>Adicella reducta</i> (McLachlan, 1865) | Indifferent | 8 | 0 | 2 | 0 | 0 | 0 | 0 |
| Trichoptera | <i>Chaetopteryx villosa</i> (Fabricius, 1798) | Rheo-Limnophile | 4 | 2 | 3 | 0 | 0 | 0 | 0 |
| Trichoptera | <i>Chaetopteryx major</i> (McLachlan, 1876) | Rheophile | 6 | 0 | 2 | 0 | 0 | 2 | 0 |
| Trichoptera | <i>Drusus annulatus</i> (Stephens, 1837) | Rheobiont | 1 | 1 | 8 | 0 | 0 | 0 | 0 |
| Trichoptera | <i>Glyphotaenius pellucidus</i> (Retzius, 1783) | Limnophile | 6 | 0 | 1 | 0 | 0 | 3 | 0 |
| Trichoptera | <i>Halesus digitatus/tesselatus</i> | Limno-Rheophile | 7 | 0 | 1 | 0 | 0 | 2 | 0 |
| Trichoptera | <i>Halesus radiatus</i> (Curtis, 1834) | Rheo-Limnophile | 7 | 0 | 1 | 0 | 0 | 2 | 0 |
| Trichoptera | <i>Chaetopterygini/Stenop hylacini Gen. sp.</i> | Indifferent | 7 | 0 | 1 | 0 | 0 | 2 | 0 |
| Trichoptera | <i>Limnephilini Gen. sp.</i> | Indifferent | 5 | 1 | 2 | 0 | 0 | 2 | 0 |
| Trichoptera | <i>Limnephilus lunatus</i> (Curtis, 1834) | Limno-Rheophile | 5 | 0 | 2 | 0 | 0 | 3 | 0 |
| Trichoptera | <i>Limnephilus rhombicus</i> (Linnaeus, 1758) | Limno-Rheophile | 5 | 0 | 2 | 0 | 0 | 3 | 0 |
| Trichoptera | <i>Potamophylax cingulatus</i> (Stephens, 1837) | Rheophile | 6 | 0 | 2 | 0 | 0 | 2 | 0 |

| Order | Taxa | Water Velocity Preference | Shredders | Gatherers | Grazers | Active Filter Feeders | Passive Filter Feeders | Predators | Others |
|-------------|---|---------------------------|-----------|-----------|---------|-----------------------|------------------------|-----------|--------|
| Trichoptera | <i>Potamophylax latipennis</i> (Curtis, 1834) | Rheo-Limnophile | 6 | 0 | 2 | 0 | 0 | 2 | 0 |
| Trichoptera | <i>Potamophylax luctuosus</i> (Piller & Mitterpacher, 1783) | Rheo-Limnophile | 6 | 0 | 2 | 0 | 0 | 2 | 0 |
| Trichoptera | <i>Odontocerum albicorne</i> (Scopoli, 1763) | Rheophile | 3 | 0 | 3 | 0 | 0 | 4 | 0 |
| Trichoptera | <i>Philopotamus ludificatus</i> (McLachlan, 1878) | Rheobiont | 0 | 0 | 0 | 0 | 10 | 0 | 0 |
| Trichoptera | <i>Philopotamus montanus</i> (Donovan, 1813) | Rheobiont | 0 | 0 | 0 | 0 | 10 | 0 | 0 |
| Trichoptera | <i>Philopotamus variegatus</i> (Scopoli, 1763) | Limno-Rheophile | 0 | 0 | 0 | 0 | 10 | 0 | 0 |
| Trichoptera | <i>Wormaldia occipitalis</i> (Pictet, 1834) | Rheophile | 0 | 0 | 0 | 0 | 10 | 0 | 0 |
| Trichoptera | <i>Plectrocnemia conspersa</i> (Curtis, 1834) | Rheophile | 0 | 0 | 0 | 0 | 1 | 9 | 0 |
| Trichoptera | <i>Lype reducta</i> (Hagen, 1868) | Rheophile | 0 | 0 | 8 | 0 | 0 | 0 | 2 |
| Trichoptera | <i>Rhyacophila sensu stricto</i> | Rheophile-Rheobiont | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Trichoptera | <i>Oecismus monedula</i> (Hagen, 1859) | Rheophile | 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| Trichoptera | <i>Sericostoma flavicorne/personatum</i> | Limno-Rheophile | 9 | 0 | 0 | 0 | 0 | 1 | 0 |
| Turbellaria | <i>Dugesia sp.</i> | Indifferent | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Turbellaria | <i>Polycelis sp.</i> | Indifferent | 0 | 0 | 0 | 0 | 0 | 10 | 0 |

Table S4 Indicator taxa of the pondside and streamside of abandoned and maintained dams, as identified with the IndVAL-Index (%) (Dufrêne & Legendre, 1997). In addition, value A-Specificity (taxon occurrence within the different dam categories) and value B-Fidelity (taxon occurrence within a specific dam category). The p-value shows significance of a taxon association with a dam category, * = 0.05; ** = 0.01; *** = 0.001

| pondside-abandoned | | | | |
|--|----------------------|-------------------|---------------------|----------------|
| Taxa | A-Specificity | B-Fidelity | IndVal-Index | p value |
| <i>Potamophylax cingulatus</i> | 0.67 | 1.00 | 82% | 0.001 *** |
| <i>Chaetopterygini/Stenophylacini</i> Gen. sp. | 0.57 | 1.00 | 76% | 0.003 ** |
| <i>Habrophlebia lauta</i> | 0.86 | 0.25 | 47% | 0.008 ** |
| <i>Sialis</i> sp. | 0.56 | 0.38 | 46% | 0.044 * |
| pondside-maintained | | | | |
| <i>Baetis rhodani</i> | 0.67 | 1.00 | 82% | 0.002 ** |
| <i>Limnephilini</i> Gen. sp. | 0.63 | 0.88 | 74% | 0.009 ** |
| <i>Nemoura</i> sp. | 0.53 | 1.00 | 73% | 0.007 ** |
| <i>Halesus radiatus</i> | 0.60 | 0.88 | 73% | 0.023 * |
| <i>Halesus digitatus/tesselatus</i> | 0.64 | 0.75 | 70% | 0.009 ** |
| <i>Limnephilus lunatus</i> | 0.96 | 0.50 | 69% | 0.001 *** |
| <i>Radix balthica</i> | 0.54 | 0.63 | 58% | 0.022 * |
| <i>Physa fontinalis</i> | 0.87 | 0.25 | 47% | 0.031 * |
| <i>Eloeophila</i> sp. | 0.57 | 0.38 | 46% | 0.043 * |
| streamside-abandoned | | | | |
| <i>Paraleptophlebia submarginata</i> | 0.64 | 0.67 | 65% | 0.036 * |
| <i>Dianous coerulescens</i> Ad. | 0.60 | 0.73 | 67% | 0.007 ** |
| <i>Philopotamus montanus</i> | 0.61 | 0.77 | 68% | 0.010 ** |
| <i>Wormaldia occipitalis</i> | 0.73 | 0.83 | 78% | 0.001 *** |
| <i>Lumbriculidae</i> Gen. sp. | 0.47 | 0.88 | 64% | 0.026 * |
| <i>Lipsothrix</i> sp. | 0.60 | 0.53 | 57% | 0.050 * |
| streamside-maintained | | | | |
| <i>Prosimulium</i> sp. | 0.72 | 0.83 | 77% | 0.004 ** |
| <i>Simulium</i> sp. | 0.56 | 0.86 | 70% | 0.011 * |
| <i>Hydropsyche saxonica</i> | 0.87 | 0.27 | 49% | 0.034 * |

4 General discussion

4.1 Summary

With the aim of exploring changes in the aquatic ecosystem due to beaver activities, I investigated three streams in the low mountain range and thoroughly examined them over a period of two years. For each stream, a 200 m section within a beaver territory and an equally long section without beaver influence (non-beaver territory), at least 200 m upstream, were considered. Thus, data from six stream sections were included in the analysis. Aerial drone images were captured for each stream section, and transect mapping were concluded (10 transects with 100 measurement points per section). Through the mapping, environmental variables such as water depth, flow velocity, and substrate types were systematically recorded. Additionally, I investigated habitat-specific macrozoobenthos species using Surber samplers or the beaver dam suction device developed for the study. In the first chapter, I addressed the question of the type and availability of aquatic habitats and their environmental conditions. Subsequently, the second chapter examined which macrozoobenthos community colonize habitats created by beavers and how these communities differ in terms of species richness, abundance and flow preferences from those in non-beaver territories. In the final chapter, I placed a special focus on beaver dams, attributing them a unique position in the aquatic ecosystem due to their hydraulic properties and diverse habitat offerings.

The results of this dissertation partly confirm findings from previous studies, for example, the reconnection of the aquatic ecosystem with the terrestrial through beaver activities. The transferability of these results indicates that certain mechanisms and effects resulting from beaver activities are transferable regardless of local environmental conditions. Thus, these results contribute to a better understanding and therefore predictability of the effects of beaver engineering. Further results represent completely new findings and thus expand our knowledge of habitat formation and its colonization by macrozoobenthos due to beaver activity. In the following, I will point out for each chapter, what these new data indicate for the overarching research question.

4.2 Implications of the results

In my comprehensive investigation, the first chapter sheds light on the remarkable influence of beaver activities on aquatic ecosystems. The research reveals that beaver not only significantly increase wetted surface areas (six-fold), but also create a diverse complex of lentic, lotic and semi-aquatic habitats. To address the former aspect, my results confirm and expand upon previous research by demonstrating that water retention by beaver dams depend highly on the

topography (Johnston and Naiman 1987). In comparison with dam-induced water retention in flat terrain like in the study of Kaphegyi and Christoffers (2014), the average pond size was 339 times greater than in the higher altitudes of the northern Eifel. Other factors, such as the type of soil, certainly contribute to this, but we are still lacking specific studies on this topic. The creation of habitats with different flow patterns due to beaver activity has been mentioned in previous studies, but never been quantified. Thus, this study represents a major contribution in this field, and the results provide new insights into the hydrology and hydraulics of beaver territories. My findings show that the area of lotic habitats due to beaver activity has not decreased, but that the proportion of lentic and semi-aquatic areas is increasing. Although beaver dams create ponds, which have received the most attention so far, I could not determine any displacement of lotic habitats in my study area. What I can demonstrate is the transition from a homogeneously fast-flowing stream to a watercourse with very heterogeneous flow patterns due to beaver engineering. Harthun (1998) describes similar findings in his study, also conducted in higher altitudes. Additional studies must clarify whether these effects are only transferable to low mountain ranges or also apply in the lowland. Further results of my study emphasize the crucial role of beavers in enhancing the connectivity of stream-floodplain complexes, by lengthening shorelines and reducing incision depth. The ways beaver lengthening the shoreline are various (Hood and Larson 2015) and impressively enhancing biodiversity (Hood and Larson 2014; Anderson et al. 2015). An extended shoreline is a spatial feature which is accompanied by an increase in the water surface area and the trophic connectivity between the aquatic and terrestrial environment (Iwata et al. 2003). Studies by Iwata et al. (2003) and Power and Rainey (2000) show that both factors are associated with an increase in the abundance and distribution of aquatic insects. My results show that the increased water level due to beaver dams also leads to further connection of the aquatic and terrestrial habitats. These effects confirm previous studies on stream ecology and restoration by beaver dams (Fedyń et al. 2022; Munir and Westbrook 2021; Pollock et al. 2014). The presence of deadwood, riparian vegetation, and various substrates within beaver territories further elevates habitat complexity and diversity, underscoring the positive ecological effects. The results represent an extension of our previous understanding of microhabitats in beaver territories and reveal that the number and diversity of habitat complexes created by beavers is much higher than in stream sections without beavers.

Building on this foundation, the second chapter explores how beaver activities have the potential to reshape benthic communities in the aquatic ecosystem. In contrast to most studies that indicate a displacement of stream taxa by pond taxa (Naiman et al. 1988; Bush and

Wissinger 2016), my results indicates that this depends on the habitats compared. Thereby, community composition showed greater similarity between habitat types with similar flow patterns, such as beaver ponds and pools in non-beaver territories as well as side channels and riffles. The expansion of lentic habitats (beaver ponds), as well as the establishment of side channels and the construction of dams as lotic environments must be viewed as one habitat-complex as a result of beaver activities. Furthermore, my results show a higher taxonomical richness in beaver territories, which is in contrast to other results indicating a lower richness at beaver sites (Law et al. 2016). The different findings are based on the study design and show once again that the focus on beaver ponds without the inclusion of other habitats, leads to completely different results and thus different, and less accurate, conclusions are drawn. An increase of abundance of macrozoobenthos due to beaver activities is usually the case (Bush and Wissinger 2016). Beaver ponds are regarded as hotspots of abundance, but when other beaver created habitats are taken into account, the results are often different. This is also demonstrated in the study of Rolauuffs et al. (2001), where the dams had the highest invertebrate abundance. However, in my study macrozoobenthos abundance were highest in the side channels of beaver territories, which were only investigated once before (Harthun 1998).

Expanding our understanding, the final chapter delves into the varied environmental conditions and habitat types provided by beaver dams. Based on the study design and the sampled technique used, this study represents the most detailed survey of macrozoobenthos in beaver dams so far. Most of the results therefore contribute to new insights into the macrozoobenthos colonization of this fascinating habitat. Within a confined area, beaver dams create microhabitats catering to species with diverse flow preferences and feeding types, ranging from lentic to lotic and even semi-aquatic situations. Importantly, my results highlight the distinct succession of beaver dams, especially when abandoned, further enhancing the variability of habitat types. Overlooking the fauna of beaver dams leads to an underestimation of the impact of beaver activities on biodiversity. Dams emerge as a crucial component of the habitats created by beavers, significantly increasing invertebrate diversity in streams and adjacent floodplains. Recognizing the comprehensive range of habitats shaped by beaver activities becomes pivotal for effective biodiversity conservation and habitat management.

4.3 Outlook

The results of my study demonstrate that emphasizing specific habitats, like beaver ponds, may yield incomplete or inaccurate conclusions, potentially leading to insufficient assessment and underestimation of beaver engineering and its conservation potential. By reintroducing features

reminiscent of natural stream ecosystems absent from contemporary European streams, beavers play a vital role in restoring and maintaining the ecological integrity of small streams, aligning them more closely with their “potentially natural state”. In this context, further research questions arise, such as the impact of beaver activities on entire catchment areas. What is the situation in other types of water courses; are the changes I have discovered transferable to lowland streams? Furthermore, the streams I studied are in near-natural state, what are the effects of beaver engineering in non-natural streams? The expansion of the beaver in Europe is creating opportunities for biotope and species protection, but also major challenges due the high land requirements of humans. The extent to which we can exploit the benefits of beaver engineering depends on further investigations and how future coexistence will be organized.

Acknowledgements

I am immensely grateful to Daniel Hering, my supervisor, who has been the cornerstone of this study. His guidance and contributions throughout my thesis, have been invaluable throughout this journey and has challenge and encourage me as a scientist. Daniel's appreciation for ideas, his patience and ability to communicate at eye level, and his own stunning and contagious passion for nature and science have inspired me every step of the way. His support helped me navigate through challenges and kept me motivated.

I extend my heartfelt appreciation to Armin Lorenz for his support and encouragement feedback, especially with the study design, my taxonomical education, and the fun and experience he brings to fieldwork. His guidance has been instrumental in shaping this research. Peter Rolauffs deserves special thanks for his expertise in my taxonomical education of Ephemeroptera, which significantly contributed to the quality of this study.

Wim Kaijser deserves sincere gratitude for his support with data analysis and for sharing his contagious passion for statistics and science in general. His enthusiasm has been a driving force behind the analytical aspects of this work.

I am indebted to Felix Dacheneder for his expertise in aerial photography by drone and his support in processing the data, which added a unique dimension to this research.

I am also grateful to the many helping hands in the field and the constructive discussions with Paul Mausbach, Katharina Hund, and Svenja Pfeiffer. Their contributions and insights have enriched this study.

I am fortunate to be part of an exceptional working group passionate about limnology. Their helpfulness, appreciation, and passion have fostered a collaborative and supportive environment.

Lutz Dalbeck deserves recognition and my heartfelt appreciation for his support since my diploma thesis. Lutz is always an incentive to maintaining curiosity, passion, and commitment for wildlife, especially for beavers.

I am deeply thankful to my mentor and friend Glynnis Hood. Her worldwide known scientific work and passion for beavers and wildlife, in general, have been the initial inspiration for my journey further into research. Every time we meet, I experience great interest, recognition and motivation from Glynnis, which has often picked me up and helped me to advance this study.

Lastly, I would like to express my heartfelt gratitude to my family and friends, especially my partner Nicolaus Seefeld, for their love, understanding, and patience throughout this journey. I am infinitely thankful for Nicolaus unwavering support which sustained me during challenging times.

References

- Andersen, D. C. & P. B. Shafroth, 2010. Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona. *Ecohydrology* 3: 325–338. <https://doi.org/10.1002/eco.113>
- Anderson, N. L.; Paszkowski, C. A.; Hood, G. A. (2015): Linking aquatic and terrestrial environments: can beaver canals serve as movement corridors for pond-breeding amphibians? In *Anim Conserv* 18 (3), pp. 287–294. DOI: 10.1111/acv.12170.
- Arndt, E. and Domdei, J. (2011). Influence of beaver ponds on the macroinvertebrate benthic community in lowland brooks. *Polish Journal of Ecology*, 59(4), 799–811
- Arens, W., 1990. Wear and tear of mouthparts: a critical problem in stream animals feeding on epilithic algae. *Canadian Journal of Zoology* 68: 1896–1914. <https://doi.org/10.1139/z90-269>
- AQEM Consortium, 2002. Manual for the application of the AQEM system: A comprehensive method to assess European streams using benthic macroinvertebrates, developed for the purpose of the Water Framework Directive (No. Version 1.0). [http://: www.aqem.de](http://www.aqem.de)
- Barnes, D. M. & A. U. Mallik, 1996. Use of woody plants in construction of beaver dams in northern Ontario. *Canadian Journal of Zoology* 9: 1781–1786. <https://doi.org/10.1139/z96-197>
- Beisel, J.-N.; Usseglio-Polatera, Ph.; Thomas, S.; Moreteau, J.-C. (1998): Stream community structure in relation to spatial variation: The influence of mesohabitat characteristics. In *Hydrobiologia* 389 (1/3), pp. 73–88. DOI: 10.1023/A:1003519429979.
- Billings, W. D.; Golley, F.; Lange, O. L.; Olson, J. S.; Remmert, H.; Turner, Monica Goigel (Eds.) (1987): *Landscape Heterogeneity and Disturbance*. New York, NY: Springer New York (Ecological Studies).
- Blersch, D. M. & P. C. Kangas, 2014. Signatures of self-assembly in size distributions of wood members in dam structures of *Castor canadensis*. *Global Ecology and Conservation* 2: 204-213. <https://doi.org/10.1016/j.gecco.2014.08.011>
- Brazier, R. E.; Puttock, A.; Graham, H. A.; Auster, R. E.; Davies, K. H.; Brown, Ch. (2021): Beaver: Nature's ecosystem engineers. In *WIREs Water* 8 (1), p. 149. DOI: 10.1002/wat2.1494.
- Brooks, M. E., Kristensen, K., Benthem, K. J., van Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J.,

- Brown, D. J.; Hubert, W. A.; Anderson, St. H. (1996): Beaver ponds create wetland habitat for birds in mountains of southeastern Wyoming. In *Wetlands* 16 (2), pp. 127–133. DOI: 10.1007/BF03160686.
- Burchsted, D., Daniels, M., Thorson, R. and Vokoun, J. (2010). The River Discontinuum: Applying Beaver Modifications to Baseline Conditions for Restoration of Forested Headwaters. *BioScience*, 60(11), 908–922. doi: 10.1525/bio.2010.60.11.7.
- Burchsted, D.; Daniels, M. D. (2014): Classification of the alterations of beaver dams to headwater streams in northeastern Connecticut, U.S.A. In *Geomorphology* 205, pp. 36–50. DOI: 10.1016/j.geomorph.2012.12.029.
- Bush, B. & S. Wissinger, 2016. Invertebrates in Beaver-Created Wetlands and Ponds. *Invertebrates in Freshwater Wetlands*. Springer, Cham., 129: 411-449. https://doi.org/10.1007/978-3-24978-0_12
- Bush, B., C. Stenert, L. Maltchik & D. Batzer, 2019. Beaver-created successional gradients increase β -diversity of invertebrates by turnover in stream-wetland complexes. *Freshwater Biology* 64: 1265-1274. <https://doi.org/10.1111/fwb.13302>
- Butler, D. R. & G. P. Malanson, 1995. Sedimentation rates and patterns in beaver ponds in a mountain environment. *Geomorphology* 13: 255-269. [https://doi.org/10.1016/0169-555X\(95\)00031-Y](https://doi.org/10.1016/0169-555X(95)00031-Y)
- Butler, D. R.; Malanson, G. P. (2005): The geomorphic influences of beaver dams and failures of beaver dams. In *Geomorphology* 71 (1-2), pp. 48–60. DOI: 10.1016/j.geomorph.2004.08.016.
- Bylak, A., K. Kukuła & J. Mitka, 2014. Beaver impact on stream fish life histories: the role of landscape and local attributes. *Canadian Journal of Fisheries and Aquatic Sciences* 71: 1603-1615. <https://doi.org/10.1139/cjfas-2014-0105>
- Bylak, A. & K. Kukuła, 2018. Living with an engineer: fish metacommunities in dynamic patchy environments. *Marine and Freshwater* 69: 883-893. <https://doi.org/10.1071/MF17255>
- Bylak, A.; Kukuła, K. (2022): Impact of fine-grained sediment on mountain stream macroinvertebrate communities: Forestry activities and beaver-induced sediment management. In *The Science of the total environment* 832, p. 155079. DOI: 10.1016/j.scitotenv.2022.155079.
- Carpenter, St. R.; Lodge, D. M. (1986): Effects of submersed macrophytes on ecosystem processes. In *Aquatic Botany* 26, pp. 341–370. DOI: 10.1016/0304-3770(86)90031-8.

- Chao, A., Gotelli, N. J., Hsieh, T. C.; Sander, E. L., Ma, K. H., Colwell, R. K., Ellison, A. M. (2014): Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. In *Ecological Monographs* 84 (1), pp. 45–67. DOI: 10.1890/13-0133.1.
- Collen, P. & R. J. Gibson, 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects. *Reviews in Fish Biology and Fisheries* 10: 439-461
- Clifford, H. F., G. M. Wiley & R. J. Casey, 1993. Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. *Canadian Journal of Zoology* 71: 1439–1447. <https://doi.org/10.1139/z93-199>
- Curran, J. C.; Cannatelli, K. M. (2014): The impact of beaver dams on the morphology of a river in the eastern United States with implications for river restoration. In *Earth Surf. Process. Landforms* 39 (9), pp. 1236–1244. DOI: 10.1002/esp.3576.
- Cutting, K., J. Ferguson, M. Anderson, K. Cook, S. Davis & R. Levine, 2018. Linking beaver dam affected flow dynamics to upstream passage of Arctic grayling. *Ecology and Evolution* 8: 12905-12917. <https://doi.org/10.1002/ece3.4728>
- Czerniawski, R., L. Sługocki & M. Kowalska-Górska, 2017. Effects of beaver dams on the zooplankton assemblages in four temperate lowland streams (NW Poland). *Biologia* 4: 417-430. <https://doi.org/10.1515/biolog-2017-0047>
- Dalbeck, L. (2022). Ergebnisse der Bibererfassung im Kreis Düren in 2022. <https://biostation-dueren.de>
- Dalbeck, L., 2021. Bestandsentwicklung des Bibers am Beispiel des Kreises Düren. In *Wald und Holz NRW* (Ed.), 40 Jahre Biber-Wiederansiedlung in Nordrhein-Westfalen: 14–17. Retrieved from <http://www.wald-und-holz.nrw.de/>.
- Dalbeck, L. (2020): A review of the influence of beaver *Castor fiber* on amphibian assemblages in the floodplains of European temperate streams and rivers. In *HJ* (Volume 30, Number 3), pp. 135–146. DOI: 10.33256/hj30.3.135146.
- Dalbeck, L., J. Janssen & L. S. Völsgen, 2014. Beavers (*Castor fiber*) increase habitat availability, heterogeneity and connectivity for common frogs (*Rana temporaria*). *Amphibia-Reptilia* 35: 321–329. <https://doi.org/10.1163/15685381-00002956>

- Danilov, P., V. Kanshiev & F. Fyodorov, 2011. Characteristics of North American and Eurasian beaver ecology in Karelia. In: Sjöberg, G. & J.P. Ball, 2011. Restoring the European beaver 2011: 50 years of experience. Section 2 – Biology of two beaver species in Europe. Chapter 6: 55-72. Sofia. Pensoft
- Dauwalter, D. C.; Walrath, J. D. (2018): Beaver dams, streamflow complexity, and the distribution of a rare minnow, *Lepidomeda copei*. In *Ecology of Freshwater Fish* 27 (2), pp. 606–616. DOI: 10.1111/eff.12374.
- DeCáceres, M., 2020. Package 'indicspecies'. Retrieved from <http://cran.r-project.org/web/packages/indicspecies/vignettes/indicspecies>
- Dittbrenner, B. J.; Pollock, M. M.; Schilling, J. W.; Olden, J. D.; Lawler, J. J.; Torgersen, Ch. E. (2018): Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation. In *PloS one* 13 (2), e0192538. DOI: 10.1371/journal.pone.0192538.
- Dittbrenner, B.J., Schilling, J.W., Torgersen, C.E. and Lawler, J.J. (2022). Relocated beaver can increase water storage and decrease stream temperature in headwater streams. *Ecosphere*, 13(7). doi: 10.1002/ecs2.4168.
- Duan, X.; Wang, Z.; Xu, M.; Zhang, K. (2009): Effect of streambed sediment on benthic ecology. In *International Journal of Sediment Research* 24 (3), pp. 325–338. DOI: 10.1016/S1001-6279(10)60007-8.
- Dufrêne, M. & P. Legendre, 1997. Species Assemblages and Indicator Species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.
- Dugmore, A. R., 1914. The romance of the beaver: being the history of the beaver in the Western Hemisphere. JB Lippincott.
- Edington, J. M., 1968. Habitat Preferences in Net-Spinning Caddis Larvae with Special Reference to the Influence of Water Velocity. *The Journal of Animal Ecology* 37: 1-675. <https://doi.org/10.2307/3081>
- Eiseler, B. (2020). Bestimmungshilfen - Makrozoobenthos (3) Köcherfliegenlarven: LANUV-Arbeitsblatt 46. Recklinghausen.

- Fairfax, E. and Whittle, A. (2021). Smokey the Beaver: Beaver-Dammed Riparian Corridors Stay Green During Wildfire Throughout the Western USA. *The Bulletin of the Ecological Society of America*, 102(1). doi: 10.1002/bes2.1795.
- Fedyń, I.; Przepióra, F.; Sobociński, W.; Wyka, J.; Ciach, M. (2022): Eurasian beaver - A semi-aquatic ecosystem engineer rearranges the assemblage of terrestrial mammals in winter. In *The Science of the total environment* 831, p. 154919. DOI: 10.1016/j.scitotenv.2022.154919.
- Ford, T. E.; Naiman, R. J. (1988): Alteration of carbon cycling by beaver: methane evasion rates from boreal forest streams and rivers. In *Can. J. Zool.* 66, pp. 529–533.
- Flores, L.; Giorgi, A.; González, J. M.; Larrañaga, A.; Díez, J. R.; Elosegi, A. (2017): Effects of wood addition on stream benthic invertebrates differed among seasons at both habitat and reach scales. In *Ecological Engineering* 106, pp. 116–123. DOI: 10.1016/j.ecoleng.2017.05.036.
- Fritz, S. & M. Gangloff, 2022. The effects of beaver impoundments on montane stream fish communities. *Aquatic Conservation: Marine and Freshwater Ecosystems* 32: 1618-1633. <https://doi.org/10.1002/aqu.3876>
- Fuller, M. R. & B. L. Peckarsky, 2011a. Does the morphology of beaver ponds alter downstream ecosystems? *Hydrobiologia* 1: 35-48. <https://doi.org/10.1007/s10750-011-0611-x>
- Fuller, M. R. & B. L. Peckarsky, 2011b. Ecosystem engineering by beavers affects mayfly life histories. *Freshwater Biology* 5: 969-979. <https://doi.org/10.1111/j.1365-2427.2010.02548.x>
- Garcia, X.-F.; Schnauder, I.; Pusch, M. T. (2012): Complex hydromorphology of meanders can support benthic invertebrate diversity in rivers. In *Hydrobiologia* 685 (1), pp. 49–68. DOI: 10.1007/s10750-011-0905-z.
- Gepp, J., 2003. Der Bachhaft *Osmylus fulvicephalus* - 240 Jahre nach seiner Beschreibung durch Johannes Antonius Scopoli - Österreichs Insekt des Jahres (Osmylidae, Neuroptera). *Carinthia* II 193/113: 325–334.
- Green, K.C. and Westbrook, C.J. (2009). Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams', *Journal of Ecosystems and Management*. doi: 10.22230/jem.2009v10n1a412.
- Gurnell, A. M., 1998. The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography* 22: 167–189. <https://doi.org/10.1177/030913339802200202>

- Hafen, K. C., J. M. Wheaton, B. B. Roper, P. Bailey & N. Bouwes, 2020. Influence of topographic, geomorphic, and hydrologic variables on beaver dam height and persistence in the intermountain western United States. *Earth Surf. Process. Landforms (Earth Surface Processes and Landforms)* 11: 2664–2674. <https://doi.org/10.1002/esp.4921>
- Halley, D. J., A. P. Saveljev, F. Rosell, 2021: Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia. *Mammal Review* 51, 1: 1-24. <https://doi.org/10.1111/mam.12216>
- Harrod, J. J., 1965. Effect of current speed on the cephalic fans of the larva of *Simulium ornatum* var. *nitidifrons* Edwards (Diptera: Simuliidae). *Hydrobiologia* 26: 8–12. <https://doi.org/10.1007/BF00142248>
- Hart, J., M. Rubinato & T. Lavers, 2020: An Experimental Investigation of the Hydraulics and Pollutant Dispersion Characteristics of a Model Beaver dam. *Water* 9: 1-22. <https://doi.org/10.3390/w12092320>
- Harthun, M., 1998. Biber als Landschaftsgestalter - Einfluß des Bibers (*Castor fiber albus* Matschie, 1907) auf die Lebensgemeinschaft von Mittelgebirgsbächen. 1-199. Schriftenreihe der Horst-Rohde-Stiftung. Maecenata. München
- Harthun, M., 1999. Der Einfluss des Bibers (*Castor fiber albus*) auf die Fauna (Odonata, Mollusca, Trichoptera, Ephemeroptera, Diptera) von Mittelgebirgsbächen in Hessen (Deutschland). *Limnologica* 29: 449-464. [https://doi.org/10.1016/S0075-9511\(99\)80052-8](https://doi.org/10.1016/S0075-9511(99)80052-8)
- Hartman, G. (1994): Long-Term Population Development of a Reintroduced Beaver (*Castor fiber*) Population in Sweden. In *Conservation Biology* 8 (3), 713-117.
- Hägglund, A. & G. Sjöberg, 1999. Effects of beaver dams on the fish fauna of forest streams. *Forest Ecology and Management* 115:259-266. [https://doi.org/10.1016/S0378-1127\(98\)00404-6](https://doi.org/10.1016/S0378-1127(98)00404-6)
- Hering, D., Buffagni, A., Moog, O., SANDIN, L., Sommerhäuser, M., Stubauer, I., Feld, C., Johnson, R., Pinto, P., Skoulikidis, N., Verdonschot, P. and Zahradkova, S. (2003). The Development of a System to Assess the Ecological Quality of Streams Based on Macroinvertebrates - Design of the Sampling Programme within the AQUEM Project. *Internat. Rev. Hydrobiol.*, 88(3), 345–361.

- Hering, D., Gerhard, M., Kiel, E., Ehlert, T. and Pottgießer, T. (2001). Review Study on Near-natural Conditions of Central European Mountain Streams, with Particular Reference to Debris and Beaver Dams: Results of the "REG Meeting" 2000. *Limnologica*, 31, 81–92.
- Hoffmann, A. & D. Hering, 2000. Wood-Associated Macroinvertebrate Fauna in Central European Streams. *International Review Hydrobiology* 85: 25–48. [https://doi.org/10.1002/\(SICI\)1522-2632\(200003\)85:1<25::AID-IROH25>3.0.CO;2-R](https://doi.org/10.1002/(SICI)1522-2632(200003)85:1<25::AID-IROH25>3.0.CO;2-R)
- Hood, G. A. (2020): Semi-aquatic mammals. Ecology and biology. Baltimore, MD: Johns Hopkins University Press. Available online at <https://search.ebscohost.com/login.aspx?direct=true&scope=site&db=nlebk&db=nlabk&AN=2446096>.
- Hood, G.A. and Bayley, S.E. (2008). Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation*, 141(2), 556–567. doi: 10.1016/j.biocon.2007.12.003.
- Hood, G. A. & D. G. Larson, 2014. Beaver-Created Habitat Heterogeneity Influences Aquatic Invertebrate Assemblages in Boreal Canada. *Wetlands* 34: 19-29. <https://doi.org/10.1007/s13157-013-0476-z>
- Hood, G. A.; Larson, D. G. (2015): Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. In *Freshw Biol* 60 (1), pp. 198–208. DOI: 10.1111/fwb.12487.
- Hsieh, T. C., Ma, K. H., Chao, A. (2016): iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). In *Methods in Ecology and Evolution* 7 (12), pp. 1451–1456. DOI: 10.1111/2041-210X.12613.
- Hsieh T. C., Ma KH, Chao, A. (2022). iNEXT: Interpolation and Extrapolation for Species Diversity. R package version 3.0.0, http://chao.stat.nthu.edu.tw/wordpress/software_download/.
- Iwata, T.; Nakano, Sh.; Murakami, M. (2003): Stream meanders increase insectivorous bird abundance in riparian deciduous forests. In *Ecography* 26 (3), pp. 325–337. DOI: 10.1034/j.1600-0587.2003.03355.x.

- Jähnig, S.C., Brunzel, S., Gacek, S., Lorenz, A.W. and Hering, D. (2009). Effects of re-braiding measures on hydromorphology, floodplain vegetation, ground beetles and benthic invertebrates in mountain rivers. *Journal of Applied Ecology*, 46(2), 406–416. doi: 10.1111/j.1365-2664.2009.01611.x.
- Johansson, A. (2014): Effects of beaver dams on benthic macroinvertebrates. Master of science. Biology Education Centre, Uppsala University, and Department of Aquatic Sciences and Assessment SLU, Uppsala, Sweden.
- John, S. and Klein, A. (2003). Beaver pond development and its hydrogeomorphic and sedimentary impact on the Jossa floodplain in Germany. *Lutra*, 46(2), 183–188.
- Johnston, C. A.; Naiman, R. J. (1987): Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. In *Landscape Ecology* 1 (1), pp. 47–57.
- Johnston, C., 2017. *Beavers: Boreal Ecosystem Engineers*. Springer International Publishing: 1-272. Cham. <https://doi.org/10.1007/978-3-319-61533-2>
- Kaphegyi, T.; Christoffers, Y. (2014): Vom Prozessschutz zu adaptiven Naturschutzstrategien in Kulturlandschaften. Die Rückkehr des Bibers (*Castor fiber*) als Motor neuer Managementkonzepte für Schutzgebiete. Der Biber als Faktor im Moorschutz. Edited by Albert-Ludwigs-Universität Freiburg Professur für Landespflege.
- Kaufmann, P. R.; Faustini, J. M. (2012): Simple measures of channel habitat complexity predict transient hydraulic storage in streams. In *Hydrobiologia* 685 (1), pp. 69–95. DOI: 10.1007/s10750-011-0841-y.
- Koch, K., 1989. *Die Käfer Mitteleuropas*. Krefeld: Goecke & Evers.
- Kovalenko, K. E.; Thomaz, S. M.; Warfe, D. M. (2012): Habitat complexity: approaches and future directions. In *Hydrobiologia* 685 (1), pp. 1–17. DOI: 10.1007/s10750-011-0974-z.
- Kroes, D. E. & C. W. Bason, 2015. Sediment-trapping by Beaver Ponds in Streams of the Mid-Atlantic Piedmont and Coastal Plain, USA. *Southeastern Naturalist* 14: 577–595.
- Laurel, D. and Wohl, E. (2019). The persistence of beaver-induced geomorphic heterogeneity and organic carbon stock in river corridors. *Earth Surface Processes and Landforms*, 44(1), 342–353. doi: 10.1002/esp.4486.

- Law, A.; McLean, F.; Willby, N. J. (2016): Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. In *Freshwater Biology* 61 (4), pp. 486–499. DOI: 10.1111/fwb.12721.
- Lenth, R. V., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., Singmann, H. (2023). emmeans: Estimated Marginal Means, aka Least-Square Means. <https://github.com/rvlenth/emmeans>.
- Lenz, F., 1920. Thaumastoptera calceata Mik. Eine gehäusetragende Tipulidenlarve. *Archiv für Naturgeschichte* 85: 114-136
- Lokteff, R., B. Roper & J. Wheaton, 2013. Do Beaver Dams Impede the Movement of Trout? *Transactions of the American Fisheries Society* 142: 1114-1125. <https://doi.org/10.1080/00028487.2013.797497>
- Margolis, B. E.; Raesly, R. L.; Shumway, D. L. (2001): The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two appalachian streams. In *Wetlands* 21 (4), pp. 554–563. DOI: 10.1672/0277-5212(2001)021[0554:TEOBCW]2.0.CO;2.
- Mächler, M., Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J.* 9, 378. <https://doi.org/10.32614/RJ-2017-066>
- McCaffery, M. and Eby, L. (2016). Beaver activity increases aquatic subsidies to terrestrial consumers. *Freshwater Biology*, 61(4), 518–532. doi: 10.1111/fwb.12725.
- McComb, W. C., J. R. Sedell & T. D. Buchholz, 1990. Dam-Site selection by beavers in an eastern Oregon basin. *Great Basin Naturalist* 50: 273–281.
- McDowell, D. M. & R. J. Naiman, 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia* 68: 481-489
- Meier, C., Böhmer, J., Biss, R., Feld, C., Haase, P., Lorenz, A., Rawer-Jost, C., Rolaufts, P., Schindehütte, K., Schöll, F., Sundermann, A., Zenker, A. and Hering, D. (2006). Weiterentwicklung und Anpassung des nationalen Bewertungssystems für Makrozoobenthos an neue internationale Vorgaben. Essen.

- Meier, C., P. Haase, P. Rolauffs, K. Schindehütte, F. Schöll, A. Sundermann & D. Hering, 2006. Methodisches Handbuch Fließgewässerbewertung zur Untersuchung und Bewertung von Fließgewässern auf der Basis des Makrozoobenthos vor dem Hintergrund der EG-Wasserrahmenrichtlinie. <http://www.fliessgewaesserbewertung.de>
- Mocq, J.; Soukup, P. R.; Näslund, J.; Boukal, D. S. (2021): Disentangling the nonlinear effects of habitat complexity on functional responses. In *The Journal of Animal Ecology* 90 (6), pp. 1525–1537. DOI: 10.1111/1365-2656.13473.
- Moog, O., 2019. Der Europäische Bachhaft - ein Ufer-Insekt mit Höhlenaffinität? *Osmylus fulvicephalus* - a shore insect with cave affinity? *Höhlenkundliche Mitteilungen des Landesvereins Für Höhlenkunde in Wien und Niederösterreich*. (5-6): 94–95.
- Munir, Tariq M.; Westbrook, Cherie J. (2021): Beaver dam analogue configurations influence stream and riparian water table dynamics of a degraded spring-fed creek in the Canadian Rockies. In *River Res. Applic.* 37 (3), pp. 330–342. DOI: 10.1002/rra.3753.
- Müller, G., 2014. Ingenieurtechnische Aspekte der Biberdämme. *KW Korrespondenz Wasserwirtschaft* 7: 158–163.
- Müller, G. & J. Watling, 2016. The engineering in beaver dams. In Constantinescu, G., M. Garcia & D. Hanes (Eds.), *A Balkema book, River flow 2016: Proceedings of the International Conference on Fluvial Hydraulics (River Flow 2016)*. St. Louis, USA. 11-14 July 2016 (pp. 2094–2099). Boca Raton: CRC Press. <https://doi.org/10.1201/9781315644479-326>
- Müller-Schwarze, D., 2011. *The beaver: Its life and impact* (2nd ed.). Cornell University Press, p. 216
- Naiman, R. J., D. M. McDowell & B. Farr, 1984. The influence of beaver (*Castor canadensis*) on the production dynamics of aquatic insects. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* 22: 1801-1810. <https://doi.org/10.1080/03680770.1983.11897578>
- Naiman, R. J.; Melillo, J. M.; Hobbie, J. E. (1986): Ecosystem Alteration of Boreal Forest Streams by Beaver (*Castor Canadensis*). In *Journal of Wildlife Management* 67 (5), pp. 1254–1269. DOI: 10.2307/1938681.
- Naiman, R. J., C. A. Johnston & J. C. Kelley, 1988. Alteration of North American Streams by Beaver. *BioScience* 11: 753-762. <https://doi.org/10.2307/1310784>

- Naiman, R. J.; Bailan, E.; Bartz, K.; Bilby, R.; Latterell, J. (2002): Dead wood dynamics in stream ecosystems. In USDA Forest Service General Technical Report 181.
- Naumann, G., 1991. Aussetzen von Bibern in der Eifel - Ein Beispiel für die Problematik von Wiedereinbürgerungen. Naturschutz Im Rheinland, Rheinischer Verein für Denkmalpflege und Landschaftsschutz, Jahrbuch 1989-1991: 137–150.
- Nolet, B. A.; Rosell, F. (1998): Comeback of the Beaver Castor fiber: An Overview of Old and New Conservation Problems. In *Biological Conservation* 83 (2), pp. 165–173.
- Nummi, P., 1989. Simulated effects of the beaver on vegetation, invertebrates and ducks. *Annales Zoologici Fennici* 26: 43-52.
- Nummi, P., W. Liao, J. van der Schoor, J. Loehr, 2021. Beaver creates early successional hotspots for water beetles. *Biodiversity and Conservation* 30: 2655-2670. <https://doi.org/10.1007/s10531-021-02213-8>
- Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. Stevens, E. Szoecs & H. Wagner, 2020. Package 'vegan'. Community Ecology Package. (Version R package version 2.5-7.) Cran.R-project.org: Cran.R-project.org. <https://CRAN.R-project.org/package=vegan>
- Orazi, V., Hagge, J., Gossner, M.M., Müller, J. and Heurich, M. (2022). A Biodiversity Boost From the Eurasian Beaver (*Castor fiber*) in Germany's Oldest National Park. *Frontiers in Ecology and Evolution*, 10. doi: 10.3389/fevo.2022.873307.
- Patil, I., 2021. Visualizations with statistical details: The ggstatsplot approach. *Journal of Open Source Software*, 6(61), 3167. <https://doi.org/10.21105/joss.03167>
- Pliūraitė, V. and Kesminas, V. (2012). Ecological impact of Eurasian beaver (*Castor fiber*) activity on macroinvertebrate communities in Lithuanian trout streams. *Open Life Sciences*, 7(1), 101–114. doi: 10.2478/s11535-011-0084-y.
- Pollock, Michael M.; Beechie, Timothy J.; Jordan, and Chris E. (2007): Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. In *Earth Surf. Process. Landforms* 32 (8), pp. 1174–1185. DOI: 10.1002/esp.1553.

- Pollock, M. M.; Beechie, T. J.; Wheaton, J. M.; Jordan, Ch. E.; Bouwes, N.; Weber, N.; and Volk, C. (2014): Using Beaver Dams to Restore Incised Stream Ecosystems. In *BioScience* 64 (4), pp. 279–290. DOI: 10.1093/biosci/biu036.
- Pollock, M., S. Witmore & E. Yokel, 2022. Field experiments to assess passage of juvenile salmonids across beaver dams during low flow conditions in a tributary to the Klamath River, California, USA. *PloS one* 17: 1-24. <https://doi.org/10.1371/journal.pone.0268088>
- Polvi, L.E. and Wohl, E. (2012). The beaver meadow complex revisited - the role of beavers in post-glacial floodplain development. *Earth Surface Processes and Landforms*, 37(3), 332–346. doi: 10.1002/esp.2261.
- Power, M. E.; Rainey, W. E. (2000): Food webs and resources sheds: towards spatially delimiting trophic interactions. In *Ecological consequences of habitat heterogeneity*, pp. 291–314.
- Pringle, C.; Naiman, R. J.; Bretschko, G.; Karr, J. R.; Oswood, M. W.; Webster, J. R. et al. (1988): Patch dynamics in lotic systems: the stream as a mosaic. In *J. N. Am. Benthol. Soc.* 7 (4), pp. 503–524.
- R Core Team, 2021. R: A language and environment for statistical computing. Freeware. R Foundation for statistical computing. Vienna, Austria. <http://www.R-project.org/>
- Redin, A. & G. Sjöberg, 2013. Effects of Beaver Dams on Invertebrate Drift in Forest Streams. *Sumarski list* 11-12: 597-607
- Reice, S. R. (1974): Environmental Patchiness and the Breakdown of Leaf Litter in a Woodland Stream. In *Journal of Wildlife Management* 55 (6), pp. 1271–1282. DOI: 10.2307/1935455.
- Renik, K. M. & A. W. Hafs, 2020. Effect of Beaver on Brook Trout Habitat in North Shore, Lake Superior, Streams. *North American Journal of Fisheries Management* 40: 427-445. <https://doi.org/10.1002/nafm.10422>
- Richard, P. B., 1967. Le déterminisme de la construction des barrages chez le Castor du Rhône. *Revue D'Ecologie, Terre Et Vie, Société Nationale De Protection De La Nature*: 339–470.
- Robinson, C.T., Schweizer, P., Larsen, A., Schubert, C.J. and Siebers, A.R. (2020). Beaver effects on macroinvertebrate assemblages in two streams with contrasting morphology. *The Science of the Total Environment*, 722. doi: 10.1016/j.scitotenv.2020.137899.

- Rolauffs, P., 1999. Untersuchungen zur Besiedlung von Biberdämmen durch Insekten unter besonderer Berücksichtigung der Emergenz. Diploma Thesis: 1-160. Faculty of Biology, University Essen.
- Rolauffs, P., D. Hering & S. Lohse, 2001. Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. *Hydrobiologia* 459: 201–212.
- Ronnquist, A. L. & C. J. Westbrook, 2021. Beaver dams: How structure, flow state, and landscape setting regulate water storage and release. *The Science of the Total Environment* 785: 1-12. <https://doi.org/10.1016/j.scitotenv.2021.147333>
- Rosell, F.; Bozser, O.; Collen, P.; Parker, H. (2005): Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. In *Mammal Review* 35 (3-4), pp. 248–276. DOI: 10.1111/j.1365-2907.2005.00067.x.
- RStudio Team (2023). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL <http://www.rstudio.com/>.
- Rurek, M. (2021): Characteristics of Beaver Ponds and Landforms Induced by Beaver Activity, S Part of the Tuchola Pinewoods, Poland. In *Water* 13 (24), p. 3641. DOI: 10.3390/w13243641.
- Scamardo, J. E.; Marshall, S.; Wohl, E. (2022): Estimating widespread beaver dam loss: Habitat decline and surface storage loss at a regional scale. In *Ecosphere* 13 (3). DOI: 10.1002/ecs2.3962.
- Schloemer, S. & A. Hoffmann, 2018. The Beaver Dam Vacuum Sampler - a new sampling method to investigate the invertebrate fauna in beaver dams. *Lauterbornia* 85: 117–121.
- Schloemer, S., Hörren, T., Lorenz, A.W. and Hering, D. (2023). The macroinvertebrate fauna of maintained and abandoned beaver dams. *Hydrobiologia*, 850(8), 1763–1778. doi: 10.1007/s10750-023-05176-9.
- Schmedtje, U. & M. Colling, 1996. Ökologische Typisierung der aquatischen Makrofauna (Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft No. 4). München. https://www.gewaesserbewertung-berechnung.de/files/downloads/perlodes/PerlodesOnline_Dokumentation_Teil_III_Beschreibung_Indizes.pdf

- Schmidt-Kloiber, A. & D. Hering, 2015. www.freshwaterecology.info – An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators* 53: 271-282. <https://doi.org/10.1016/j.ecolind.2015.02.007>
- Smith, M. E., C. T. Driscoll, B. J. Wyskoski, C. M. Brooks & C. C. Cosentini, 1991. Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Canadian Journal of Zoology* 69: 55-61. <https://doi.org/10.1139/z91-009>
- Sommerhäuser, M. & T. Pottgiesser, 2002. *Fließgewässertypenatlas Nordrhein-Westfalens* (Merkblätter Nr. 36). Essen.
- Speiser, B., 2001. Food and Feeding Behaviour. In G. M. Barker (Ed.), *The biology of terrestrial molluscs*: 259–288. Wallingford, Oxon, UK, New York, NY, USA: CABI Pub.
- Sternberg, K., R. Buchwald & U. Stephan, 2000. *Cordulegaster boltonii*. In: Sternberg, K. & R. Buchwald, 2000. *Die Libellen Baden-Württembergs – Band 2: Großlibellen (Anisoptera)*: 191-208. Verlag Eugen Ulmer
- Spitzenberg, D., Schöne, A., Klausnitzer, B. and Malchau, W. (2021). *Die wasserbewohnenden Käfer Sachsen-Anhalts*. Rangsdorf: Natur + Text.
- Stout, T.L., Majerova, M. and Neilson, B.T. (2017). Impacts of beaver dams on channel hydraulics and substrate characteristics in a mountain stream. *Ecohydrology*, 10(1), e1767. doi: 10.1002/eco.1767.
- Strahler, A. N., 1954. Statistical Analysis in Geomorphic Research. *The Journal of Geology* 62: 1–25. <https://doi.org/10.1086/626131>
- Thie, J., 2022. Exploring Beaver Habitat in Canada: The Longest Beaver Dam in the World. https://www.geostrategis.com/p_beaver-longestdam.htm
- Thompson, S., Vehkaoja, M. and Nummi, P. (2016). Beaver-created deadwood dynamics in the boreal forest. *Forest Ecology and Management*, 360, 1–8. doi: 10.1016/j.foreco.2015.10.019.
- Thompson, S., Vehkaoja, M. and Nummi, P. (2016). Beaver-created deadwood dynamics in the boreal forest. *Forest Ecology and Management*, 360, 1–8. doi: 10.1016/j.foreco.2015.10.019.

- Törnblom, J.; Angelstam, P.; Hartman, G.; Henrikson, L.; Sjöberg, G. (2011): Toward a Research Agenda for Water Policy Implementation: Knowledge about Beaver (*Castor fiber*) as a Tool for Water Management with a Catchment Perspective. In *Baltic Forestry* 17 (1), pp. 154–161.
- Townsend, J. E., 1953. Beaver Ecology in Western Montana with Special Reference to Movements. *Journal of Mammalogy* 34: 459. <https://doi.org/10.2307/1375861>
- Van Stuijvenberg, F., 1997. Tabel en verspreidingsatlas van de Nederlandse Steninae (Coleoptera: Staphylinidae). *Nederlandse Faunistische Mededelingen* 6: 3–60.
- Visscher, M. de; Nyssen, J.; Pontzele, J.; Billi, P.; Frankl, A. (2012): Spatio-temporal sedimentation patterns in beaver ponds along the Chevral River, Ardennes, Belgium. In *Hydrological Processes* 28 (4), pp. 1–12.
- Warren, E. R., 1932. Position of wood in beaver dams. *Science (New York, N.Y.)* 75, 1937: 194–195. <https://doi.org/10.1126/science.75.1937.194-b>
- Wegener, P., Covino, T. and Wohl, E. (2017). Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism. *Water Resources Research*, 53(6), 4606–4623. doi: 10.1002/2016WR019790.
- Westbrook, C.J., Cooper, D.J. and Baker, B.W. (2006). Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. *Water Resources Research*, 42(6), 288. doi: 10.1029/2005WR004560.
- Wiese, V., 2016. *Die Landschnecken Deutschlands: Finden - erkennen - bestimmen* (2., durchgesehene Auflage). Quelle & Meyer Bestimmungsbücher. Wiebelsheim: Quelle & Meyer Verlag
- White, D.S. (1990). Biological relationships to convective flow patterns within stream beds. *Hydrobiologia*, 196(2), 149–158. doi: 10.1007/BF00006106.
- Wilke, C.O., 2019. cowplot: Streamlined Plot Theme and Plot Annotations for “ggplot2.” R Package Version 094 <https://CRAN.R-project.org/package=cowplot>.
- Willby, N. J., A. Law, O. Levanoni, G. Foster & F. Ecke, 2018. Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. *Philosophical transactions of the Royal Society, Series B, Biological Sciences* 373: 1–8. <https://doi.org/10.1098/rstb.2017.0444>

- Wohl, E., D. N. Scott & S. E. Yochum, 2019. Managing for large wood and Beaver dams in stream corridors. General Technical Report-Rocky Mountain Research Station. USDA Forest Service, (RMRS-GTR-404):136
- Wojton, Andrzej; Kukuła, Krzysztof (2021): Transformation of benthic communities in forest lowland streams colonised by Eurasian beaver *Castor fiber* (L.). In *Int. Revue ges. Hydrobiol. Hydrogr.* 106 (2), pp. 131–143. DOI: 10.1002/iroh.202002043.
- Woo, M.-K. & J. M. Waddington, 1990. Effects of Beaver Dams on Subarctic Wetland Hydrology. *Arctic* 43: 223–230.
- Wright, J. P.; Jones, Clive G.; Flecker, Alexander S. (2002): An ecosystem engineer, the beaver, increases species richness at the landscape scale. In *Oecologia* 132, pp. 96–101.
- Wróbel, M., 2020. Population of Eurasian beaver (*Castor fiber*) in Europe. *Global Ecology and Conservation* 23: 1-4. <https://doi.org/10.1016/j.gecco.2020.e01046>
- Zahar, A. R., 1951. The Ecology and Distribution of Black-Flies (Simuliidae) in South-East Scotland. *The Journal of Animal Ecology* 20: 33. <https://doi.org/10.2307/1643>
- Zavyalov, N. A., 2014. Beavers (*Castor fiber* and *Castor canadensis*), the founders of habitats and phytophages. *Biology Bulletin Reviews* 4: 157–180. <https://doi.org/10.1134/S207908641402008X>

Der Lebenslauf ist aus Gründen des Datenschutzes in der Online-Version nicht enthalten

Declarations

Erklärung:

Hiermit erkläre ich, gem. § 7 Abs. (2) d) + f) der Promotionsordnung der Fakultät für Biologie zur Erlangung des Dr. rer. nat., dass ich die vorliegende Dissertation selbständig verfasst und mich keiner anderen als der angegebenen Hilfsmittel bedient, bei der Abfassung der Dissertation nur die angegebenen Hilfsmittel benutzt und alle wörtlich oder inhaltlich übernommenen Stellen als solche gekennzeichnet habe.

Essen, den 05.02.2024

Unterschrift des/r Doktoranden/in

Erklärung:

Hiermit erkläre ich, gem. § 7 Abs. (2) e) + g) der Promotionsordnung der Fakultät für Biologie zur Erlangung des Dr. rer. nat., dass ich keine anderen Promotionen bzw. Promotionsversuche in der Vergangenheit durchgeführt habe und dass diese Arbeit von keiner anderen Fakultät/Fachbereich abgelehnt worden ist.

Essen, den 05.02.2024

Unterschrift des Doktoranden

Erklärung:

Hiermit erkläre ich, gem. § 6 Abs. (2) g) der Promotionsordnung der Fakultät für Biologie zur Erlangung der Dr. rer. nat., dass ich das Arbeitsgebiet, dem das Thema „*European beaver (Castor fiber) engineered habitats and their invertebrate community in mountain streams*“ zuzuordnen ist, in Forschung und Lehre vertrete und den Antrag von (Sara Schloemer) befürworte und die Betreuung auch im Falle eines Weggangs, wenn nicht wichtige Gründe dem entgegenstehen, weiterführen werde.

Herr Prof. Dr. Daniel Hering

Name des Mitglieds der Universität Duisburg-Essen in Druckbuchstaben

Essen, den 05.02.2024 _____

Unterschrift eines Mitglieds der Universität Duisburg-Essen

Die Veröffentlichung soll erfolgen durch die unentgeltliche Abgabe von:

3 Belegexemplaren bei Veröffentlichung in einer wissenschaftlichen Zeitschrift, Schriftenreihe oder als Monographie mit Vertrieb über den Buchhandel

Essen, den 05.02.2024

Unterschrift des/r Doktoranden/in

Essen, den _____

Unterschrift des Betreuers