

1 The positive response of small terrestrial and semi-aquatic mammals to beaver damming

3 ¹Zuzanna Wikar, ¹Mateusz Ciechanowski, ¹Adrian Zwolicki

4 Department of Vertebrate Ecology and Zoology, University of Gdańsk, Wita Stwosza 59, 80-
5 308 Gdańsk, Poland

7 ORCID numbers: Wikar 0000-0003-2747-3222; Ciechanowski 0000-0002-5390-7971;
8 Zwolicki 0000-0003-2710-681X

10 E-mail of corresponding author: zuzanna.wikar@gmail.com

12 Abstract

13 Ecosystem engineers, such as the Eurasian beaver, *Castor fiber*, transform habitats, thereby
14 creating favourable conditions for other species and increasing biodiversity. Multiple studies
15 have revealed that beaver ponds are valuable habitats for invertebrates and vertebrates,
16 including other mammals, but the impact of watercourse damming on the fauna of small
17 terrestrial rodents and shrews has not yet been documented. We aimed at testing the hypothesis
18 that the presence of beaver dams and consequent flooding enriches the small mammal
19 assemblage both quantitatively and qualitatively. We live-trapped small mammals at nine
20 beaver-modified sites on 300 metre transects alongside dammed watercourses, starting from the
21 dam through to the pond to the sections with unmodified lotic conditions. The abundance and
22 species richness of trapped small mammals were highest near the dams and declined with
23 distance. Additionally, five out of 12 trapped species significantly decreased their abundance
24 with distance from the dam and none revealed the opposite trend. Four species were more
25 abundant on plots subjected to damming (especially *Sorex minutus* and *Micromys minutus*),

while none were present solely on undammed plots. Among the semi-aquatic species, two water shrews benefited from beavers' activity in different ways. *Neomys milleri* occurred only in flooded sections, while *N. fodiens* preferred unmodified sections, but was the most numerous closer to the dams, following the already known patterns of competitive displacement observed in Central Europe. An important factor affecting small mammals, the herbaceous layer cover, appeared to be interdependent with damming. We provide the first unequivocal evidence that beaver dams facilitate the abundance and diversity of small mammals, presumably due to increased food abundance, availability of shelters and habitat connectivity. Beaver-created wetlands may act as potential refuges for the species most susceptible to the consequences of anthropogenic climate change, while revealing a critically low range-shift capacity.

Keywords

Castor fiber; Keystone species; Intraspecific interactions; Whole-community facilitation; Ecosystem engineering

Highlights

- Impact of beaver ponds on small mammals has remained understudied
- Shrews and rodents at beaver-modified watercourses were studied by live-trapping
- Abundance and richness of small mammals were higher on dammed sections of streams
- Number of species and individuals decreased with distance from the dam

1. Introduction

Ecosystem engineers are organisms that are capable of modifying their environment to a 'significant extent' and therefore, directly or indirectly modulating the availability of resources to other species and affecting the distribution of those species (Jones et al., 1994).

51 They appear to be widespread in all terrestrial biomes; up until now, at least 121 such organisms
52 have been recognised and their impact results from burrowing, nest-building, herbivory, soil
53 manipulation and leaf-structuring. The majority of the already recognised ecosystem engineers
54 have been mammals (Coggan et al., 2018). Some of the ecosystem engineers can also be
55 considered keystone species, i.e. organisms whose impact on other taxa is disproportionately
56 high, compared to their abundance, density and share in the community (Paine, 1969). The
57 North American *Castor canadensis* and Eurasian beaver *Castor fiber* belong to the most
58 prominent ecosystem engineers and keystone species at the higher latitudes of the Northern
59 Hemisphere (Rosell and Campbell-Palmer 2022). Their engineering function results partially
60 from their herbivory focused on woody plants (Johnston and Naiman, 1990; Nolet et al., 1994;
61 Levin and Meyer, 2019), but mostly from damming and consequent flooding, necessary to
62 cover the entrances to dens and lodges (Rosell and Campbell-Palmer 2022), which allows the
63 classification of beavers as ‘nest-building’ engineers (Coggan et al., 2018). Although beavers
64 inhabit various types of freshwater habitats, including lakes, ponds, estuaries, bogs, large and
65 small rivers, streams, small seepages and ditches (Rosell and Campbell-Palmer 2022), they
66 build dams only on narrow and shallow water courses, where one may expect at least a
67 minimum current (Hartman and Törnlov, 2006). Thus, depending on the geographic location,
68 usually 10–53% of Eurasian beaver sites have active dams (Żurowski and Kasperczyk, 1986;
69 Parker and Rønning, 2007; Rosell and Campbell-Palmer 2022) and this is why, at least
70 considering damming activities only, beavers should be classified as facultative ecosystem
71 engineers if following the definition by Coggan et al. (2018). Despite that facultative nature,
72 the function of these rodents as modifiers of landscape and hydrological systems is important
73 on a continental or even global scale, as beaver ponds recently cover 952 600–1 109 000 ha in
74 the whole Northern Hemisphere, including 24 600–181 000 in the Palearctic (Thompson et al.,
75 2020).

The engineering effects of damming by beavers extend to various ecosystem functions and taxa. It attenuates stream flow even during strong rainstorms (Westbrook et al., 2020), improves water storage and provides standing water during periods of drought (Westbrook et al., 2006), creates sediment and nutrient traps, thus improving water quality below beaver sites (Bason et al., 2017), buffering changes in water temperature (Weber et al., 2017) and mitigates the effects of wildfires (Fairfax and Whittle, 2020). The creation of ponds by beavers increases diversity and/or abundance of plants (Willby et al., 2018), water beetles (Nummi et al., 2021) and molluscs (Bashinskiy and Stojko, 2022), amphibians (Dalbeck et al., 2007), reptiles (Russell et al., 1999), birds (Grover and Baldassarre, 1995; Orazi et al., 2022), bats (Ciechanowski et al., 2010; Orazi et al., 2022), as well as medium-sized and large mammals (Nummi et al., 2019; Fedyń et al., 2022). As many of those effects result in substantial benefits for environmental and climate protection, biological conservation and local economies, both species of beavers are responsible for providing ecosystem services worth about 330 million US dollars annually in their native ranges (Thompson et al., 2020). Not all species benefit from beaver damming, however. As beavers increase the area of lenitic habitats at the expense of lotic ones, reophilous taxa, like stoneflies Plecoptera (Washko et al., 2022) may decline because of damming, while a substantial corpus of studies on fish presents conflicting results (Kemp et al., 2011). Proper estimation of those effects is, however, possible only at coarser spatial scales – beavers can reduce the alpha diversity of some groups but they always increase gamma diversity (Washko et al., 2022). Among negatives from a conservation point of view, beavers may also facilitate the spread of alien invasive plants in occupied riparian zones (Perkins and Wilson, 2005; Piętka and Misiukiewicz, 2022).

Despite an impressive number of studies on the function of beavers as keystone species, reflected in an equally unparalleled number of review papers (Rosell et al., 2005; Janiszewski et al., 2014; Brazier et al., 2021; Larsen et al., 2021; Grudzinski et al., 2022; Rosell and

Campbell-Palmer 2022), there are still significant, unexplored gaps in that body of knowledge. One of the groups of organisms that has evaded sufficient attention in research on ecosystem effects of beaver-created wetlands are small terrestrial mammals, despite their worldwide importance in trophic networks and soil processes (Hayward and Phillipson, 1979). Scarce, already available studies either failed to reveal any significant effect on abundance or lack proper statistical treatment and none revealed any significant effect on diversity. That applies even to the North American beaver, which, in general, seems to have much better scientific coverage for most aspects of its ecology (Rosell and Campbell-Palmer 2022). Medin and Clary (1991) found a 2.7 greater biomass of rodents and shrews around beaver ponds than in adjacent riparian habitats of Idaho but differences in species richness and diversity were negligible and none of the effects were tested statistically. On contrary, differences in abundance and richness of small mammals between beaver-occupied and unoccupied streams in Oregon were tested but none of them appeared significant (Suzuki and McComb, 2005). The abundance of the deer mouse, *Peromyscus maniculatus*, was significantly higher at beaver sites compared to controls in Montana, as was the contribution of aquatic-derived carbon in mice from the first group, revealed by stable isotope analysis (McCaffery and Eby, 2016). Finally, Frey and Malaney (2009) found that beaver ponds contribute to persistence of the threatened New Mexico meadow jumping mouse, *Zapus hudsonius luteus*.

The state of knowledge about the effect of Eurasian beavers on small mammals is even less satisfying. Sundell et al. (2021) trapped small mammals over two years in ten beaver sites and ten control sites in Finland, finding no differences in abundance nor diversity. Results from the Russian Karelia appear inconsistent, with small mammal abundance being lower at one abandoned beaver site, compared to an adjacent control, while at the other site, the opposite effect was found but the differences were not tested statistically (Fyodorov and Yakimova, 2012). Orazi et al. (2022), in their multidisciplinary study, compared abundance and diversity

of various taxonomic groups not only between beaver ponds and non-beaver sections of streams but also between both of them and surrounding forests in Germany. Unfortunately, any material of small mammals in that study was obtained as bycatch in pitfall traps used to capture terrestrial invertebrates and was analysed together with amphibians and reptiles trapped in a similar manner, without producing any significant results. Two Lithuanian studies focused not on beaver-created wetlands but rather on beaver lodges. Ulevičius and Janulaitis (2007) captured nine species of small rodents and shrews visiting those constructions but did not compare them to any control sites. Samas and Ulevičius (2015) found a significantly higher abundance of small mammals at beaver lodges than in adjacent forests but the effect should rather be attributed to the provided shelters, not the flooding itself. The latter study is also the only one that reveals notably higher diversity indices at beaver constructions but, again, those differences were not statistically tested.

The aim of this study was to determine how damming of small water courses (rivers, streams and ditches) by Eurasian beavers affects assemblages of small terrestrial mammals, including rodents and shrews. We hypothesised that beaver damming enriches the small mammal assemblage quantitatively and qualitatively, leading to the following predictions: 1) abundance and species richness would decline with increasing distance from a dam along the stream channel; 2) species richness would attain higher values in sections of the valley subjected to flooding by beavers (increased water table) than in those with unmodified hydrology.

2. Material and methods

2.1. Study area

We conducted the study at nine wetland sites in the Pomeranian Lakeland and three at the Baltic Sea Coast, Northern Poland, all located approximately between meridians 17° 02' E and 18° 34' E, and between parallels 54° 39' N and 53° 39' N, at an altitude of 0.2–178.2 m

a.s.l. (Fig. 1). The climate, according to the Köppen classification, is a humid continental one, with a warm summer subtype (*Dbf*). The mean annual temperature is 8.1–8.8 °C, with a mean temperature in January of –1.5–0.2 °C and a mean temperature in July of 17.5–18.0 °C. The mean annual precipitation is 571–746 mm, with 38–40 days of snow on average. The area comprises mostly young, postglacial landscape, while land cover is dominated by a mosaic of arable land and meadows (~50%), forests, mostly managed (~36%) and human settlements (~6%). A dense network of lakes and small rivers cover ~5% of the region.

Particular study sites differed in geomorphological, hydrological and geobotanical features. Beaver dams were built on small rivers and streams, either rapid and of sub-montane character or slow flowing, but also on drainage ditches with minimum current. Vegetation along the shores of water courses and beaver ponds consisted of alder-ash forest *Fraxino-Alnetum* (usually swampy), alder carrs *Ribeso nigri-Alnetum* and *Sphagno squarrosi-Alnetum* (usually flooded), often with a lush herbaceous layer, willow-alder shrublands, reed beds *Phragmitetum australis*, tall-herb fens, dominated by tussocks of large sedges *Carex* and wet meadows, either mowed or abandoned. Vegetation on valley slopes was dominated by either oak-hornbeam forests *Stellario-Carpinetum* and beech forests *Fagion sylvaticae*, usually with a scarce herbaceous layer, or pine forests *Leucobryo-Pinetum*, with herbaceous stands consisting of prostrate shrubs, mosses and lichens. Both alder-ash and oak-hornbeam woodlands occurred along the sections of water courses unmodified by beavers but they were locally replaced by humid or dry, usually mowed, meadows. Tree stands varied in age and naturalness but most were managed and planted conifers formed a significant admixture even in some of the broadleaved forests. Most sites were located in rural areas, with only one at the edge of a large, urban agglomeration.

There were 1–3 dams at each site, 2.8–92.0 m long (median 7.2 m, N = 13) and 0.05–1.2 m high at the downstream face (median 0.6 m, N = 10). At most sites, beavers lived in

burrows dug in steep banks, they built a bank lodge only in one site and a typical stick lodge in another one (if applying the classification of beaver dwellings used by Rosell and Campbell-Palmer 2022). Most beaver sites were active and their dams maintained. Only one was abandoned and the water level in the pond, consequently, dropped. The fauna of small, non-volant mammals in the region consisted of 17 species, including five soricomorphs and 12 rodents (Pucek and Raczyński, 1981).

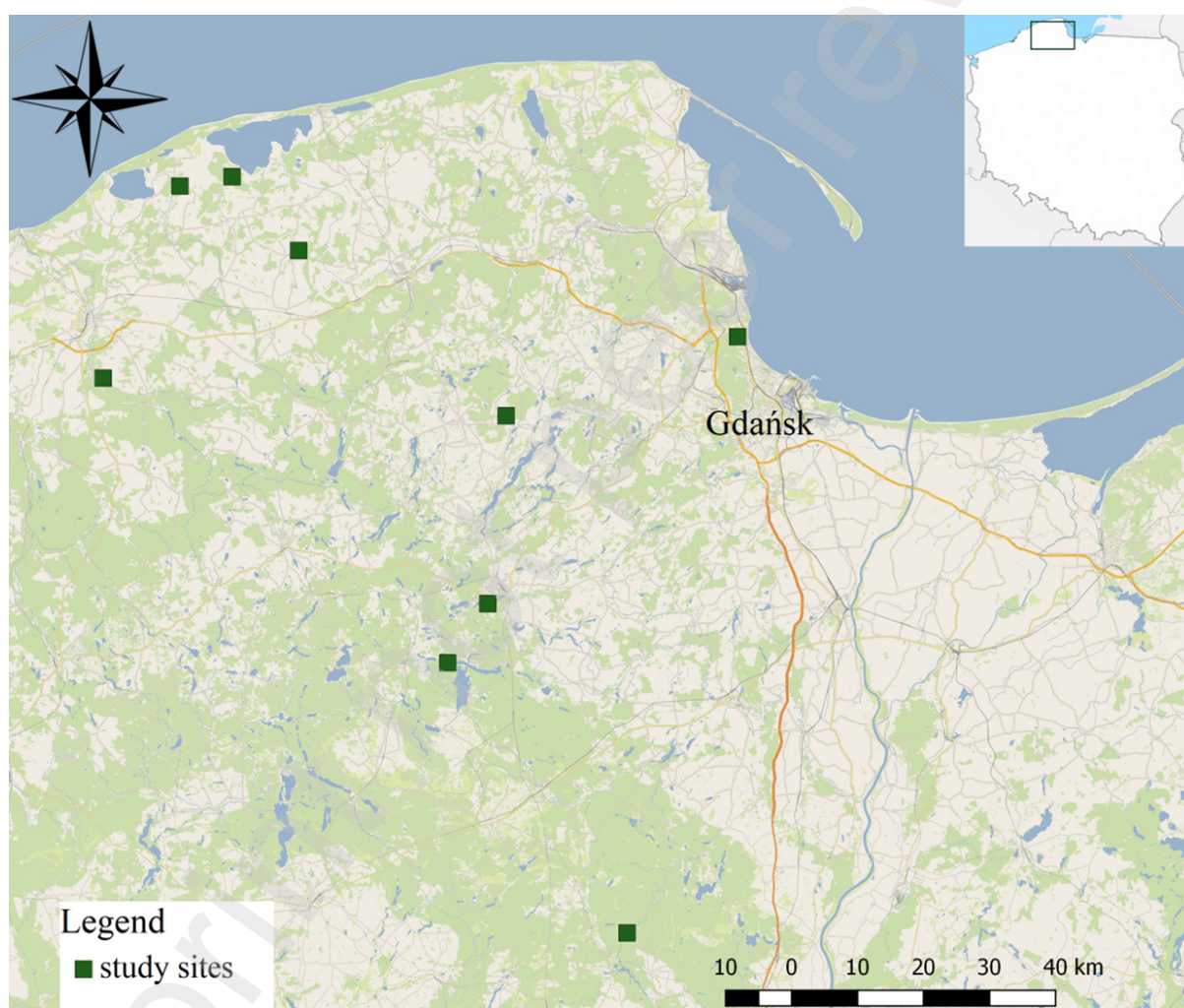


Figure 1. Locations of the study sites at nine small streams modified by Eurasian beavers (source of background map: Open Street Map).

2.2. Fieldwork

Data on the small mammals' distribution, activity and species richness were obtained by live-trapping in conical pitfall traps. Thirty traps were located on the transect alongside the watercourse starting next to a beaver dam, with 10 m distance between traps. We inspected the transect every two hours to minimise mortality of caught animals. Additionally, on the bottom of the traps, we put 2–3 cm thick plugs made of locally harvested reed or grass and two mealworm *Tenebrio molitor* larvae to further increase chances of survival of the trapped small mammals, especially shrews due to their fast metabolism and to reduce the chances of cannibalism among them and predation towards other small mammals. Plugs were removed after trapping on every site and new ones were installed in the next locality. In addition to increasing survival, the plugs collected the urine of the caught animals and their replacement allowed us to avoid attracting mammals (Andrzejewski et al., 1997). Captured small mammals were identified (Pucek, 1984; Aulagnier et al., 2009) and released on the spot. Species, time of capture and, if possible, sex and age were noted.

We trapped for three nights on the first site and for two nights on the remaining eight study sites, beginning two hours before sunset and finishing two hours after sunrise. The trapping effort involved 90 trap-nights on the first site, 60 trap-hours on the rest and 570 trap-nights overall. During the day, the traps were secured. Trapping was conducted based on licenses of Regional Directorate of Environmental Protection in Gdańsk RDOŚ-Gd-WZG.6401.2021.BP.2 (for the plots located outside protected areas), Director of Słowiński National Park ZM.611.26.2021.MG and Ministry of Climate and Environment DOP-WPN.61.163.2021.MGr (for the plots located within borders of the mentioned national park).

Each trap was described with the following features: 1) distance from a beaver dam (m); 2) presence of damming (0 – water remaining in the riverbed, 1 – water level raised, water flooding beyond the stream bed or ditch); 3) the percentage cover of herbaceous layer (1 m x 1 m quadrat with trap in the middle); 4) surface moisture of the ground (dry – the absence of

water on the surface, wet – ground at least partially covered with water or moisture on the surface); 5) tree presence (0 – no tree canopy over the trap, 1 – tree canopy over trap).

To analyse collected data, we split the traps into plots. A plot consisted of three to six traps described by the same parameters, ideally in sequence. If the trap deviated from the nearest points, it was assigned to the nearest plot with the most similar parameters.

2.3. Statistical analyses

Generalised linear mixed models (GLMMs), in which the location of the beaver site was regarded as a random factor, were used to assess the responses of: (i) the number of captures; and (ii) the number of species (S) of small mammals to beaver damming in relation to the distance from a beaver dam.

The distance-based redundancy analysis (dbRDA) was performed to demonstrate the relationship between the small mammal species' composition and the tested environmental variables. Vectors that defined response variables were created based on the Spearman rank correlation. To test the influence of selected variables on species composition, we used distance-based linear models (DistLM) with 999 permutations. As a variable selection procedure, we applied forward selection based on the adjusted R² value of the model. The Similarity Percentage (SIMPER) analysis was used to measure the contribution of abundances of particular species to the dissimilarity between 'damming' and 'no damming' groups of plots. To perform dbRDA, DistLM and SIMPER analyses, data were previously standardised by the sample and square-root transformed, after which the distance matrix was calculated based on the Bray Curtis dissimilarity scaled to 0–100%. To explore individual species' distribution across distance from a beaver dam we employed Generalised Additive Models (GAMs) with quasi-Poisson distribution and log link function.

Statistical methods were carried out using PRIMER 6.1.15 with the PERMANOVA 1.0.5 add-on (Clarke and Gorley, 2007; Anderson, 2014) and the R 4.1.0 environment (R Core

Team, 2021). The following R packages were used: ‘Tidyverse’ (Wickham et al., 2019) for data wrangling, ‘lme4’ (Bates, 2010) together with ‘lmerTest’ (Kuznetsova et al., 2017) for GLMM calculations, and ‘ggeffects’ (Lüdtke, 2018) for GLMMs’ visualisation. GAMs models were calculated and graphically presented in CANOCO 5 (Šmilauer and Lepš, 2014).

3. Results

3.1. Beaver influence on small mammal abundance and species composition

The number of captured small mammals and the number of their species were significantly higher on plots subjected to damming, compared to non-functioning dams or sections of streams and ditches with an increased water table lacking (no damming). The damming factor explained a higher fraction of variation compared to distance in both models. Moreover, in both groups, the highest values were found close to a dam and significantly decreased with the distance from a dam (Tab. 1, Fig. 2). Slopes of ‘damming’ and ‘no damming’ GLMMs’ regression were similar in both captures and species number models.

Table. 1. The results of GLMMs testing the influence of fixed factors (beavers damming and distance from a beaver dam) on the number of small mammals captured and on the number of small mammal species.

Model/Response	Factor	SS	MS	F- value	P-value
	Damming	18.4	18.4	18.4	0.0013
Number of captures	sqrt(Distance)	14.7	14.7	14.7	0.0001

	<i>Damming:sqrt(Distance)</i>	0.2	0.2	0.2	0.6835
	Damming	12.08	12.08	12.08	0.005
Number of species	sqrt(Distance)	4.03	4.03	4.03	0.045
	<i>Damming:sqrt(Distance)</i>	0.36	0.36	0.36	0.547

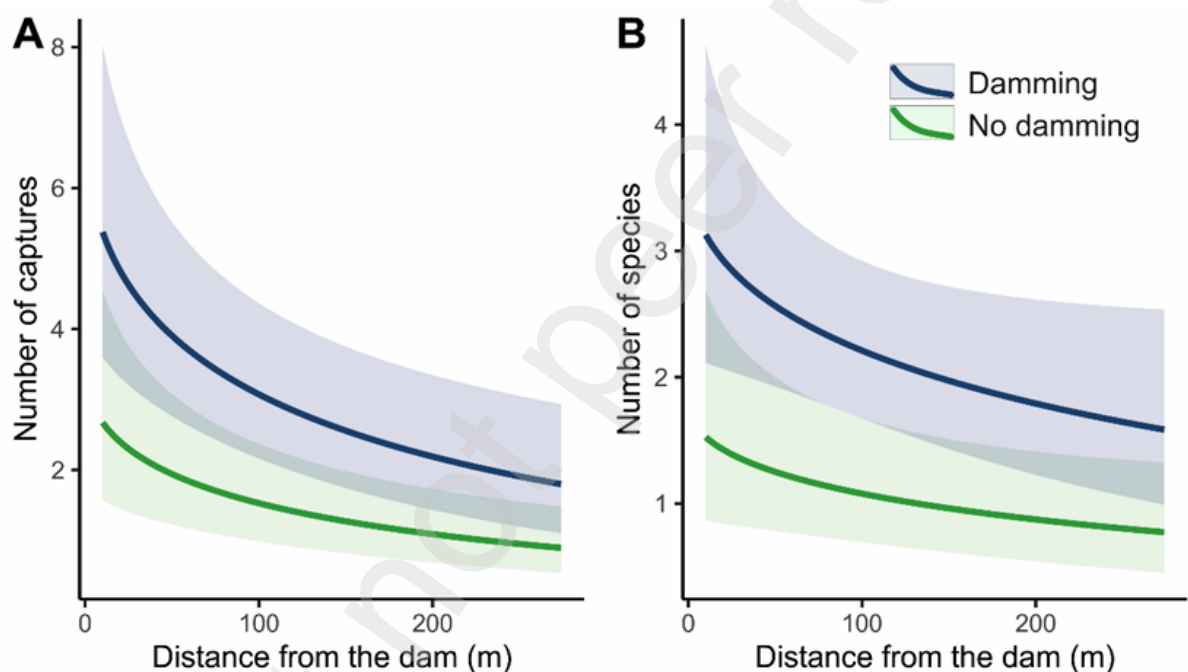


Figure 2. Generalised linear mixed models (GLMMs) plots with 95% confidence intervals (shaded area) of (A) the number of captured small mammals and (B) the number of small mammal species distributed over the distance from a beaver dam in the no damming (green) and damming (blue) factors.

The distance-based linear model revealed that the most important variable, explaining mammal species composition variation, was the percentage cover of herbaceous layer (8.1% of explained variation). Distance and damming factors were also significant and explained a similar fraction of variation, 5.9% and 5.2%, respectively. It is worth emphasising that the angle between the vectors of damming and % herbaceous layer was close to 90 degrees, which suggests that their influence on small mammals was interdependent. The remaining tree cover and ground variables had no influence on small mammals (Supplementary Table 1).

GAMs revealed that five small mammalian species, i.e. *Apodemus agrarius*, *Clethrionomys glareolus*, *Neomys fodiens*, *Micromys minutus* and *Apodemus flavicollis* were significantly related to distance from a beaver dam. In all cases, the highest numbers of captured animals were found close to a beaver dam. However, the distance of this influence was unequal. The farthest influence, reaching up to 200 m, was observed in the case of *N. fodiens* and *A. flavicollis*, while *Apodemus agrarius* and *C. glareolus* were captured only in the immediate vicinity of a dam, up to about 60 and 100 m, respectively. The remaining seven species did not change their number significantly with distance, thus no positive effect of that parameter was revealed (Fig. 3).

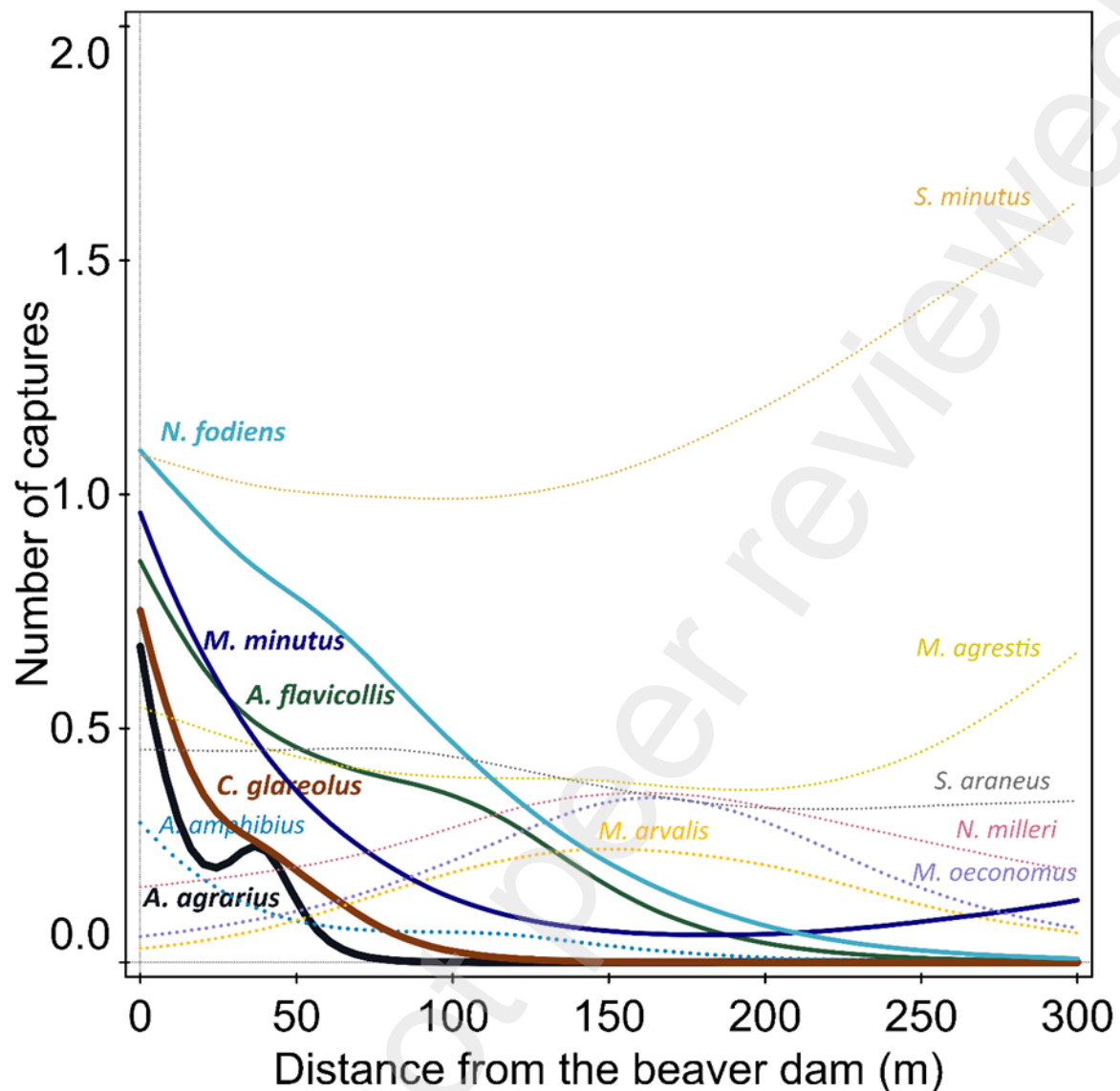


Figure 3. Generalised additive models (GAMs) response curves showing the number of captures of each small mammalian species distributed over the distance from a beaver dam. Line thickness indicates R² value of the model, solid line – significant model, dotted line – non-significant model. Details of GAMs models are presented in the Supplementary Table 2.

3.2. Species-specific responses of small mammals to beaver impact on riparian habitat

The dbRDA space shows a clear separation of sample plots from damming and no damming groups, expressing substantial differences in species composition between these groups (Fig. 4). Based on the direction of response vectors, we found that *Sorex minutus*,

Neomys milleri and *Arvicola amphibius* characterised habitats influenced by beaver damming, while *A. flavicollis*, *A. agrarius*, *C. glareolus* and *N. fodiens* avoided areas of active damming.

Differences in species composition between ‘damming’ and ‘no damming’ groups were quantified using the SIMPER analysis (Fig. 5, Supplementary Table 3). *S. minutus*, which was the most abundant species, demonstrated the greatest degree of dissimilarity between damming groups (17.1%). The second most differentiating was *A. flavicollis*, which dominated in the no damming group. Interesting differences were found within the *Neomys* genus, where *N. milleri* clearly preferred habitats with damming, while *N. fodiens* was slightly more often caught in habitats without damming. *A. agrarius* and *A. amphibius* had the lowest contribution in dissimilarity, 3.2% and 2.3%, respectively.

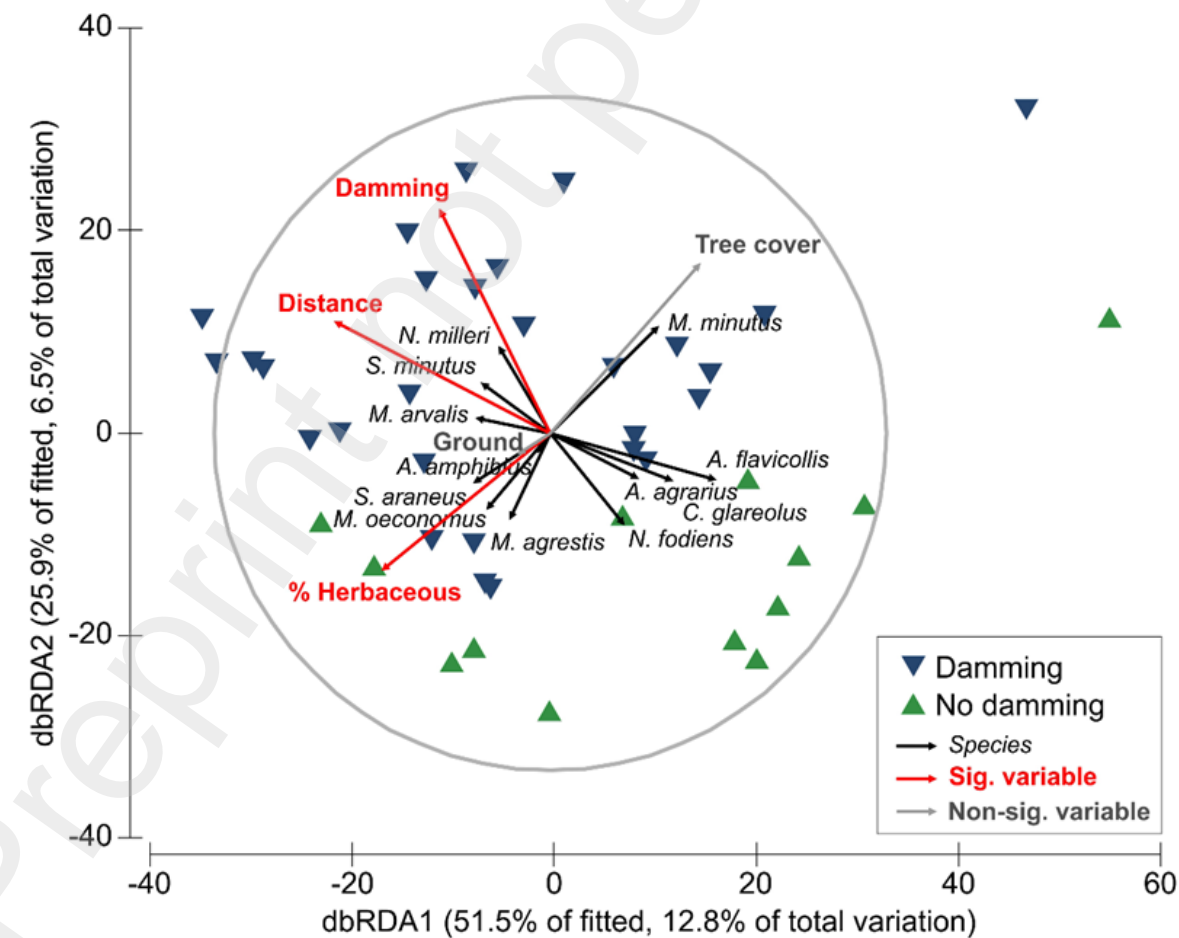


Figure 4. Distance-based redundancy plot (dbRDA) showing the relationship between small mammal species' composition and tested predictors.

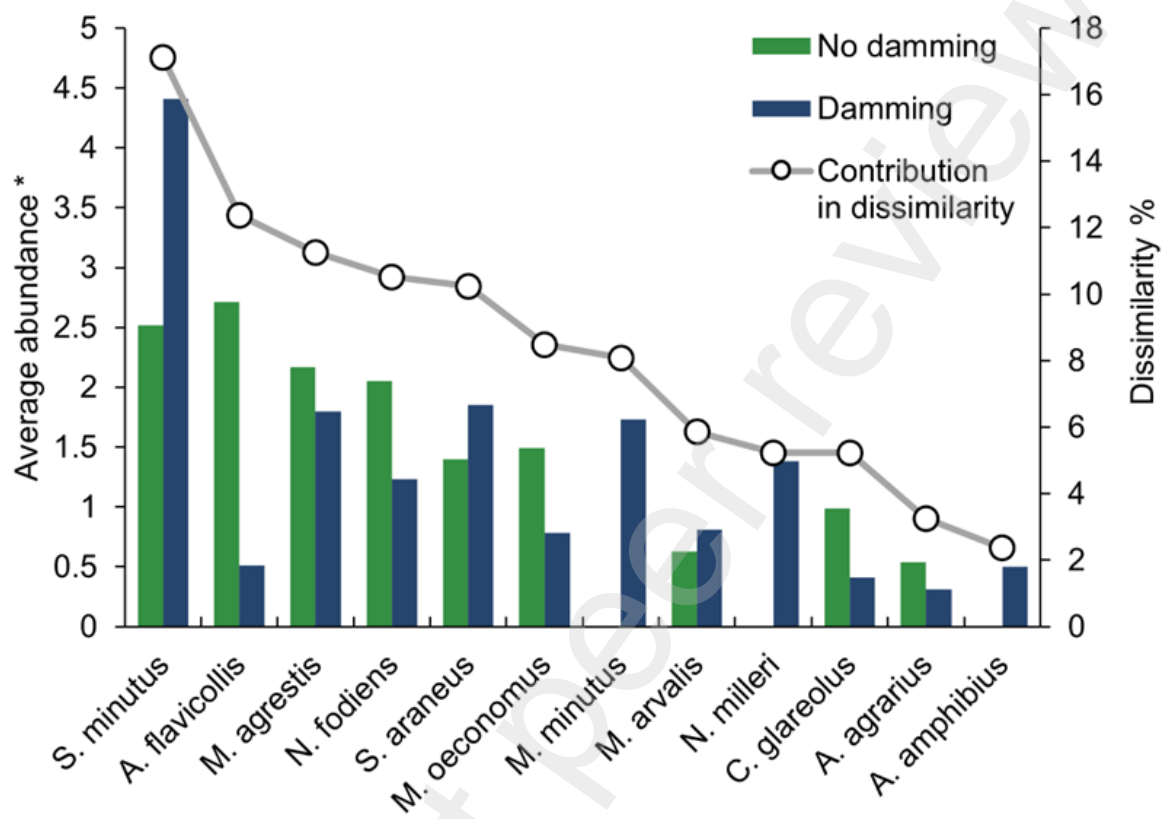


Figure 5. Analysis of similarity (SIMPER) between the damming and no damming. * values of abundance based on standardised (per sample) and transformed (sqrt) data.

3.3. Taxonomic composition of the sample

In total, we trapped 164 small mammals from 12 species: four shrews ($n = 94$) and eight rodents ($n = 70$) including five Cricetidae ($n = 40$) and three Muridae ($n = 30$). The most numerous species was *S. minutus*. Together with *Sorex araneus*, it was also caught in the largest number of sites. The least numerous species were *A. amphibius* and *A. agrarius*. *A. agrarius*

were caught only in one study site. Four identified species (n = 42, 26%) are considered to be semi-aquatic – *N. fodiens*, *N. milleri*, *A. amphibius* and *Microtus oeconomus* (Tab. 2).

Table 2. Taxonomic classification, abundance, dominance and frequency of occurrence of small mammals captured at the studied sites (*semi-aquatic taxa).

Taxonomic group	Species	Number of captures	% of captures	Number of sites
Soricomorpha	Common shrew	17	10%	7
Soricidae	<i>Sorex araneus</i>			
	Eurasian pygmy shrew	46	28%	7
	<i>Sorex minutus</i>			
	Eurasian water shrew*	20	12%	6
	<i>Neomys fodiens</i>			
	Mediterranean water shrew*	11	7%	4
	<i>Neomys milleri</i>			
Rodentia	Bank vole	5	3%	3

Cricetidae	<i>Clethrionomys glareolus</i>			
	Common vole	6	4%	3
	<i>Microtus arvalis</i>			
	Short-tailed field vole	18	11%	6
	<i>Microtus agrestis</i>			
	Root vole*	8	5%	3
	<i>Microtus oeconomus</i>			
	Water vole*	3	2%	2
	<i>Arvicola amphibius</i>			
Rodentia	Eurasian harvest mouse	11	7%	4
Muridae	<i>Micromys minutus</i>			
	Striped field mouse	3	2%	1
	<i>Apodemus agrarius</i>			
	Yellow-necked mouse	16	10%	4

Total	12	164	100%	9
-------	----	-----	------	---

4. Discussion

4.1. Factors behind the failure of previous attempts to document beaver-driven facilitation of small mammal assemblage

We provided the first unequivocal evidence that the Eurasian beaver dams and consequent flooding lead to an increase in abundance and diversity of small terrestrial rodents and shrews. We also revealed, for the first time within the range of the whole beaver genus, that the areas adjacent to beaver dams are hot-spots of small mammal diversity and abundance, with those parameters declining with distance from those constructions. Thus, we confirmed our hypothesis by obtaining results fitting into both predictions. Performing GLMM and GAM analyses validated 300 m long transects as the distance sufficient to test that hypothesis in the observed scale of beaver impact. Plots located at its ends, either upstream, above the beaver pond, or downstream, below the dam, usually acted as a control, with neither an elevated water table nor any other effect of beavers on surrounding habitats. The sampling design allowed overcoming the even strong variation among sites – in a very flat topography, the effect of damming extended far beyond the end of the transect, leaving it with no control; such a situation was sporadic however (one site only). One may wonder why the earlier studies, conducted in several geographical locations, could not reveal similar effects. The potential reasons for that might be the different spatial scale at which the effect occurs, improper selection of control

sites, use of too selective traps, preferred by taxa not affected by beavers and too small a sample size in terms of both sites and individuals.

The only European study focusing on the relationship between small mammal assemblages and beaver damming compared sites where beavers either created a pond or increased a water table in an already existing lake with natural ponds and lakes that remained unmodified by beavers (Sundell et al., 2021). Thus, the methodology of that study assumed two binary states, which precluded the detection of gradual variability with the starting point of that gradient located at the beaver dam. Details about distance between control sites and the nearest beaver ponds were not available in the Finnish study, while one may expect that the difference was simply visible on a smaller spatial scale, probably within the home range of a single beaver family (as already revealed by McCaffery and Eby, 2016, but also our study). Both experimental sites and controls represented lenitic environments, thus Sundell et al. (2021) failed to pinpoint the crucial environmental change caused by beaver damming, i.e. a shift from lotic to lenitic conditions (Brazier et al., 2021; Rosell and Campbell-Palmer 2022). As controls were not selected as random, it is quite possible that some other, presumably abiotic, phenomena reproduced the conditions present in the riparian fringe of the beaver pond. In that particular case, the only difference between experimental sites and controls that can be deduced from the text of this paper is the extensive shallow water areas near shores of beaver ponds and lakes whose outlets were dammed by beavers (Sundell et al., 2021). According to the description of the study area, emergent vegetation was sparse around the studied lakes (Sundell et al., 2021) and there was no evidence for the development of typical fen conditions with organic soils and dense, herbaceous vegetation that favour rich small mammal fauna (Aulak, 1970). On the contrary, experimental recreation of beaver pond conditions in the same region led to a decline in the biomass of herbaceous vegetation with negligible effects on its composition (Nummi, 1989). We cannot exclude that the expected effect is hard to detect in the

boreal forest zone, where most water bodies and wetlands are poor in nutrients and of low productivity; those in the study area of Sundell et al. (2021) are usually classified as oligotrophic ones (Eloranta, 1986). In such conditions, acidic peat bogs often develop and those in woodland biomes of the Palearctic are known to be inhabited by one of the poorest small mammal assemblages among those studied (Boström and Hansson, 1981; Ciechanowski et al., 2013). Vegetation of an experimental beaver pond in the same area already included *Sphagnum* moss (Nummi, 1989) and it might not be a rare case in southern Finland, judging from the extremely widespread occurrence of raised bog habitats (Seppä, 2002). Our study, conducted at lower latitudes, was much more fitted to successfully test for interactions between beaver damming and small mammals, presumably due to the higher productivity of the nemoral biome (Alexandrov and Matsunaga, 2008). This might also explain why our study (54° N) revealed statistically significant effects of beaver damming on small mammals, while that of Sundell et al. (2021) (61° N) did not.

Some of the scarce, already available studies on the subject revealed numerical differences but were not even feasible for statistical testing, leaving aside modelling and it is understandable that the authors did not attempt to undertake it. This would require either multiple beaver sites or drainages, treating single traps or parts of the trap-line as single data points (like in our study) or finally, trap mammals during many nights on two plots and treat those days as single data points as well. The latter approach would be, however, a typical example of pseudoreplication (Hurlbert, 1984). It seems that differences between individual sites sometimes outweigh the differences between broad classes of sites. This explains why, in one Russian site, Fyodorov and Yakimova (2012) found an abundance of small mammals about twice higher around an abandoned beaver pond than in a habitat unmodified by beavers, while in the other site, small mammal abundance dropped ten times. Moreover, in the second site, only two species (one rodent and one shrew) inhabited beaver pond shores, contrary to five

species in beaver-free habitats. Even in the first site, the increase in abundance was not followed by an increase in species richness, as only one species (*S. araneus*) inhabited the beaver pond, while two species were trapped in unmodified patches. The revealed structure of small mammal assemblage was not an effect of undersampling, as trapping was conducted for five years in those sites, simply methodology precluded separation of beaver effect from random effect of site. Even including five pairs of beaver-occupied and unoccupied reaches in the study design was not enough to reveal any significant differences in small mammal abundance and diversity, despite catching 1531 individuals of 16 species in Oregon. Significantly higher variability in capture rates among beaver-occupied sites than among controls, found for five species, might explain, why that study failed to document any community- or species-level facilitation by ecosystem engineer, especially when no intra-site variation in habitat structure was addressed (Suzuki and McComb, 2005). This is why the results of other studies with a similar approach should be treated with caution. An almost three-fold increase in relative density and biomass of small mammals around a beaver pond, compared to adjacent habitat, was revealed in Idaho, based on a quite impressive sample (2400 trap-nights and 203 individuals, belonging to eight species, trapped) but the study used only two plots, one representing the shores of a beaver pond and one representing a control (Medin and Clary, 1991). Judging from the negative results of the other, already mentioned studies, that difference could also be obtained by chance.

Another factor that could obscure the effect of beaver damming in the previous small mammal studies is the application of traps that are too selective and favour detection of particular taxa. Usually small terrestrial mammals are sampled with traps belonging to three types – live-traps, snap traps and pitfalls. Some papers claim that live- and snap traps are more efficient in catching rodents, and pitfalls in catching shrews (Rathke and Bröring, 2005; Nicolas and Colyn, 2006). However, other studies revealed that only snap and live-traps underestimated the abundance and dominance of shrews, while the efficiency of rodent trapping with all three

412 types of traps remained similar (Pucek, 1969; O'Brien et al., 2006). In some extremely diverse
413 biomes, using pitfalls alone may even generate higher estimates of overall small mammal
414 abundance and species richness, as well as rodent abundance and/or species richness than using
415 not only live-traps alone but also both types of traps together (Bovendorp et al., 2017). If the
416 shrews were the most affected group by beaver damming, while the reaction of rodents is
417 weaker, using exclusively those highly selective types of traps, luring mostly rodents with baits
418 (i.e. snap and live-traps) might result in failure to reveal any difference between flooded and
419 unflooded habitats at all. Unfortunately, the only Eurasian study on the subject also applied
420 snap traps, which resulted in obtaining strongly rodent-biased material with only 6.5% (N =
421 215 mammals) consisting of shrews (Sundell et al., 2021). The earlier experiments in almost
422 the same area, i.e. Finland at 60° N, already revealed that the application of cone traps provides
423 not only much higher catch indices but also a much more balanced picture of small mammal
424 assemblage, providing abundant material of both shrews and rodents. On the contrary, snap
425 traps captured not only three times less mammals but also material that remained strongly
426 rodent-biased. The difference was even stronger when analysing particular species, with not
427 only a 37-times higher catch index for *S. minutus* but a 70-times higher for the smallest
428 European rodent, *M. minutus*, in pitfalls than in snap traps (Pankakoski, 1979). Meanwhile,
429 both mentioned species benefited the most from beaver damming by beavers in our study, while
430 none of them were detected by Sundell et al. (2021), despite their frequent occurrence in
431 southern Finland (Mitchell-Jones et al., 1999). Thus, the application of snap traps not only led
432 to unnecessary sacrifice of studied animals, as all of those species could easily be identified
433 based on external features (Pucek, 1984) and released but also contributed to failure of the
434 Finnish study. The majority of methodological studies confirmed, on the other hand, that we
435 choose the optimal method of small mammal sampling to test our hypotheses, even if some

species, predominantly *A. flavicollis*, might remain undersampled with pitfalls due to their ability to jump out of the trap (Pelikan et al., 1977; Pankakoski, 1979).

4.2. Potential benefits of beaver ecosystem engineering for small mammals

Small rodents and shrews may benefit, directly or indirectly, due to various impacts of beaver activity on their habitat. As most of them should be considered rather a generalist, based on their widespread occurrence in a broad range of habitats (Aulak, 1970), several species can increase their abundance due to similar factors. In general, beavers create a disturbance in the riparian zone and surrounding woodland, switching the habitat from late (mature forest) to early or even initial stages of succession (non-forest communities), due to both flooding and tree felling. Therefore, beaver wetlands and canopy gaps resemble windthrows, clearings, landslides and post-fire areas, and all those disturbed habitats often reveal much more diverse small mammal assemblages than mature woodlands, with diversity and/or abundance decreasing with progressing succession (Grodziński, 1958; Powell and Brooks, 1981; Bogdziewicz and Zwolak, 2014; Torre et al., 2023). These effects are far from being universal however, even with the very same species usually benefiting from disturbance (Wołk and Wołk, 1982) but declining with a drop in canopy cover in some specific habitats (Benedek et al., 2021). There are also some strictly terrestrial rodents that always negatively react to logging, while arboreal species, like squirrels and dormice, always become the losers when the closed canopy vanishes (Bogdziewicz and Zwolak, 2014). The main reason for qualitative and quantitative enrichment of a small mammal assemblage after damming the stream by beavers might be an increase in cover, biomass and diversity of plants in the herbaceous layer, a crucial factor affecting the structure of that assemblage (Aulak, 1970). In the temperate woodland zone, early succession stages, like meadows were characterised by a much larger standing crop biomass of ground

vegetation, compared to mature deciduous forests on mesic soils (Jędrzejewski and Jędrzejewska, 1996). One may expect that increased plant cover provides more shelter against predation to all species, more food to herbivores and habitat for potential prey to insectivores. In our DistLM model, the % of herbaceous layer explained the variability of small mammal assemblages to an even greater extent than the direct impact of beaver damming but it also affected ordination of plots into 'damming' and 'no damming' categories, suggesting that it was responsible for an important part of that effect. This was especially visible in forest plots including traps located far upstream from a dam, where almost no effect of flooding was visible, where lush cover of herbs was replaced by an almost bare forest floor, covered by a layer of tree litter and only sparse plants. Damming can increase plant diversity but also % coverage for the majority of herbaceous species in the beaver site, leading to a decline of only a few nitrophilous species (Law et al., 2017). Not all of the impact of beaver damming on small mammals can be explained by an increase in herbaceous layer coverage induced by mature forest disturbance. First, some of our beaver ponds were established in forests growing not on mesic but on hydric soils, usually alder stands, which already had lush and tall ground vegetation in summer (Leuschner and Ellenberg, 2017a). Still, on a landscape scale, beavers can increase the extent of those woodland communities. Second, some of our sites were located in habitats anthropogenically deforested for a long time, usually mowed meadows, where herbaceous coverage almost always reached 100% (Leuschner and Ellenberg, 2017b), irrespective of beaver presence; thus, the impact of the latter must go beyond structural responses of vegetation.

Inundation of valley bottoms by beaver damming leads to increasing soil humidity in surrounding habitats (Law et al., 2017) and an increased fertility of the created wetlands by storage of nutrients (Bason et al., 2017) may lead to increased net primary production (Johnston, 2014). This probably starts a bottom-up trophic cascade, subsidising small mammals belonging

486 to different trophic levels, even if not aligned in a single trophic chain – primary (voles, mice),
487 as well as secondary and tertiary consumers (mice, shrews) (classified based on dietary data:
488 Drózd, 1966; Watts, 1968; Babińska-Werka and Garbarczyk, 1981; Faber and Ma, 1986;
489 Dickman, 1986; Churchfield and Rychlik, 2006; Lantová and Lanta, 2009; Soininen et al.,
490 2009). That cascade is, at least partially, fuelled by carbon accumulated in an aquatic
491 environment. Analysis of carbon and nitrogen stable isotopes revealed, indeed, a significant
492 aquatic subsidy to the Nearctic generalist rodent, *Peromyscus maniculatus* living on shores of
493 beaver ponds. That contribution of aquatic-derived carbon declined linearly with distance from
494 the stream banks both in sites dammed and not dammed by beavers but it extended farther
495 inland near beaver-modified locations (McCaffery and Eby, 2016). As the diet of *P.*
496 *maniculatus* consists of both plants and arthropods in a similar proportion (Wolff et al., 1985),
497 comparable to Palearctic *Apodemus* mice (Drózd, 1966), that subsidy could reach *P.*
498 *maniculatus* either directly or through at least one, additional trophic level. Abundance of
499 aquatic insects emerging from a beaver pond can also lead to a high contribution of aquatic-
500 derived carbon in predatory, terrestrial arthropods, particularly wolf spiders (Lycosidae), which
501 also occur in a 60% higher density around beaver-impounded sites than near lotic sections of
502 streams (McCaffery and Eby, 2016). Although the Eurasian counterpart of that study is lacking,
503 it is worth noting that the most abundant small mammal in our study, *S. minutus*, is an epigeal
504 insectivore, preying predominantly on spiders (Churchfield and Rychlik, 2006). It is also the
505 more hygrophilous species among the two *Sorex* species in our sample, selecting areas located
506 closer to water (Rychlik, 2000). Beavers also facilitate the occurrence of alder-dominated
507 riparian woodlands along streams, and those communities are distinguished by a high relative
508 abundance of earthworms (Lumbricidae) (Leuschner and Ellenberg, 2017a). Meanwhile,
509 another generalist shrew, common across the Eurasian beaver range, *S. araneus*, forages
510 predominantly on earthworms (Churchfield and Rychlik, 2006) and thus, might also trophically

benefit from beaver damming in some locations. As beaver ponds are usually the deepest and the most voluminous just above the dams (Karran et al., 2017), the extent of paludification may also be expected to be the highest close to a dam. Similarly, the relative thickness of sediments stored in beaver ponds attain the highest values just above the dams (De Visscher et al., 2013) and so too, probably, are nutrient storage and resulting soil fertilisation. Both effects might, therefore, be responsible not only for binary differences in small mammal occurrence between dammed and non-dammed sections but also for gradient in diversity and abundance between a dam and the areas located far from the centre of beaver territory. Some species, especially dominants (*S. minutus*, *S. araneus*) preferred dammed plots but did not decline in abundance with distance, supporting our view that both effects were not entirely co-dependent.

Beaver impact on surrounding habitats extends well beyond inundation and paludification (Rosell et al., 2005) and some of their activities may generate similar effects on small mammal assemblage, despite being unrelated to the creation of wetlands or ponds. The structure of a dam, especially its downstream face, resembles the roof and walls of a lodge (Rosell and Campbell-Palmer 2022), thus one may expect that it offers a lot of shelter among twigs and other woody debris used for construction. Lodges of Eurasian beavers are already known to be visited by a significantly higher number of common, generalist rodents and shrews than are trapped in the adjacent forest (Samas and Ulevičius, 2015) and if dams provide similar services to those mammals, they could become a nexus of their activity, generating a gradient of trapping success, similar to that observed in our study. This applied however only to higher dams, while a similar pattern occurred near the smallest and lowest dams (extending only 5 cm above the water surface on both sites), covered with mud from both sides. Still, even the small dams improve habitat connectivity for small mammals acting as bridges for river crossing (Wikar and Ciechanowski, 2023). Beavers fell a lot of trees during foraging and some of them, especially the largest trunks, remain on the spot (Rosell and Campbell-Palmer 2022),

significantly increasing the amount of deadwood, including coarse woody debris (CWD) in nearby habitats (Thompson et al., 2016). Meanwhile, high volumes of CWD facilitates the abundance of small mammals (Loeb, 1999; Fauteux et al., 2012). As beavers are the central-place foragers, they cut most of the trees and the largest of them, close to the centre of their territories (Raffel et al., 2009), which is indicated either by location of a lodge, den or winter food cache, all located usually at the deepest part of the pond, i.e. close to a dam (Rosell and Campbell-Palmer 2022). Therefore, tree felling by beavers and consequent CWD provision may contribute to the observed gradient but only at sites with mature forest adjacent to the stream banks, and not on inundated meadows.

Some more species-specific effects require additional explanation. A quarter of all captures represented semi-aquatic taxa, both insectivores (*N. fodiens*, *N. milleri*) and herbivores (*M. oeconomus*, *A. amphibius*) (Pucek, 1984). It is already known that other medium-sized and large semi-aquatic mammals benefit from beaver constructions and beaver-created wetlands (Sidorovich et al., 1996; Mott et al., 2013; Nummi et al., 2019; Fedyń et al., 2022), thus one may expect a similar effect in small rodents and shrews belonging to the same guild. Their response was, however, a mixed one. *N. milleri* appeared to be associated exclusively with beaver-inundated plots. This remains in concordance with its microhabitat preferences and foraging behaviour – the species wades in shallow water overgrown with dense, emerged vegetation, often among tufts of sedges (Rychlik, 1997), feeding on both terrestrial and aquatic prey (Churchfield and Rychlik, 2006). As beaver dams generate extensive areas of shallow water beyond the original stream channel, those newly created wetlands, in particular, fit into *N. milleri* habitat requirements (Rychlik, 2000). Astonishingly, its congeneric, *N. fodiens*, did not reveal such a strong alignment to dammed sections of the trap-lines, despite its preferences for deep water, immediate neighbourhood of stream banks and diving for aquatic prey as the predominant foraging mode (Rychlik, 1997, 2000). In our study, it was trapped even slightly

more often on plots with no visible effects of damming. As *N. fodiens* uses steep, eroded banks to dig dens for nesting (Rychlik, 1997), it may even align with unaltered lotic conditions, which do not exclude benefits from the other effects of beaver presence (see below). Among the two water shrews in Poland, that species can appear in a much broader spectrum of habitats (Aulak, 1970) to the point of being unsuitable as a bioindicator of water quality (Scott et al., 2012). Specialisation of *N. milleri* may result from competitive displacement and interspecific aggression by larger, more generalist congeneric (Rychlik and Zwolak, 2006; Kryštufek and Quadracci, 2008; Tapisso et al., 2013), therefore, beaver ponds may even increase chances to escape from potential competition.

Even if six species were trapped less frequently on plots with damming, only one of them, *A. flavicollis*, contributed strongly to the dissimilarity between both categories, with a five-fold difference in average abundance. Indeed, waterlogging may affect that taxon negatively, as – contrary to the other species – it is known to attain the highest abundance in dominance in late successional stages (Grodziński, 1958), preferring closed canopy (Benedek et al., 2021), especially beech, oak and hornbeam forests on mesic soils, providing crops of heavy seeds (Juškaitis, 2002), being its predominant food resource (Drózd, 1966). Switching from that habitat to alder-ash forests or even open wetlands due to damming may lead to local disappearance of its preferred food. However, based on the GAM analysis, we assume that *A. flavicollis* still benefits from beaver activities, probably by using dams for shelter in a similar way, as it has already been known to use lodges, visited with significantly higher frequency (Samas and Ulevičius, 2015) but also from the connective function of a dam and abundance of CWD. The same explanation may apply to the other species that do not align with inundated sections but significantly increase their abundance close to a dam, especially *N. fodiens*, the most abundant semi-aquatic taxon. Not even a single species in our study was restricted solely to the ‘no damming’ plots, while three species were trapped exclusively on ‘damming’ plots

and the only species-specific, significant effects of distance from a dam on abundance were negative. All those lines of evidence point to the fact that creation of wetlands by beavers leads to a net increase in small mammal species richness. That effect might vary with spatial scale, with the smallest dams (e.g. on small drainage ditches) benefiting small mammals only to a negligible level but we could not find such differences in our material, probably due to the limited sample size.

4.3. Conservation implications

Beaver sites may act as refuges for rare and threatened species (Bartel et al., 2010), especially in a heavily managed landscape. This also applies to small, terrestrial mammals, often a neglected element of biodiversity. Endemic subspecies of meadow jumping mouse, *Zapus hudsonicus luteus* (Zapodidae), are restricted to tall, dense, herbaceous riparian vegetation in the otherwise arid and mountainous American Southwest and have lost 70–90% of its historical range. Its decline is caused primarily by habitat loss, due to livestock grazing, against which beaver-created wetlands provide effective protection (Frey and Malaney, 2009). In one German study, the only individuals of a locally and regionally threatened northern birch mouse, *Sicista betulina* (Sminthidae), were captured at beaver ponds (Orazi et al., 2022). As revealed by our data, beavers can facilitate the availability of habitat for *N. milleri*, an uncommon species only recently distinguished from its allopatric sibling, *N. anomalus*, a stenotopic taxon (Aulak, 1970), characterised by disjunct, presumably relict distribution (Igea et al., 2015). Although classified as being of least concern in Poland (Głowaciński, 2002), it is considered highly threatened in the national red list of neighbouring Germany (Meinig et al., 2020). The other two species, restricted to ‘dammed’ plots in our sample, *M. minutus* and *A. amphibius*, are considered threatened to a various extent in some Western European countries (Meinig et al., 2020; Mathews and Harrower, 2020). Their association with beaver sites may

mitigate their decline, especially in areas where reintroduction of beavers is ongoing (Stringer and Gaywood, 2016).

Overall abundance and diversity of small mammals, especially rodents, in beaver-modified habitats may also be a crucial factor for restoration of mature woodland when disturbance by the ecosystem engineer ceases and the opportunity for secondary succession appears. In North America, upon abandonment of dams by beavers, drained ponds often turn into predominantly graminoid patches, so called 'beaver meadows' that resist colonisation by conifers due to a lack of ectomycorrhizal fungi. Spores of the latter are dispersed by the mycophagous red-backed vole, *Clethrionomys gapperi*, which deliver them to the soil with faecal pellets. The species is a forest specialist, largely absent in open beaver meadows but is present in meadow-woodland ecotones, which makes it a crucial vector of ectomycorrhizal fungi that facilitate closing the succession cycle (Terwilliger and Pastor, 1999). Although no similar study was conducted in the range of the Eurasian beaver, one may expect a similar function of small mammals in habitats the bearing long-term legacy of its impact.

5. Conclusions

Our study filled, at least partially, a significant gap in knowledge about the engineering function of the Eurasian beaver, one of the best studied keystone species and ecosystem engineers (Rosell and Campbell-Palmer 2022), providing further evidence for whole-community facilitation by that rodent (Nummi and Holopainen, 2020). The direct mechanisms of that facilitation require further studies but it is probably the increase in both heterogeneity and productivity that are responsible for most of the effect. Our key findings, i.e. the fact that beaver dams and ponds are hot-spots of small mammal abundance and diversity, may probably point to the similar function of the North American beaver and provide additional arguments for protection of both species and their reintroduction to the areas from which they were

expatriated (e.g. Gaywood, 2018). Their potential to enrich small mammal abundance may have increased in recent times, due to successful recolonisation of their former ranges (Halley et al., 2020). Many European mammals are highly exposed to the consequences of anthropogenic climate change, while revealing a critically low range-shift capacity, and small terrestrial mammals constitute a significant portion of them (Morrison et al., 2018). The expanding beaver populations may provide refuges for the most hygrophilous and oligothermophilous small rodents and soricomorphs, just as they are expected to mitigate the effects of climate change on the other elements of the ecosystem (Jordan and Fairfax, 2022).

CRedit authorship contribution statement

ZW: Conceptualization, Methodology, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Supervision. **MC:** Conceptualization, Methodology, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing. **AZ:** Methodology, Formal analysis, Writing - Review & Editing, Visualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Professional proofreading was funded by the Department of Vertebrate Ecology and Zoology. University of Gdansk. Subsidy number: 531-D050-D244-23-S0.

We are cordially thankful to Grażyna Sadowska, Grażyna Butrykowska, Elwira Ahmad and Magdalena Jędro for informations about locations of beaver dams and to Michał Pawlik, Katarzyna Borzym, Magdalena Jędro and Małgorzata Goc for help with the fieldwork.

661
662
663
664
665
666
667
668
669
670
671
672
673
674
675
676
677
678
679
680
681
682
683
684

References

- Alexandrov, G.A., Matsunaga, T., 2008. Normative productivity of the global vegetation. Carbon Balance Manag. 3, 8. <https://doi.org/10.1186/1750-0680-3-8>
- Anderson, M.J., 2014. Permutational multivariate analysis of variance (PERMANOVA). Wiley statsref: statistics reference online. 1-15.
- Andrzejewski, R., Babińska-Werka, J., Liro, A., Owadowska, E., Szacki, J., 1997. The attractiveness of conspecific and interspecific odor for bank voles *Clethrionomys glareolus*. Acta Theriol. 42, 231-234.
- Aulagnier, S., Haffner, P., Mitchell-Jones, A.J., Moutou, F., Zima, J., 2009. Mammals of Europe, North Africa and Middle East, first ed. A&C Black Publishers Ltd., London.
- Aulak, W., 1970. Small mammal communities of the Białowieża National Park. Acta Theriol. 15, 465–515.
- Babińska-Werka, J., Garbarczyk, H., 1981. Food of the striped field mouse in different types of urban green areas. Acta Theriol. <https://doi.org/10.4098/at.arch.81-24>
- Bashinskiy, I.W., Stojko, T.G., 2022. The more Diverse Beaver Ponds are Better – a Case Study of Mollusc Communities of Steppe Streams. Wetlands. 42, 104. <https://doi.org/10.1007/s13157-022-01625-8>
- Bartel, R., Haddad, N., Wright, J., 2010. Ecosystem engineers maintain a rare species of butterfly and increase plant diversity. Oikos. 119. 883 - 890. 10.1111/j.1600-0706.2009.18080.x
- Bason, C., Kroes, D., Brinson, M., 2017. The Effect of Beaver Ponds on Water Quality in Rural Coastal Plain Streams. Southeast. Nat. 16, 584. 10.1656/058.016.0408
- Bates, D.M., 2010. lme4: Mixed-effects modeling with R.

685 Benedek, A.M., Sîrbu, I., Lazăr, A., 2021. Responses of small mammals to habitat
686 characteristics in Southern Carpathian forests. Sci. Rep. 11, 12031.
687 <https://doi.org/10.1038/s41598-021-91488-6>

688 Bogdziewicz, M., Zwolak, R., 2014. Responses of small mammals to clear-cutting in temperate
689 and boreal forests of Europe: a meta-analysis and review. Eur. J. Forest. Res. 133, 1–
690 11. <https://doi.org/10.1007/s10342-013-0726-x>

691 Boström, U., Hansson, L., 1981. Small rodent communities on mires: implications for
692 population performance in other habitats. Oikos. 37: 216-224.

693 Bovendorp, R., Mccleery, R., Galetti, M., 2017. Optimising sampling methods for small
694 mammal communities in Neotropical rainforests. Mamm. Rev. 47, 148-158.
695 [10.1111/mam.12088](https://doi.org/10.1111/mam.12088).

696 Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H., Brown, C.M.L., 2021.
697 Beaver: Nature's ecosystem engineers. WIREs Water. 8:e1494.
698 <https://doi.org/10.1002/wat2.1494>

699 Churchfield, S., Rychlik, L., 2006. Diets and coexistence in Neomys and Sorex shrews in
700 Białowieża forest, eastern Poland. J. Zool. 269, 381–390.
701 <https://doi.org/10.1111/J.1469-7998.2006.00115.X>

702 Ciechanowski, M., Kubic, W., Rynkiewicz, A., Zwolicki, A., 2010. Reintroduction of beavers
703 *Castor fiber* may improve habitat quality for vespertilionid bats foraging in small river
704 valleys. Eur. J. Wildl. Res. 57, 737–747.

705 Ciechanowski, M., Cichocki, J., Ważna, A., Piłacińska, B., 2013. Small-mammal assemblages
706 inhabiting *Sphagnum* peat bogs in various regions of Poland. Biol. Lett. 49, 115–133.
707 <https://doi.org/10.2478/v10120-012-0013-4>

708 Clarke, K., Gorley, R., 2007. PRIMER-6 6.1. 10. PRIMER-E Ltd, Plymouth.

709 Coggan, N.V., Hayward, M.W., Gibb, H., 2018. A global database and “state of the field”
 710 review of research into ecosystem engineering by land animals. *J. Anim. Ecol.* 87, 974–
 711 994. <https://doi.org/10.1111/1365-2656.12819>
 712 Dalbeck, L., Lüscher, B., Ohlhoff, D., 2007. Beaver ponds as habitat of amphibian communities
 713 in a central European highland. *Amphib-Reptil.* 28, 493-501.
 714 De Visscher, M., Nyssen, J., Pontzele, J., Billi, P., Frankl, A., 2013. Spatio-temporal
 715 sedimentation patterns in beaver ponds along the Chevril river, Ardennes, Belgium.
 716 *Hydrol. Process.* 28, 1602–1615. doi:10.1002/hyp.9702
 717 Dickman, C., 1986. Habitat utilization and diet of the harvest mouse, *Micromys minutus*, in an
 718 urban environment. *Acta Theriol.* 31. 249-256. 10.4098/AT.arch.86-24
 719 Drózd, D. 1966. Food habits and food supply of rodents in the beech forest. *Acta Theriol.* 11,
 720 363-384.
 721 Eloranta, P., 1986. Phytoplankton Structure in Different Lake Types in Central Finland.
 722 *Holarct. Ecol.* 9, 214–224.
 723 Faber, J.H., Ma, W., 1986. Observations on seasonal dynamics in diet composition of the field
 724 vole, *Microtus agrestis*, with some methodological remarks. *Acta Theriol.* 31, 479-490.
 725 10.4098/AT.arch.86-43
 726 Fairfax, E., Whittle, A., 2020. Smokey the Beaver: beaver-dammed riparian corridors stay
 727 green during wildfire throughout the western USA. *Ecol. Appl.* 30. e02225.
 728 10.1002/eap.2225
 729 Fauteux, D., Imbeau, L., Drapeau, P., Mazerolle, M.J., 2012. Small mammal responses to
 730 coarse woody debris distribution at different spatial scales in managed and unmanaged
 731 boreal forests. *For. Ecol. Manag.* 266, 194-205.
 732 <https://doi.org/10.1016/j.foreco.2011.11.020>

733 Fedyń, I., Przepióra, F., Sobociński, W., Wyka, J., Ciach, M., 2022. Eurasian beaver – A semi-
734 aquatic ecosystem engineer rearranges the assemblage of terrestrial mammals in winter.
735 Sci. Total Environ. 831, 154919. <https://doi.org/10.1016/j.scitotenv.2022.154919>
736

737 Frey, J., Malaney, J., 2009. Decline of the Meadow Jumping Mouse (*Zapus hudsonius luteus*)
738 in two Mountain Ranges in New Mexico. Southwest. Nat. 54, 31-44. 10.1894/MLK-
739 07.1

740 Fyodorov, F., Yakimova, A., 2012. Changes in ecosystems of the middle taiga due to the impact
741 of beaver activities, Karelia, Russia. Balt. For. 18, 278-287.

742 Gaywood, M.J., 2018. Reintroducing the Eurasian beaver *Castor fiber* to Scotland. Mamm.
743 Rev. 48, 48-61. <https://doi.org/10.1111/mam.12113>

744 Głowaciński, Z., 2002. Czerwona lista zwierząt ginących i zagrożonych w Polsce. Instytut
745 Ochrony Przyrody PAN, Kraków.

746 Grodziński, W., 1958. The succession of small mammal communities on an overgrown clearing
747 and landslip in the Western Carpathians. – Bull. Acad. Pol. Sci., Cl. II, Ser. Sci. Biol. 9,
748 493-499.

749 Grover, A., Baldassarre, G., 1995. Bird species richness within beaver ponds in south-central
750 New York. Wetlands. 15, 108–118.

751 Grudzinski, B.P., Fritz, K., Golden, H.E., Newcomer-Johnson, T.A., Rech, J.A., Levy, J., Fain,
752 J., McCarty, J.L., Johnson, B., Vang, T.K., Maurer, K., 2022. A global review of beaver
753 dam impacts: Stream conservation implications across biomes. Glob. Ecol. Conserv. 37,
754 e02163, <https://doi.org/10.1016/j.gecco.2022.e02163>

755 Halley, D.J., Saveljev, A.P., Rosell, F., 2020. Population and distribution of beavers *Castor*
756 *fiber* and *Castor canadensis* in Eurasia. Mamm. Rev. 51, 1-24.
757 <https://doi.org/10.1111/mam.12216>

758 Hartman, G., Törnlov, S., 2006. Influence of watercourse depth and width on dam-building
 759 behaviour by Eurasian beaver (*Castor fiber*). J. Zool. 268, 127-131.
 760 <https://doi.org/10.1111/j.1469-7998.2005.00025.x>
 761 Hayward, G. F., Phillipson, J., 1979. Community structure and functional role of small
 762 mammals in ecosystems. In: Stoddart, M.D. (Eds.), Ecology of Small Mammals.
 763 Springer, Dordrecht, pp. 135–211. doi:10.1007/978-94-009-5772-5_4
 764 Hurlbert, S.H., 1984. Pseudoreplication and the Design of Ecological Field Experiments. Ecol.
 765 Monogr. 54, 187-211. <https://doi.org/10.2307/1942661>
 766 Igea, J., Aymerich, P., Bannikova, A., Gosálbez, J., Castresana, J., 2015. Multilocus species
 767 trees and species delimitation in a temporal context: Application to the water shrews of
 768 the genus *Neomys*. BMC Evol. Biol. 15. 10.1186/s12862-015-0485-z
 769 Janiszewski, P., Hanzal, V., Misiukiewicz, W., 2014. The Eurasian Beaver (*Castor fiber*) as a
 770 Keystone Species – a Literature Review. Balt. For. 20(2): 277-286.
 771 Jędrzejewski, W., Jędrzejewska, B., 1996. Rodent cycles in relation to biomass and productivity
 772 of ground vegetation and predation in the Palearctic. Acta Theriol. 41, 1-34.
 773 10.4098/AT.arch.96-1
 774 Johnston, C.A., Naiman, R.J., 1990. Browse selection by beaver: effects on riparian forest
 775 composition. Can. J. For. Res. 20, 1036-1043. <https://doi.org/10.1139/x90-138>
 776 Johnston, C.A., 2014. Beaver pond effects on carbon storage in soils. Geoderma. 213, 371–378.
 777 doi:10.1016/j.geoderma.2013.08.025
 778 Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69,
 779 373-386.
 780 Jordan, C.E., Fairfax, E., 2022. Beaver: The North American freshwater climate action plan.
 781 WIREs Water. 9, e1592. <https://doi.org/10.1002/wat2.1592>

782 Juškaitis, R., 2002. Spatial distribution of the yellow-necked mouse (*Apodemus flavicollis*) in
 783 large forest areas and its relation with seed crop of forest trees, Mamm. Biol. 67, 206-
 784 211. <https://doi.org/10.1078/1616-5047-00031>.
 785 Karran, D., Westbrook, C., Wheaton, J, Johnston, C., Bedard-Haughn, A., 2017. Rapid surface-
 786 water volume estimations in beaver ponds. Hydrol. Earth Sys. Sci. 21, 1039-1050.
 787 10.5194/hess-21-1039-2017
 788 Kemp, P., Worthington, T., Langford, T., Tree, A., Gaywood, M., 2011. Qualitative and
 789 quantitative effects of reintroduced beavers on stream fish. Fish Fish. 13, 158-181.
 790 10.1111/j.1467-2979.2011.00421.x
 791 Kryštufek, B., Quadracci, A., 2008. Effects of latitude and allopatry on body size variation in
 792 European water shrews. Acta Theriol. 53, 39–46. <https://doi.org/10.1007/BF0319427>
 793 Kuznetsova, A., Brockhoff, P.B., Christensen, R.H., 2017. lmerTest package: tests in linear
 794 mixed effects models. Journal of statistical software. 82, 1-26.
 795 Lantová, P., Lanta, V., 2009. Food selection in *Microtus arvalis*: the role of plant functional
 796 traits. Ecol. Res. 24, 831-838. <https://doi.org/10.1007/s11284-008-0556-3>
 797 Larsen, A., Larsen, J.R., Lane, S.N., 2021. Dam builders and their works: Beaver influences on
 798 the structure and function of river corridor hydrology, geomorphology, biogeochemistry
 799 and ecosystems. Earth Sci. Rev. 218. <https://doi.org/10.1016/j.earscirev.2021.103623>
 800 Law, A., Gaywood, M., Jones, K., Ramsay, P., Willby, N., 2017. Using ecosystem engineers
 801 as tools in habitat restoration and rewilding: beaver and wetlands. Sci. Total Environ.
 802 605-606. 1021-1030. 10.1016/j.scitotenv.2017.06.173
 803 Leuschner, C., Ellenberg, H., 2017a. Ecology of Central European Forests. Vegetation Ecology
 804 of Central Europe Vol. I. Revised and Extended Version of the 6th German Edition
 805 Translated by Laura Sutcliffe. Springer International Publishing, Cham, 992 pp.

- 806 Leuschner, C., Ellenberg, H., 2017b. Ecology of Central European Non-Forests Vegetation:
807 Coastal to Alpine, Natural to Man-Made Habitats. Vegetation Ecology of Central
808 Europe Vol. II. Revised and Extended Version of the 6th German Edition Translated by
809 Laura Sutcliffe. Springer International Publishing, Cham, 992 pp.
- 810 Loeb, S. C., 1999. Responses of Small Mammals to Coarse Woody Debris in a Southeastern
811 Pine Forest. *J. Mamm.* 80, 460–471. <https://doi.org/10.2307/1383293>
- 812 Lüdecke, D., 2018.ggeffects: Tidy data frames of marginal effects from regression models. *J.*
813 *Open Source Softw.* 3, 772.
- 814 McCaffery, M., Eby, L., 2016. Beaver activity increases aquatic subsidies to terrestrial
815 consumers. *Freshw. Biol.* 61, 518-532. <https://doi.org/10.1111/fwb.12725>
- 816 Mathews, F., Harrower, C., 2020. IUCN – compliant Red List for Britain’s Terrestrial
817 Mammals. Assessment by the Mammal Society under contract to Natural England,
818 Natural Resources Wales and Scottish Natural Heritage. Natural England,
819 Peterborough.
- 820 Medin, D. E., Clary, W. P., 1991. Small mammals of a beaver pond ecosystem and adjacent
821 riparian habitat in Idaho. United States Department of Agriculture, Forest Service,
822 Intermountain Research Station, Research Paper INT-445: 1-5.
- 823 Meinig, H., Boye, P., Dähne, M., Hutterer, R., Lang, J., 2020. Rote Liste und Gesamtartenliste
824 der Säugetiere (Mammalia) Deutschlands. *Naturschutz und Biologische Vielfalt.* 170,
825 73.
- 826 Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H.,
827 Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V., Zima, J., 1999. The atlas
828 of European mammals. Poyser natural history, Poyser.

829 Morrison, L., Estrada, A., Early, R., 2018. Species traits suggest European mammals facing the
830 greatest climate change are also least able to colonize new locations. *Divers. Distrib.* 24,
831 1321– 1332. <https://doi.org/10.1111/ddi.12769>

832 Mott, C., Bloomquist, C., Nielsen, C., 2013. Within-lodge interactions between two ecosystem
833 engineers, beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*). *Behaviour.*
834 150. 10.1163/1568539X-00003097

835 Nicolas, V., Colyn, M., 2006. Relative efficiency of three types of small mammal traps in an
836 African rainforest. *Belg. J. Zool.* 136.

837 Nolet, B.A., Hoekstra, A., Ottenheim, M.M., 1994. Selective foraging on woody species by the
838 beaver *Castor fiber*, and its impact on a riparian willow forest, *Biol. Conserv.* 70, 117-
839 128. [https://doi.org/10.1016/0006-3207\(94\)90279-8](https://doi.org/10.1016/0006-3207(94)90279-8)

840 Nummi, P., 1989. Simulated effects of the beaver on vegetation, invertebrates and ducks. *Ann.*
841 *Zool. Fenn.* 26, 43–52. <http://www.jstor.org/stable/23734551>

842 Nummi, P., Holopainen, S., 2020. Restoring wetland biodiversity using research: Whole-
843 community facilitation by beaver as framework. *Aquatic Conserv: Mar. Freshw.*
844 *Ecosyst.* 30, 1798– 1802. <https://doi.org/10.1002/aqc.3341>

845 Nummi, P., Liao, W., Huet, O., Scarpulla, E., Sundell, J., 2019. The beaver facilitates species
846 richness and abundance of terrestrial and semi-aquatic mammals. *Glob. Ecol. Conserv.*
847 e00701. doi:10.1016/j.gecco.2019.e00701

848 Nummi, P., Liao, W., Schoor, J., Loehr, J., 2021. Beaver creates early successional hotspots for
849 water beetles. *Biodivers. Conserv.* 30. 10.1007/s10531-021-02213-8

850 O'Brien, C., McShea, W., Guimondou, S., Barrière, P., Carleton, M., 2006. Terrestrial Small
851 Mammals (Soricidae and Muridae) from the Gamba Complex of Protected Areas,
852 Gabon: Species Composition and Comparison of Sampling Techniques. *Proc. Biol. Soc.*
853 *Wash.* 12, 353-363.

- 854 Orazi, V., Hagge, J., Gossner, M.M., Müller, J., Heurich, M., 2022. A Biodiversity Boost From
855 the Eurasian Beaver (*Castor fiber*) in Germany's Oldest National Park. *Front. Ecol.*
856 *Evol.* 10, 873307. doi: 10.3389/fevo.2022.873307
- 857 Paine, R.T., 1969. The *Pisaster–Tegula* interaction: prey patches, predator food preference, and
858 intertidal community structure. *Ecology.* 50, 950–961. doi:10.2307/1936888
- 859 Pankakoski, E., 1979. The cone trap — a useful tool for index trapping of small mammals. *Ann.*
860 *Zool. Fenn.* 16, 144–150. <http://www.jstor.org/stable/23734422>
- 861 Parker, H., Rønning, Ø., 2007. Low potential for restraint of anadromous salmonid reproduction
862 by beaver *Castor fiber* in the Numedalslågen River Catchment, Norway. *River Res.*
863 *Appl.* 23, 752 - 762. 10.1002/rra.1008
- 864 Perkins, T.E., Wilson, M.V. 2005. The impacts of *Phalaris arundinacea* (reed canarygrass)
865 invasion on wetland plant richness in the Oregon Coast Range, USA depend on beavers.
866 *Biol. Conserv.* 124, 291-295. <https://doi.org/10.1016/j.biocon.2005.01.023>
- 867 Piętko, S., Misiukiewicz, W., 2022. Impact of European Beaver (*Castor fiber* L.) on Vegetation
868 Diversity in Protected Area River Valleys. *Conservation.* 2, 613-626.
869 <https://doi.org/10.3390/conservation2040040>
- 870 Pelikan, J., Zejda, J., Holisova, V., 1977. Efficiency of different traps in catching small
871 mammals. *Folia Zool.* 26, 1-13.
- 872 Powell, R.A., Brooks, W.S., 1981. Small Mammal Changes in Populations Following Tornado
873 Blowdown in Northern Mixed Forest. *J. Mammal.* 62, 397–400.
874 <https://doi.org/10.2307/1380723>
- 875 Pucek, Z., 1969. Trap response and estimation of number of shrews in removal catches. *Acta*
876 *Theriol.* 28: 403-426. 10.4098/AT.arch.69-30
- 877 Pucek, Z., 1984. Keys to Vertebrates of Poland: Mammals. PWN, Poland, Warsaw.
- 878 Pucek, Z. Raczyński, J., 1981. Atlas of Polish Mammals. PWN, Poland, Warsaw.

879 R Core Team, 2021. R: A language and environment for statistical computing. R Foundation
 880 for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>

881 Raffel, T., Smith, N., Cortright, C., Gatz, J., 2009. Central Place Foraging by Beavers (*Castor*
 882 *canadensis*) in a Complex Lake Habitat. Am. Midl. Nat. 162, 62-73. 10.1674/0003-
 883 0031-162.1.62

884 Rathke, D., Bröring, U., 2005. Colonization of post-mining landscapes by shrews and rodents
 885 (Mammalia: Rodentia, Soricomorpha). Ecol. Eng. 24, 149-156.

886 Rosell, F., Bozser, O., Collen, P., Parker, H., 2005. Ecological impact of beavers *Castor fiber*
 887 and *Castor canadensis* and their ability to modify ecosystems. Mamm. Rev. 35, 248–
 888 276. doi:10.1111/j.1365-2907.2005.00067.x

889 Rosell, F., Campbell-Palmer, R., 2022. Beavers. Ecology, behaviour, conservation and
 890 management. Oxford University Press, Oxford.

891 Russell, K.R., Moorman, C.E., Edwards, J.K., Metts, B.S., Guynn, D.C., 1999. Amphibian and
 892 Reptile Communities Associated with Beaver (*Castor canadensis*) Ponds and
 893 Unimpounded Streams in the Piedmont of South Carolina. J. Freshw. Ecol. 14, 149-158.
 894 10.1080/02705060.1999.9663666

895 Rychlik, L., 1997. Differences in foraging behaviour between water shrews: *Neomys anomalus*
 896 and *Neomys fodiens*. Acta Theriol. 42, 351-386.

897 Rychlik, L., 2000. Habitat preferences of four sympatric species of shrews. Acta Theriol. 45,
 898 173-190.

899 Rychlik, L., Zwolak, R., 2006. Interspecific aggression and behavioural dominance among four
 900 sympatric species of shrews. Can. J. Zool. 84, 434-448.

901 Samas, A., Ulevičius, A., 2015. Eurasian Beaver Building Activity Favours Small Mammals
 902 Common for the Forest. Balt. For. 21, 244-252.

903 Scott, D.M., Southgate, F., Overall, A.J., Waite, S., Tolhurst, B.A., 2012. The Eurasian water
 904 shrew: an unsuitable candidate species for a vertebrate bio-indicator of aquatic
 905 pollution. *J. Zool.* 286, 30-37. <https://doi.org/10.1111/j.1469-7998.2011.00845.x>

906 Seppä, H., 2002. Mires of Finland: Regional and local controls of vegetation, landforms, and
 907 long-term dynamics. *Fennia*. 180, 43–60.

908 Sidorovich, V., Jedrzejewska, B., Jedrzejewski, W., 1996. Winter distribution and abundance
 909 of mustelids and beavers in the river valleys of Białowieża Primeval Forest. *Acta*
 910 *Theriol.* 41, 155-170. 10.4098/AT.arch.96-15.

911 Šmilauer, P., Lepš, J., 2014. Multivariate analysis of ecological data using CANOCO 5.
 912 Cambridge university press.

913 Soininen, E., Valentini, A., Coissac, É., Miquel, C., Gielly, L., Brochmann, C., Brysting, A.,
 914 Sønstebo, J.H., Ims, R., Yoccoz, N., Taberlet, P., 2009. Analysing diet of small
 915 herbivores: The efficiency of DNA barcoding coupled with high-throughput
 916 pyrosequencing for deciphering the composition of complex plant mixtures. *Front. Zool.*
 917 6. 10.1186/1742-9994-6-16

918 Stringer, A.P., Gaywood, M.J., 2016. The impacts of beavers *Castor* spp. on biodiversity and
 919 the ecological basis for their reintroduction to Scotland, UK. *Mamm. Rev.* 46, 270-283.
 920 <https://doi.org/10.1111/mam.12068>

921 Sundell, J., Liao, W., Nummi, P., 2021. Small mammal assemblage in beaver-modified habitats.
 922 *Mammal Res.* 66, 181-186. <https://doi.org/10.1007/s13364-020-00545-4>

923 Suzuki, N., McComb, B., 2005. Associations of small mammals and amphibians with beaver-
 924 occupied streams in the Oregon Coast Range. *Northwest Sci.* 78, 286-293.

925 Tapisso, J. T., Ramalhinho, M. G., Mathias, M. L., Rychlik, L., 2013. Ecological release:
 926 swimming and diving behavior of an allopatric population of the Mediterranean water
 927 shrew. *J. Mamm.* 94, 29–39. <https://doi.org/10.1644/11-MAMM-A-364.1>

928 Terwilliger, J., Pastor, J., 1999. Small Mammals, Ectomycorrhizae, and Conifer Succession in
 929 Beaver Meadows. *Oikos*. 85, 83–94. <https://doi.org/10.2307/3546794>

930 Thompson, S., Vehkaoja, M., Nummi, P., 2016. Beaver-created deadwood dynamics in the
 931 boreal forest. *For. Ecol. Manag.* 360, 1–8. doi:10.1016/j.foreco.2015.10.019

932 Thompson, S., Vehkaoja, M., Pellikka, J., Nummi, P., 2020. Ecosystem services provided by
 933 beavers *Castor* spp.. *Mamm. Rev.* 51, 25-39. <https://doi.org/10.1111/mam.12220>

934 Torre, I., Ribas, A., Puig-Gironès, R., 2023. Effects of Post-Fire Management on a
 935 Mediterranean Small Mammal Community. *Fire* 6, 34.
 936 <https://doi.org/10.3390/fire6010034>

937 Ulevičius, A., Janulaitis, M. 2007. Abundance and species diversity of small mammals on
 938 beaver lodges. *Ekologija*. 53, 38–43.

939 Watts, C.H.S., 1968. The Foods Eaten by Wood Mice (*Apodemus sylvaticus*) and Bank Voles
 940 (*Clethrionomys glareolus*) in Wytham Woods, Berkshire. *J. Anim. Ecol.* 37, 25–41.
 941 <https://doi.org/10.2307/2709>

942 Washko, S., Willby, N., Law, A., 2022. How beavers affect riverine aquatic macroinvertebrates:
 943 a review. *PeerJ*. 10:e13180. doi: 10.7717/peerj.13180

944 Weber, N., Bouwes, N., Pollock, M.M., Volk, C., Wheaton, J.M., Wathen, G., Wirtz, J., Jordan,
 945 C.E., 2017. Alteration of stream temperature by natural and artificial beaver dams.
 946 *PLOS ONE*. 12, e0176313. <https://doi.org/10.1371/journal.pone.0176313>

947 Westbrook, C.J., Cooper, D.J., Baker, B.W., 2006. Beaver dams and overbank floods influence
 948 groundwater–surface water interactions of a Rocky Mountain riparian area. *Water*
 949 *Resour. Res.*, 42, W06404. doi:10.1029/2005WR004560

950 Westbrook, C.J., Ronnquist, A., Bedard-Haughn, A., 2020. Hydrological functioning of a
 951 beaver dam sequence and regional dam persistence during an extreme rainstorm.
 952 *Hydrol. Process.* 34, 3726– 3737. <https://doi.org/10.1002/hyp.13828>

- 953 Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Golemund, G.,
 954 Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller,
 955 K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke,
 956 C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. *J. OpenSource Softw.* 4, 1686.
- 957 Wikar, Z., Ciechanowski, M., 2023. Beaver dams and fallen trees as ecological corridors
 958 allowing movements of mammals across water barriers—a case study with the
 959 application of novel substrate for tracking tunnels. *Animals.* 13, 1302.
 960 <https://doi.org/10.3390/ani13081302>
- 961 Willby, N., Law, A., Levanoni, O., Foster, G., Ecke, F., 2018. Rewilding wetlands: beaver as
 962 agents of within-habitat heterogeneity and the responses of contrasting biota. *Philos.*
 963 *Trans. R. Soc. Lond., B, Biol. Sci.* 373, 20170444. 10.1098/rstb.2017.0444
- 964 Wolff, J.O., Dueser, R.D., Berry, K.S., 1985. Food Habits of Sympatric *Peromyscus leucopus*
 965 and *Peromyscus maniculatus*. *J. Mammal.* 66, 795–798. doi:10.2307/1380812
- 966 Wołk, E., Wołk, K., 1982. Responses of small mammals to the forest management in the
 967 Białowieża Primeval Forest. *Acta Theriol.* 27, 45-59.
- 968 Żurowski, W., Kasperczyk, B., 1986. Characteristics of a European beaver population in the
 969 Suwałki Lakeland. *Acta Theriol.* 31, 311-325.