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ORIGINAL RESEARCH

General patterns of beavers' selective foraging: how to evaluate the effects of a re-emerging driver of vegetation change along Central European small watercourses

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Abstract

Along small watercourses, the growth and renewal of native willows and poplars (*Salicaceae* species) are hindered by the effects of past and recent man-made landscape alteration and climate change, while the selective foraging of the beaver (*Castor fiber*) is also becoming an increasingly important driver. Knowledge about foraging decisions can refine predictions about vegetational processes and help to develop better nature conservation and forest management strategies. We surveyed the woody plant supply (13,304 units) and its utilization by the beaver at 11 study sites along Central European small watercourses, at two fixed distances from the water. We collected information about the taxon, trunk diameter, and type of utilization (cutting, carving, debarking) of each unit. We built (generalized) linear mixed models aimed at answering questions regarding taxon and diameter preference, their interrelatedness, and their importance in foraging decisions. All of the factors examined had a significant effect on foraging decisions. Utilization was mostly explained by the taxon, with *Salicaceae* species being generally preferred and utilized in all diameter classes with a high ratio. Several further genera were frequently utilized (mainly *Cornus* and *Ulmus*), while others were almost completely avoided (including invasive *Amorpha* and *Robinia*). The beavers preferred units with a diameter of 5–9 cm. The type of utilization depended primarily on diameter class. Because native softwoods are the most affected by beaver impact, regardless of trunk diameter, their survival and regrowth should be consciously supported by increasing the water table and improving hydrological conditions.

Keywords Browsing impact · *Castor fiber* · Ecosystem engineer species · Forest management · Optimal foraging strategy · Riparian woodland

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Introduction

All over the world, large-scale water regulations were conducted in recent centuries, often resulting in drastic transformations of lowland streams and wetlands, with consequences still felt today (Davidson 2014; Jakubínský 2014; Reis et al. 2017). Small watercourses and their adjacent lands in Central and Southern Europe are threatened with a decrease of streamflow and hydrological drought due to climate change, water abstraction, and drainage (Feyen and Dankers 2009; Borics et al. 2016; Peña-Angulo et al. 2022). Furthermore, land-cover change (e.g., the development of settlements and the intensification of agriculture) reduces the size of areas covered by native vegetation in the stream corridors (Vörösmarty et al. 2010), thereby hindering their function as green corridors (Ristić et al. 2013). However, regulated and artificial watercourses (channelized streams and drainage canals) might still preserve species of conservation interest (Harabiš and Dolný 2015) and retain important components of the former biodiversity, as refugia in intensively managed landscapes (Tölgyesi et al. 2022).

Willows and poplars (*Salix* and *Populus* spp.—*Salicaceae* family) are foundational species of stream corridors: they provide a stable habitat structure and fundamental ecosystem functions (Briggs et al. 2021). Their growth and competition with other species are largely influenced both by the hydrology of the stream (Lite and Stromberg 2005; Shafroth et al. 2000; Stella et al. 2010) and the browsing of herbivore mammals (Painter and Ripple 2012; Runyon et al. 2014). Abrupt water table decline and soil water depletion have a negative effect on the survival of *Salicaceae* species, especially willows, which may induce a shift in the composition of the woody vegetation toward species better adapted to drier conditions (Amlin and Rood 2002; Hultine et al. 2010).

Softwood leaves and shoots, besides being frequently consumed by ungulate species (De Jager et al. 2013; Moritz et al. 2018), are also utilized by beavers (*Castor* spp.) to a great extent (Nolet et al. 1994; DziČeciołowski and Misiukiewicz 2002). The poplar and willow preference of beavers has been noted several times in different parts of the northern hemisphere (Gallant et al. 2004; Salandre et al. 2017; Juhász et al. 2020a; Mikula et al. 2022). Beavers are ecosystem engineer species (Hood and Larson 2015; Brazier et al. 2021; Larsen et al. 2021). Their selective foraging has the capacity to alter species composition and forest structure (Jones et al. 2009; Dvořák 2013), which can have remarkable nature conservation consequences (Juhász et al. 2022). Besides this impact of beavers, which is the focus of this study, the hydrological impact of their dams can also be an important factor in vegetation change along shorelines and in flooded areas (Wolf et al. 2007; McColley et al. 2012; Willby et al. 2018).

The Eurasian beaver (*Castor fiber*) almost became extinct in the nineteenth century, but thanks to protection efforts their global population now numbers at least 1.5 million (Halley et al. 2021). The selective foraging of the species is an important but still poorly understood, old-and-new driver of vegetation change across Eurasia. To understand this impact, it is essential to describe not only the beaver's taxon preference, but also its complex foraging strategy: to what extent and in what ways are different species and different diameter classes affected by foraging. In this paper, we examine the beaver's foraging decisions, aiming for a deeper understanding of the patterns of the species' disturbance.

Previously we reported that beavers avoid invasive woody species, which might indirectly enhance the proliferation of such species along the waterbanks of large rivers, where the renewal ability of softwood species is relatively low (Juhász et al. 2020a). We also explored the foraging strategy of beavers in this environment considering the four main genera (*Salix*, *Populus*, *Fraxinus* and *Acer*) (Juhász et al. 2022). Here, we deal with a wider range of genera, representing the most common woody species growing along Central European small watercourses. Our main objectives are to describe: (1) the beaver's taxon preference; (2) the genus-level differences in trunk diameter selectivity and the type of utilization; (3) the diameter-dependency of the type of utilization; and (4) the order of importance of the variables influencing the intensity and type of utilization.

Study area and methods

Study area

Hungary is a Central European country with an area of 93,030 km^2. The climate is subcontinental; the mean annual precipitation is between approx. 500 and 800 mm, and the mean annual temperature is 10–11 °C (Kocsis 2018). All of the Hungarian watercourses belong to the Danube River Basin. The Danube is the second longest river in Europe; its main tributaries are the Tisza, Dráva, Rába, Körös, Maros, Ipoly, Zagyva, and Rábca rivers (McCaffrey 2006). In the nineteenth–twentieth centuries, most of the lowland floodplains were drained. Many natural streams were straightened and deepened, and an extensive network of artificial canals was created to promote the efficient drainage of water (Borics et al. 2016). Nowadays, Hungary is strongly affected by climate change, as the soil water table is sinking continuously and substantially in some regions in the middle part of the country (Kovács Székely and Szalai 2009). 32% of Hungary's surface-water bodies are of intermittent water supply (General Directorate of Water Management 2015).

57% of the country is agricultural land including grasslands (KSH 2019), where the sides of streams and canals are mostly lined by narrow (5–20 m in width) woody vegetation strips. Forest cover is approx. 21–24% in Hungary (KSH 2019; Biró et al. 2022). The most important non-native tree species used for plantations are *Robinia pseudoacacia, Populus* × *euramericana* and *Pinus sylvestris* (Forest Europe 2015), the first two of which are popularly planted along small watercourses. In the narrow waterfront line, native softwood (mainly *Salix alba*, *S. fragilis*, *Populus alba*, *P. canescens* and *P. nigra*) and hardwood trees (e.g., *Alnus glutinosa*, *Acer* spp., *Fraxinus* spp., *Ulmus* spp.) are also typical. Among these hardwood species, *Alnus glutinosa*, *Ulmus laevis* and *U. minor* are native, while *Acer* and *Fraxinus* genera have both native (e.g., *A. campestre*, *F. excelsior*, *F. angustifolia* ssp. *danubialis*) and non-native members (*A. negundo*, *F. pennsylvanica*) in this environment. The shrub layer of these narrow vegetation strips consists of mainly native species (*Cornus sanguinea*, *Crataegus monogyna, Prunus cerasifera*, *P. spinosa*, *Rosa spp. Salix cinerea*, and *Sambucus nigra* etc.), but in several locations, the invasive *Amorpha fruticosa* is spreading rapidly.

The Eurasian beaver became extinct in Hungary in the middle of the nineteenth century, and its return began in the early 1990s (Bajomi 2011). Key roles in this process were played both by spontaneous colonization and by the beaver reintroduction campaigns between 1996 and 2008 (Juhász et al. 2019). In Hungary, data from comprehensive beaver population monitoring are not available. Prior to our study, in 2016, the population was estimated at 4000–5000 individuals (Čanády et al. 2016).

Study sites

Study sites were selected along small watercourses strongly impacted by beaver activity, with the help of local expert guidance. To gain detailed information about the distribution process and activity of the beaver in the country, we conducted structured interviews with conservationists and researchers (Juhász et al. 2019, 2020b). At the end of the interviews, we asked the informants to suggest small watercourses with intensive beaver activity. We visited all the suggested watercourses and detected beaver sites along watercourse sections at least 10 km in length.

After this preliminary fieldwork, altogether 11 study sites were chosen along 10 watercourses, shown in Fig. 1. The map was created using online data sources (Natural Earth 2022; Open Maps for Europe 2023). Each site met the following criteria:

(1) fresh signs of intensive beaver activity were clearly visible along a waterbank section with a minimum length of 300 m;
(2) woody vegetation was continuous along a 500-m-long section of the waterbank;
(3) no recent human water management interventions were visible along the waterbank section;
(4) the canopy layer was not monodominant (the estimated proportion of softwoods was 10–60%).

The watercourses showed a clear similarity in the following parameters during the field work period (2017–2020): (1) All of them were permanent watercourses. (2) They are located in lowland or hilly landscapes. (The sites are located between 74 and 360 m above sea level.) (3) Their water has a slight or medium slope (General Directorate of Water Management 2015). (4) None of them had long "bank wall" sections (bank slope > 80%), which could influence access to the woody plant supply. (5) None of them had side channels or stream branches along the surveyed sections. (6) Their maximum width at the

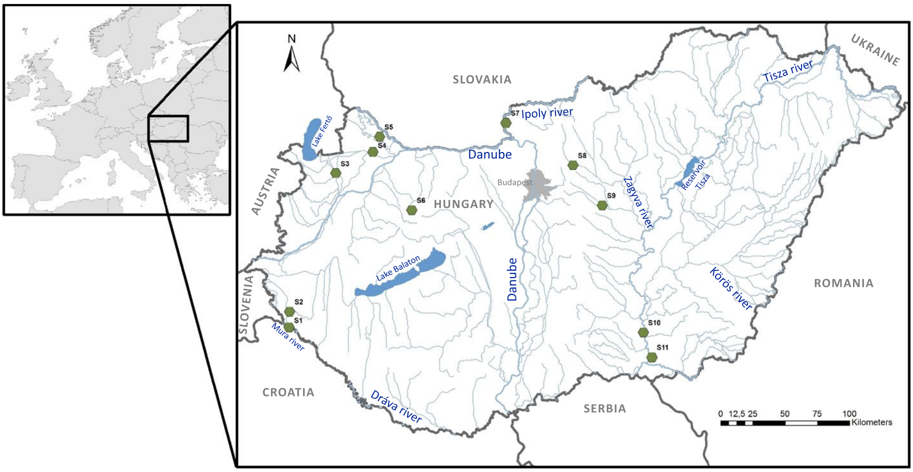

Fig. 1 Location of the study sites in Hungary. Sites were located along streams and canals. Thin blue lines: rivers and small watercourses (streams and canals); thick grey lines: national borders; light grey: capital of Hungary; blue: main lakes (sources: Natural Earth 2022; Open Maps For Europe 2023). Source of inset map: ArcGIS 10.1. online base maps, ESRI 2012 S

selected area was 3 to 5 m in the study period. (7) Their maximum depth was 1.2 to 1.5 m. Data about elevation, slope of the bank, length of beaver occupation, and population density are reported in Table 1 to illustrate slight differences in factors, which were not limited by selection criteria. It is important to highlight that we studied stream sections where the beaver did not modify the accessibility of trees and shrubs, as it had no or only moderate influence on the original shoreline. Small dams were created at 4 sites (S6, S7, S8, S9), but they did not lead to overbank flooding in this early stage (first two years) of the beaver habitat development. At one site (S8) a beaver canal was registered which led to the creation of a beaver meadow. However, no additional woody plant supply was made available by this activity in the study period.

Data collection

The study sites were surveyed once between 2017 and 2020 (always in March/April). At each study site, a waterbank transect (WBT) was surveyed along the first line of woody plants. Along one bank of the stream, 50 sampling circles were located at a distance of 10 m from each other. In the case of four study sites (S1, S2, S5 and S7), where the woody plant supply of the two watercourse banks differed considerably, the waterbank transect was supplemented by 15–25 additional sampling circles on the opposite bank. A parallel transect, the outer transect (OT), was designated at a distance of 10 m from the waterbank transect. Several sites did not have continuous woody plant cover at this distance from the water. At two sites (S6, S11) no woody plant units were found along the OT, so only a WBT survey was conducted there. The sampling circles had a radius of 2 m.

Within the sampling circles, we registered the woody plant supply available at a height of 0–70 cm above the soil and its utilization by the beaver, using the protocol described in Juhász et al. (2020a). Branches and trunks were treated together, and categorized only by taxon and diameter. In total, 13,304 units were registered at species or genus level as woody plant supply. We distinguished between thin branches, with a thickness of at least 0.8 cm but less than 5 cm, and thicker units (trunks and branches) reaching a thickness of 5 cm. In the case of the thicker units, we measured the diameter to the nearest cm. We registered the diameter at a height of 40 cm, except in the case of units branching from the trunk above this height (at a height of 40–70 cm). For the latter, the diameter was measured at the branching point, in line with Juhász et al. (2022).

Three types of utilization were defined: *cutting*, *carving*, and *debarking*. *Cutting* means the felling of trees and removal of thin branches. *Carved* units have damage to a depth of over 3 cm, while *debarked* units have only surface damage. In the case of thin branches, as carving was an irrelevant category, only *cutting* and *debarking* were registered. *Cutting*, *carving* and *debarking* together were referred to as "*summarized utilization*".

We distinguished between *fresh* and *old* signs of utilization. Utilized units with a light-coloured chewing surface were considered *fresh* (estimated age: up to 4 months), while those with a browned surface and uneroded teeth marks were considered *old* (estimated age: up to 2 years, rotting trunks were excluded).

Data analysis

During the preparation of the statistical analysis and visualization, each of the units was categorized into six diameter classes. The first diameter class (d1) was equivalent to the thin branches category (0.8–4.9 cm), and five more diameter classes (d2–d6) were

Table 1 Information about the study sites

Site	Location	Stream	Mouth	Year OBS	Year SURV	Nr. of sites/10 km	Elevation [m]	Slope of the bank		Beaver dam	Lodge/burrow		Beaver meadow
								0–4 m	4–12 m		Active lodge	Active burrow	
S1	46.477584 N 16.592607 E	Kerka stream	Mura river	1999	2019	9	148	Moderate slope	Flat	X	X	X	X
S2	46.585828 N 16.591832 E	Kerka stream	Mura river	2005	2019	7	162	Steep slope	Flat	X	X	X	X
S3	47.561416 N 17.022119 E	Répce stream	Rábca river	2013	2017	5	121	Slight slope	Steep slope	X	X	✓	X
S4	47.716679 N 17.399439 E	Kettős canal	Rábca river	2011	2017	4	113	Flat	Flat	X	✓	X	X
S5	47.824507 N 17.468102 E	Zsejkei canal	Mosoni-Danube	2010	2017	6	119	Slight slope	Slight slope	X	X	✓	X
S6	47.314728 N 17.812282 E	Hódos stream	Cuha stream	2016	2017	2	360	Moderate slope	Flat	✓	✓	✓	X
S7	47.929544 N 18.777373 E	Cserge stream	Ipoly river	2017	2018	1	115	Moderate slope	Slight slope	✓	✓	X	X

Table 1 (continued)

Site	Location	Stream	Mouth	Year OBS	Year SURV	Nr. of sites/10 km	Elevation [m]	Slope of the bank		Beaver dam	Lodge/burrow		Beaver meadow
								0–4 m	4–12 m		Active lodge	Active burrow	
S8	47.634976 N 19.469750 E	Egres stream	Galga stream	2018	2020	1	132	Moderate slope	Steep slope	✓	X	X	✓
S9	47.352279 N 19.768949 E	Tápió stream	Zagyva river	2017	2019	2	102	Moderate slope	Flat	✓	✓	✓	X
S10	46.462140 N 20.171968 E	Percsorai canal	Tisza river	2013	2017	2	79	Moderate slope	Flat	X	X	✓	X
S11	46.289922 N 20.254947 E	Hódtó-Nagyfai canal	Tisza river	2013	2017	1	74	Moderate slope	Flat	X	X	X	X

Key: Year OBS—the year of the first observation of beaver signs at the study sites; Year SURV—the year of the survey; Nr. of sites/10 km—density data based on the survey of watercourse sections at least 10 km in length. At 50–75 locations, the slope of the bank was estimated for each site using an ordinal scale (flat: $x < 5\%$, slight slope: $5\% \leq x < 20\%$, moderate slope: $20\% \leq x < 50\%$, steep slope: $50\% \leq x < 80\%$, bank wall: $x \geq 80\%$) at two distances from the waterbank (0–4 m, 4–12 m), and median values were calculated at site level. In columns showing signs of beaver activity (beaver dam, active lodge, active burrow, and beaver meadow) ✓ means at least one registered sign, while X means the absence of such signs (not registered) defined using Jenks natural breaks method (Jenks 1967): d2—5–9 cm, d3—10–18 cm, d4—19–32 cm, d5—33–54 cm, d6—55–146 cm. Meanwhile, we also defined two taxon groups: softwood species (*Salix* and *Populus* spp.) and other species.

Aiming to illustrate differences in the supply and utilization of certain genera and diameter classes, we present the following data in the figures: (1) Relative supply of the most frequent 15 genera in each diameter class. Relative supply means the ratio of the number of units in the supply of the given genus to the number of units in the supply of all genera. (2) Utilization ratio in the different diameter classes of the most frequent 15 genera. Utilization ratio means the number of utilized units/number of units in the supply of the given genus. (3) Utilization ratio of the most frequent 15 genera at 11 study sites. (4) The mean diameter of cut, carved, debarked, and intact units of the most frequent genera.

Three datasets were defined, which we used when building the models:

(1) *Full dataset*, containing intact units, units with fresh signs of utilization (light-coloured surface) and units with old signs of utilization (browned surface)
(2) *Fresh dataset*, containing intact units, units with fresh signs of utilization, and formerly beaver-harmed but living trees
(3) *Fresh utilized dataset,* containing units with fresh signs of utilization

Three response variables were used:

(1) Presence of the signs of any kind of utilization ("*summarized utilization*"), as a binary variable
(2) Presence of the signs of cutting ("*cutting*"), as a binary variable
(3) *Diameter*, as a continuous variable

With the objective of understanding the foraging strategy of beavers, binomial generalized linear mixed models (GLMMs) and a linear mixed model (LMM) were built using the R package "lme4" (Bates et al. 2015) (Table 2).

Equations used during the model building:

$$summarized\ utilization \sim Tg + D + Tr + \overline{S} \tag{1}$$

$$cutting \sim Tg + D + Tr + \overline{S} \tag{2}$$

$$summarized\ utilization \sim G + D + \overline{S} \tag{3}$$

$$cutting \sim G + D + \overline{S} \tag{4}$$

$$diameter \sim Ty + \overline{S} \tag{5}$$

In these equations, Tg stands for taxon group, D for diameter, Tr for transect, Ty for type of utilization (cut, carved, debarked, and intact) and S for site. Taxon group, diameter and transect were treated as fixed factors, and the site as a random factor (displayed overlined).

Applying Eqs. 1 and 2 to the fresh dataset (M1, M2), we examined what determines utilization (summarized utilization and cutting) within the supply. Then, applying Eq. 2 to the

Table 2 Information about the models applied during the data analysis

Model	Equation	Model type	Distribution family	Dataset	Response variable	Importance of variables	Tukey test
M1	Equation 1	GLMM	Binomial	Fresh dataset	Summarized utilization	Tested	Not conducted
M2	Equation 2	GLMM	Binomial	Fresh dataset	Cutting	Tested	Not conducted
M3	Equation 2	GLMM	Binomial	Fresh utilized dataset	Cutting	Tested	Not conducted
M4T1	Equation 3	GLMM	Binomial	Fresh dataset	Summarized utilization	Not tested	Diameter preference on genus subsets
M5T1	Equation 4	GLMM	Binomial	Fresh dataset	Cutting	Not tested	Diameter preference on genus subsets
M4T2	Equation 3	GLMM	Binomial	Fresh datasetet	Summarized utilization	Not tested	Genus preference on site subsets
M5T2	Equation 4	GLMM	Binomial	Fresh dataset	Cutting	Not tested	Genus preference on site subsets
M6T1	Equation 5	LMM	Gaussian	Full dataset	Diameter	Not tested	Tukey test for the type of utilization, excluding diameter class d1, without subsetting
M6T2	Equation 5	LMM	Gaussian	Full dataset	Diameter	Not tested	Tukey test for the type of utilization, excluding diameter class d1, on genus subsets

“Importance of variables” means the calculation of the following four metrics: likelihood ratio, the significance of the likelihood ratio, the difference in Akaike Information Criterion, and the difference in Bayesian Information Criterion, while “Tukey test” means multiple comparison of means performed by Tukey’s contrast fresh utilized dataset (M3), we examined what determines the frequency of cutting within the summarized utilization.

Four metrics were calculated to estimate the importance of variables in models M1–M3: likelihood ratio, the significance of the likelihood ratio, the difference in Akaike Information Criterion (Akaike 1974), and the difference in Bayesian Information Criterion (Schwarz 1978). For each of the fixed factors, two nested models were compared: (1) the original one detailed above, which includes all fixed factors; and (2) a reduced model, from which the studied fixed factor was excluded. The effects of fixed factors in M1-M3 models were visualised using the R package "effects" (Fox and Weisberg 2019).

The trunk diameter preference and genus preference were studied preforming multiple comparison of means by Tukey's contrast (hereinafter "Tukey test"), using R packages "emmeans" (Lenth 2020) and "multcomp" (Hothorn et al. 2008). We studied the diameter preference at genus level, that is, in the genus subsets of the fresh dataset (M4T1 and M5T1). Meanwhile, in the case of taxon preference, site-level taxon preference analyses were carried out (M4T2 and M5T2) because of the markedly different woody plant supply of the sites and the possible difference in the preferences of the individual beaver colonies.

The diameter dependency of the type of utilization was also examined by Tukey test (M6T1 and M6T2), on a subset of the full dataset, where the smallest diameter class d1 was excluded due to the unreliable recognition of old signs of utilization and the interpretation difficulties of the carving category in this class.

Results

The importance of the factors influencing utilization

The likelihood ratio values revealed that foraging decisions were mostly explained by the taxon group, in the case of both summarized utilization and cutting (Table 3). This was followed in importance by the transect and then the diameter.

Factors influencing utilization

The effect of taxon and transect proved to be significant at a level of $\alpha = 0.001$ in the case of both summarized utilization and cutting (Table 4). The beaver preferred softwood species

Table 3 Likelihood ratio, likelihood ratio significance, ΔAIC and ΔBIC values calculated for the fixed factors in the models M1 and M2

	Likelihood ratio	Likelihood ratio significance	ΔAIC	ΔBIC
Summarized utilization				
Taxon group	467.443	< 0.001	465.443	457.973
Diameter	52.611	< 0.001	42.611	5.262
Transect	246.715	< 0.001	244.715	237.245
Cutting				
Taxon group	418.058	< 0.001	416.058	408.588
Diameter	143.639	< 0.001	133.638	96.289
Transect	199.064	< 0.001	197.064	189.594

Table 4 Results of generalized linear mixed models M1 and M2

	Estimate	Standard Error	z value	p value
Summarized utilization				
Intercept (reference levels: taxon_softwood, diameter d1, transect_WBT)	−0.962	0.235	−4.097	< 0.001
taxon_other	−1.739	0.081	−21.433	< 0.001
diameter_d2	0.454	0.091	5.009	< 0.001
diameter_d3	−0.171	0.122	−1.401	0.16131
diameter_d4	−0.417	0.177	−2.360	< 0.01
diameter_d5	−0.742	0.234	−3.168	< 0.005
diameter_d6	−0.705	0.340	−2.072	< 0.05
transect_OT	−1.652	0.125	−13.248	< 0.001
Cutting				
(Intercept)	−0.970	0.215	−4.523	< 0.001
taxon_other	−1.752	0.086	−20.430	< 0.001
diameter_d2	−0.014	0.103	−0.137	0.890913
diameter_d3	−0.703	0.145	−4.857	< 0.001
diameter_d4	−1.466	0.259	−5.668	< 0.001
diameter_d5	−2.163	0.396	−5.459	< 0.001
diameter_d6	−3.417	1.001	−3.412	< 0.001
transect_OT	−1.658	0.141	−11.773	< 0.001

Reference level of taxon, diameter and transect categorical variables were softwood species, diameter_d1 (< 5 cm), and waterbank transect, respectively. Key: taxon_softwood—softwood species, taxon_other—other (non-softwood) species, diameter_d1 < 5 cm, diameter_d2—5–9 cm, diameter_d3—10–18 cm, diameter_d4—19–32 cm, diameter_d5—33–54 cm, diameter_d6—55–146 cm, transect_OT—outer transect, transect_WBT—waterbank transect

and units closer to the waterbank (Fig. 2). In the case of two sites, there was no utilization along the outer transect, and in the case of 4 other sites, a maximum of 5 units were utilized there by the beaver. Above diameter class d2, the utilization rate decreased with the increase of the trunk diameter. Based on the summarized utilization, diameter class d2 proved to be significantly preferred, but the same was not true in the case of cutting. In the case of cutting, larger diameters were increasingly avoided by the beaver compared to d1 (based on the Estimate values), and this was significant from class d3 upwards.

Supply and utilization of different taxa

At the 11 sites together, we registered the presence of woody species from a total of 30 genera. The 15 most common genera among these were the following: *Acer*, *Alnus*, *Amorpha*, *Cornus*, *Corylus*, *Crataegus*, *Fraxinus*, *Populus*, *Prunus*, *Quercus*, *Robinia*, *Rosa*, *Salix*, *Sambucus*, and *Ulmus* (Table 5). The average relative supply of these genera is shown in Fig. 3, by trunk diameter classes. 28 genera were present along the waterbank transect and 22 along the outer transect (Online Appendix A). While 28 genera occurred in the thin branches diameter class (d1), this value was 10 genera in the case of diameter class d5, and only 4 genera in the case of the thickest units (d6). The average relative supply of softwood species showed an increase along both transects with the increase of diameter class. The woody plant supply at the sites was highly variable: the number and relative supply of each

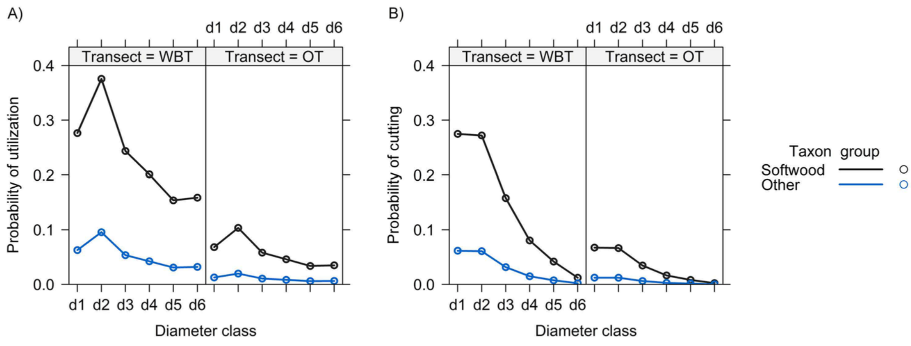

Fig. 2 Effect plots of generalized linear mixed models M1 (subfigure **A**) and M2 (subfigure **B**). Key for taxon groups: softwood—softwood species, other—other (non-softwood) species. Diameter classes: d1 < 5 cm, d2—5–9 cm, d3—10–18 cm, d4—19–32 cm, d5—33–54 cm, d6—55–146 cm. Transects: WBT—waterbank transect, OT—outer transect

genus is summarized in Online Appendix A, by trunk diameter classes, for both transects of each site separately.

The highest mean utilization and cutting ratio was achieved by the softwoods in each diameter class (Fig. 4 and Online Appendix B). Among the most frequent 15 genera, the following ten were utilized in more than one diameter class: *Acer*, *Alnus*, *Cornus*, *Fraxinus*, *Populus*, *Prunus*, *Quercus*, *Salix*, *Sambucus*, and *Ulmus* (Table 5). *Amorpha* and

Table 5 Supply and utilization of the most common 15 genera at the study sites, based on the fresh dataset

	Supply		Utilization	
Genus	Total number	Mean number ± SD	Total number	Mean number ± SD
Acer	765	69.55 ± 99.27	23	2.09 ± 3.86
Alnus	1070	97.27 ± 221.06	95	8.64 ± 21.68
Amorpha	745	67.73 ± 200.42	14	1.27 ± 4.22
Cornus	1994	181.27 ± 178.18	253	23 ± 25.12
Corylus	106	9.64 ± 25.29	0	0
Crataegus	179	16.27 ± 19.2	0	0
Fraxinus	417	37.91 ± 48.18	16	1.45 ± 3.59
Populus	920	83.64 ± 112.92	155	14.09 ± 17.24
Prunus	2382	216.55 ± 253.1	131	11.91 ± 18.21
Quercus	50	4.55 ± 8.17	5	0.45 ± 0.82
Robinia	293	26.64 ± 39.76	0*	0*
Rosa	573	52.09 ± 73.16	3	0.27 ± 0.9
Salix	1683	153 ± 181.22	483	43.91 ± 48.95
Sambucus	1390	126.36 ± 133.31	17	1.55 ± 2.62
Ulmus	155	14.09 ± 18.93	34	3.09 ± 5.34

Key: Supply—Total number: number of units in the summarized supply of all sites; Supply—Mean number ± SD: the mean number of units per site and its standard deviation; Utilization—Total number: the total number of units utilized at all sites altogether; Utilization—Mean number ± SD: the mean number of units utilized per site and its standard deviation. Asterisks in the utilization columns mean that only old signs of utilization were found in the case of the species

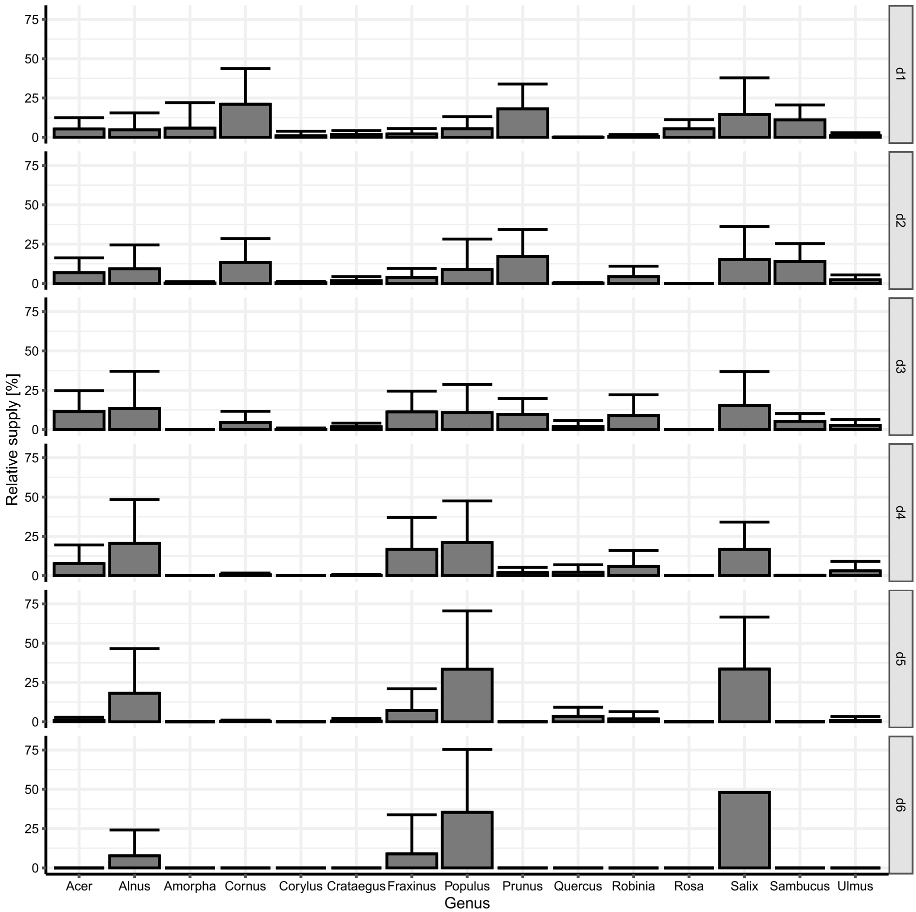

Fig. 3 Relative supply of the most frequent 15 genera (number in the summarized supply of all sites ≥ 50), based on the fresh dataset. Relative supply means the ratio of the number of units in the supply of the given genus to the number of units in the supply of all genera. Error bars display the standard deviation of site-level values. Diameter classes: d1 < 5 cm, d2—5–9 cm, d3—10–18 cm, d4—19–32 cm, d5—33–54 cm, d6—55–146 cm

Rosa were utilized rarely and only in diameter class d1. In the case of *Robinia*, only one old sign of utilization was registered, while *Crataegus* and *Corylus* were not utilized at all. Utilization was also found among some genera that were only sporadically present at the sites: *Malus*, *Carpinus*, *Celtis*, *Euonymus*, and *Juglans* (Online Appendix A).

Salix and *Populus* were utilized in all diameter classes. In diameter class d6, utilization occurred exclusively within these two genera. Besides softwoods, only *Quercus* was utilized in diameter class d5, but in its case just old signs of utilization were found. The spectrum of the utilized genera was wider along the WBTs (17 genera) than along the OTs (9 genera) (Online Appendix A).

Examining the summarized utilization within the trunk diameter classes by genus, we confirmed a significant preference for trunk diameter class d2 (units exceeding a thickness of 5 cm) compared with both d1 class and thicker units in the case of *Alnus* and *Prunus* genera (Online Appendix B). With regard to cutting, the d1-d2 difference

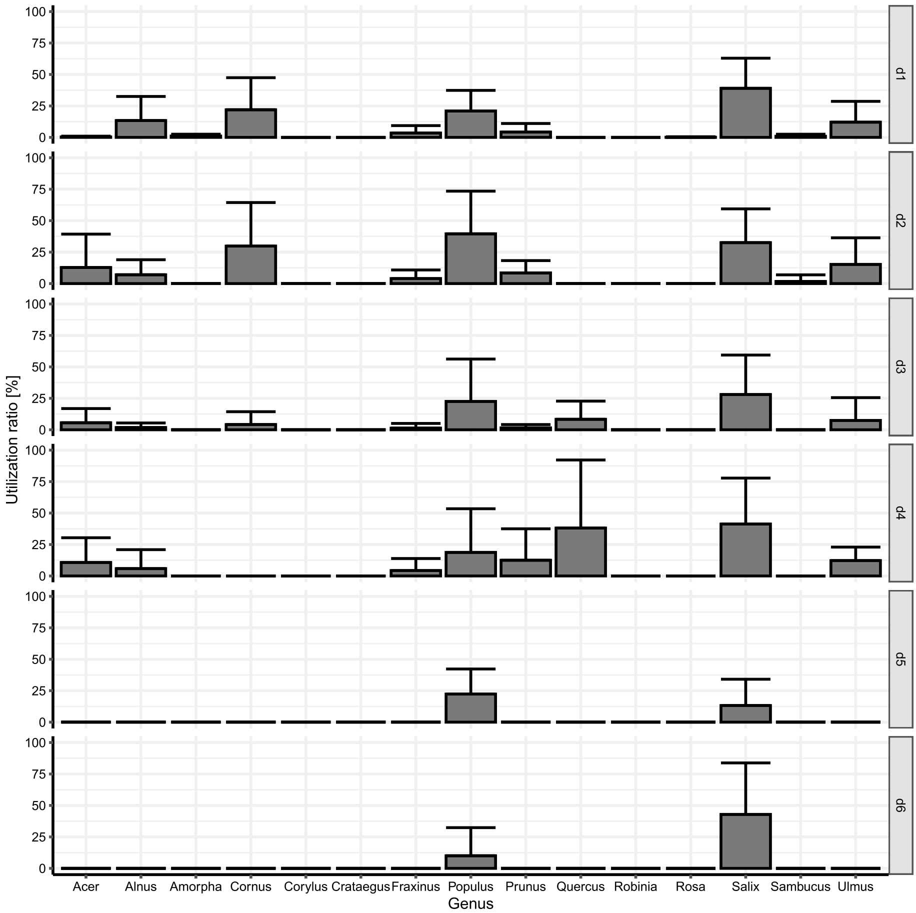

Fig. 4 Utilization ratio in the different diameter classes of the most frequent 15 genera, based on the fresh dataset. Utilization ratio means the number of utilized units/number of units in the supply of the given genus. Error bars display the standard deviation of site-level values. Diameter classes: d1 < 5 cm, d2—5–9 cm, d3—10–18 cm, d4—19–32 cm, d5—33–54 cm, d6—55–146 cm

was never significant, but in the case of *Alnus*, *Populus* and *Salix*, the beaver significantly avoided at least one larger trunk diameter class.

Softwood species (*Salix* and/or *Populus* spp.) proved to be the preferred species in site-specific analyses as well. Based on summarized utilization, we confirmed a significant preference for one or both of these genera in the case of 8 sites (Fig. 5). The utilization ratio of the *Salix* or *Populus* genera also stood out for the remaining 3 sites. The pairwise preference difference of these two taxa is not clear, based on the site-level data. In some cases, *Acer*, *Cornus*, *Ulmus* and *Malus* were also significantly preferred based on summarized utilization. In the case of cutting, *Acer* and *Malus* never proved to be preferred genera (Online Appendix B). (*Malus* is not displayed in Fig. 5 and Online Appendix B, because the genus was present only at one site, S11 as a rare genus in the supply.)

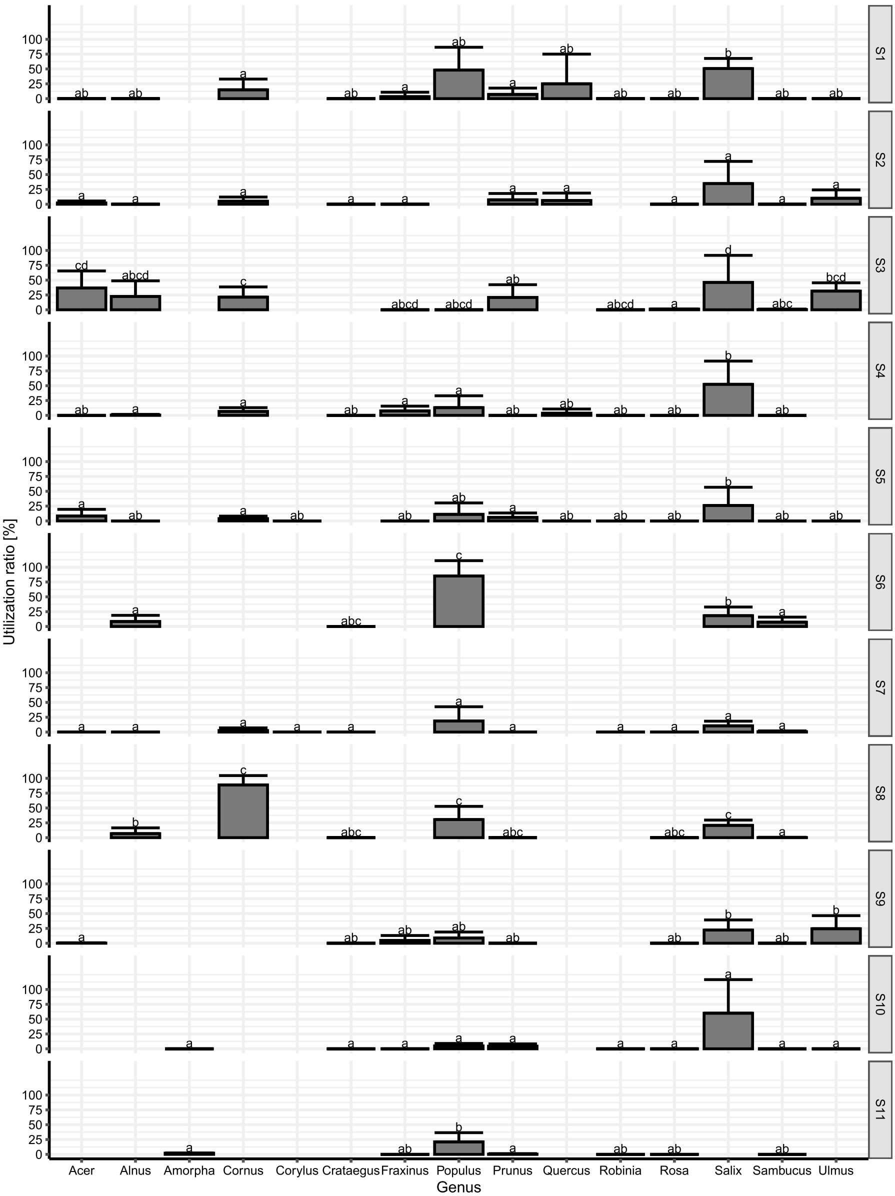

Fig. 5 Utilization ratio of the most frequent 15 genera at 11 study sites, based on the fresh dataset. Utilization ratio means the number of utilized units/number of units in the supply of the given genus. The average of the values obtained for the trunk diameter classes was calculated for each site. Error bars display the standard deviation of site-level values. Significance groups (i.e., letters) were generated by means of Tukey according to the model M4T2, where two groups sharing no common letter(s) differed significantly at level $\alpha = 0.05$

Table 6 Likelihood ratio, likelihood ratio significance, AIC and BIC values calculated for the fixed factors in the model M3

	Likelihood ratio	Likelihood ratio significance	AIC difference	BIC difference
Taxon group	7.861	< 0.01	5.861	0.736
Diameter	436.567	< 0.001	426.567	400.945
Transect	1.304	0.253	− 0.696	− 5.820

Table 7 Results of the generalized linear mixed model M3

	Estimate	Standard error	z value	p value
Intercept (reference levels: taxon_softwood, diameter d1, transect_WBT)	4.5183	0.4523	9.990	< 0.001
taxon_other	− 0.7290	0.2633	− 2.769	< 0.01
diameter_d2	− 2.9768	0.2653	− 11.222	< 0.001
diameter_d3	− 4.0518	0.3341	− 12.128	< 0.001
diameter_d4	− 4.6717	0.4415	− 10.582	< 0.001
diameter_d5	− 5.7634	0.5725	− 10.067	< 0.001
diameter_d6	− 7.1615	1.1324	− 6.324	< 0.001
transect_OT	− 0.4676	0.4035	− 1.159	0.247

Reference level of taxon, diameter and transect categorical variables were softwood species, diameter_d1 (< 5 cm), and waterbank transect, respectively. Key: taxon_softwood—softwood species, taxon_other—other (non-softwood) species, diameter_d1—d < 5 cm, diameter_d2—5–9 cm, diameter_d3—10–18 cm, diameter_d4—19–32 cm, diameter_d5—33–54 cm, diameter_d6—55–146 cm, transect_OT—outer transect, transect_WBT—waterbank transect

Type of utilization

Based on the likelihood ratio, the diameter had a more than 50-fold greater effect on the frequency of cutting within the utilization than the taxon group (Table 6). The cutting/utilization ratio was significantly influenced by the diameter and the taxon group (Table 7). It decreased monotonically with the increasing diameter and was higher in the case of softwoods than in the case of other species (Fig. 6). The effect of the transect was not significant.

The average trunk diameter of the cut units was significantly smaller than that of the intact units in the *Alnus*, *Cornus*, *Fraxinus*, *Populus*, *Prunus* and *Salix* genera (Fig. 7). The average trunk diameter of carved and debarked units was generally larger than that of cut units, and sometimes even that of intact units. In the case of *Populus*, the average diameter of the debarked units was significantly larger than that of the cut and carved units. In the case of *Prunus*, carved units were significantly larger than cut units, and in the case of *Salix*, the following order was confirmed with significant results: carved > debarked, intact > cut. Considering all genera together (model M6T1), it can be concluded that there was a significant difference in trunk diameter between the four categories of utilization type as follows: carved > debarked > intact > cut.

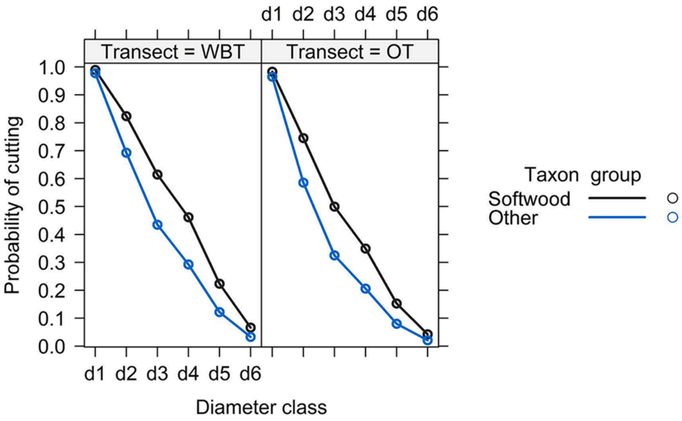

Fig. 6 The effect plot of generalized linear mixed model M3. Key for taxon groups: softwood—softwood species, other—other (non-softwood) species. Diameter classes: d1 < 5 cm, d2—5–9 cm, d3—10–18 cm, d4—19–32 cm, d5—33–54 cm, d6—55–146 cm. Transects: WBT—waterbank transect, OT—outer transect

Discussion

General patterns of beavers' selective foraging

The most influential factor in the foraging decisions of the beaver was the taxon, the importance of which exceeded that of trunk diameter and distance from the water (transect in our models). *Salix* and *Populus* genera were generally preferred, but at some sites we also proved a preference for *Acer*, *Cornus*, *Ulmus*, and *Malus* spp. Studies carried out in other areas of Europe also showed that, in addition to *Salicaceae* species, other taxa can also be positively selected (Nolet et al. 1994; Haarberg et al. 2006; Vorel et al. 2015).

Notwithstanding the fact that there are clear tendencies in their preference, beaver species are generalist herbivores (Jenkins 1975; Vorel et al. 2015). This is further supported by our results. The beaver utilized 14 of the 15 most common genera to varying degrees, and utilization even occurred in the case of some taxa that were only sporadically present at the sites. However, the following genera, despite being in relatively high supply at some sites, were utilized to a remarkably low extent: *Amorpha* and *Robinia* (representing invasive species), *Crataegus*, *Rosa*, and *Sambucus* (representing native species). A few studies reported the possibility of seasonal or year-to-year differences in taxon selectivity (Jenkins et al. 1979; Fustec et al. 2001; Dvořák 2013); bearing this possibility in mind, it may be worth repeating the study in other seasons.

Moving away from the water, the foraging intensity of the beavers decreased even on the small spatial scale we examined: along the transect situated 10 m from the water, foraging intensity was significantly lower than directly along the waterbank. Along Central European watercourses, utilization tends to occur within 10–20 m of the water (Juhász et al. 2020a; Mikula et al. 2022).

Treating all genera together, we showed that the beaver preferred units with a trunk diameter of 5–9 cm. The ratio of utilization of this diameter class significantly exceeded not only that of thicker units, but also that of units thinner than 5 cm. Conducting this analysis for each genus separately, the same difference was confirmed with significant results only in the case of *Alnus* and *Prunus*. The avoidance of thicker units can be explained by

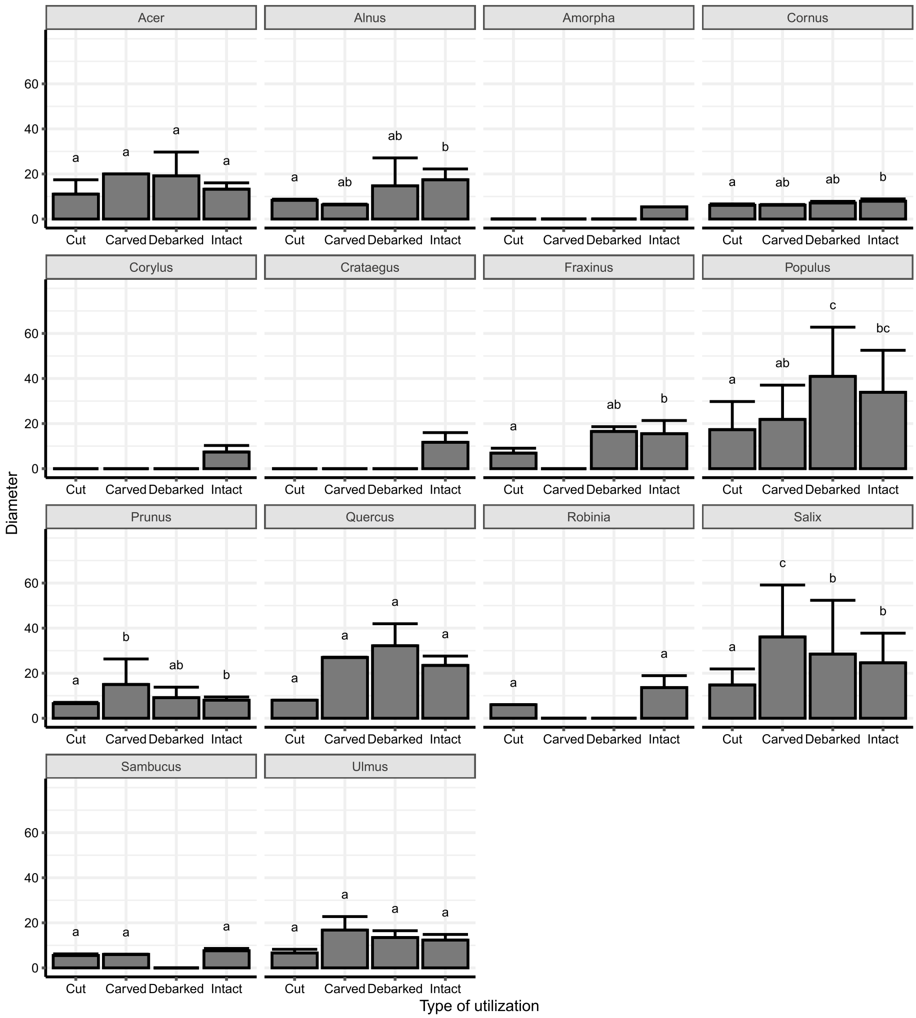

Fig. 7 The mean diameter of cut, carved, debarked and intact units of the most frequent genera, based on the full dataset. Units with a trunk diameter reaching at least 5 cm were taken into account, therefore the *Rosa* genus, present only in the thin branch category, was excluded. Error bars display the standard deviation of site-level values. Significance groups (i.e., letters) were generated by means of Tukey according to the model M6T2, where two groups sharing no common letter(s) differed significantly at level $\alpha = 0.05$

the fact that the time and work required for cutting down, processing, and mobilizing a tree increases with trunk diameter (Fryxell and Doucet 1991; Gallant et al. 2004). Avoidance of the thinnest units may be explained by the higher concentration of certain chemical substances with anti-herbivore properties in the younger units and shoots (Basey et al. 1988). In line with the results of our previous research conducted in active floodplains of larger rivers (Juhász et al. 2022), we found that the utilized trunk diameter range of the preferred *Salix* and *Populus* species was wider than that of other species. Although cutting was indeed more often completed in the case of *Salicaceae* species, the ratio of felling within the different types of utilization was not primarily determined by taxon group, but by trunk diameter. Hence, in the case of thicker trunks, carving and debarking were more typical. In the case of *Salicaceae* species, as the trunk diameter increased, the degree of utilization did not always decrease; instead, the type of utilization changed.

How to evaluate the effects of a re-emerging driver of vegetation change

Overall, the selective foraging of the beaver affected the *Salicaceae* species the most intensively within each trunk diameter class, and their thick specimens may disappear step by step along the stream corridor. However, this gradual disappearance does not necessary imply that the utilized individuals will die, as members of the *Salix* and *Populus* genera are characterized by good resprouting abilities given suitable hydrological conditions (Fustec et al. 2001; Runyon et al. 2014). At the same time, trends related to the decrease in streamflow are not favourable for the regeneration of drought-intolerant species (Hughes et al. 2001; Stella et al. 2010). The avoidance of certain taxa by the beaver may indirectly increase the proportion of these taxa (see also Lesica and Miles 2004; Deardorff and Gorchov 2021 [North America] and Juhász et al. 2020a, 2022 [Europe]). With the reduction of streamflow and the concomitant decline of *Salicaceae* species, it is expected that more and more habitats will become favourable for more drought-tolerant species along the stream corridors. Meanwhile, their spread is not hindered by the beaver's selective foraging in the studied environment. Here, the advance of trees and shrubs (*Acer*, *Amorpha*, *Crataegus*, *Fraxinus*, *Prunus*, *Robinia*, *Rosa*, *Sambucus*, and *Ulmus* spp.) better adapted for drier conditions can be predicted.

However, beaver dams can enhance water tables and create new establishment sites for willow shrubs and young *Salix* and *Populus* stands (Wolf et al. 2007; McColley et al. 2012). Softwoods can also be supported by artificial water retention, e.g., beaver dam analogues (Orr et al. 2020). During a future assessment of long-term foraging impact, it would also be necessary to distinguish the type of cut units (main stem or branch) and analyse the number of affected branches per tree/shrub, as well as the survival and sprouting ability of individual plants. The latter data should be quantitatively compared with the hydrological parameters of the beaver-transformed habitat. Here, we described in detail the general patterns of the beaver's selective foraging, which is an important driver of vegetation change. However, the impact of the species' disturbance largely depends on environmental factors, including water availability in the root zone, which may be influenced by both beavers and humans.

Ensuring the presence and renewal of native softwoods is recommended not only from the point of view of nature conservation but also with regard to forest management: dense softwood stands in the narrow waterbank section can act as a distraction zone in front of plantations, thus helping to reduce beaver damage in commercially valuable *Quercus* and *Fraxinus* stands, lying further from the water (Mikula et al. 2022). However, if *Populus* plantations are located in this narrow section, significant damage can occur, which is one of the main sources of conflict in the study area (Juhász et al. 2020b; Ulicsni et al. 2020). The order of importance of the variables indicates that if softwood supply consists of old trees of the same age, selective foraging will result in their destruction, even if there is a dense shrub layer with other species, due to the foremost importance of taxon preference.

Beavers avoided the invasive *Robinia pseudoacacia*, which fact also has forest management and conservation importance. Even though the spread of *Robinia* is causing ecological problems throughout Central Europe, the species is still popularly used in tree plantations because of its economic benefits (Vítková et al. 2017). Replacing woody vegetation along waterbanks with monodominant stands of species not utilized by beavers has the potential to further exacerbate the effects of beaver on the remaining softwood stands along the banks.

The distance from water of the foraging activity should be taken into account during landscape-scale planning of both forest management and the conservation of old softwood trees and stands. It should be noted that beavers, by building dams, can modify the original shoreline and depending on the physical landscape they may be able to create extensive wetlands, as well (Larsen et al. 2021). Therefore, along watercourses where this landscape-transforming activity of the beaver is possible, the size of the beaver-influenced area may be significantly larger. At our study sites, the shoreline was not modified by the beaver, but at one site a beaver meadow was created in the adjacent part of the landscape. The four beaver habitats where we registered beaver dams were in the early phase of their development. In Hungary, the real, experienced impact of dam-building behaviour is affected not only by the length of beaver occupation and the environmental characteristics, but also by human interventions, as large numbers of beaver dams are demolished year by year with permits from the conservation agencies, and often even without such permits (Czabán and Gruber 2018; Juhász et al. 2019). This phenomenon significantly hinders development of the beavers' beneficial effect on water retention.

Management implications

The highest foraging intensity was observed among the *Salicaceae* species for all trunk diameter classes, and the taxon was the most influential factor in the foraging decisions. In the presence of the beaver, the preservation and support of these species is possible in the following three ways:

(1) By helping the natural renewal of willows and poplars, in which a key role is played by improving hydrological conditions. Unlike larger rivers, in the case of small watercourses, the water table can be managed through moderate effort: reducing water abstraction; artificial water retention; protection of beaver dams.
(2) By ensuring the presence of a diverse age group structure, and thus the presence of thin trunk diameter classes.
(3) By ensuring the presence of beaver-utilized native species in the shrub and canopy layer along a narrow waterbank section, not intended to directly serve economic interests. Besides *Salicaceae* species, *Cornus* should be highlighted, which is also one of the most frequently utilized genera, and can occur in large quantities in the shrub layer of the stream corridors.

The fact that beaver activity is mainly limited to the waterbank also indicates that the band situated 10–20 m from the water should be considered not primarily as an area of forest management objectives, but rather as a green corridor, a means of preserving part of aquatic and riparian biodiversity. The owners of such areas could be granted support in order to motivate them to implement ecological and sustainability measures.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-023-02598-8.

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Author contributions EJ: Conceptualization (lead); Data collection (lead); Data curation (lead); Visualization (lead); Writing—original draft (lead); Methodology (equal); Formal analysis (supporting). ZM: Writing—original draft (supporting); Supervision (supporting). ÁB-F: Formal analysis (lead); Methodology (equal); Data curation (supporting); Writing—original draft (supporting). MB: Supervision (lead); Conceptualization (supporting); Visualization (supporting); Writing—original draft (supporting).

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Data availability The authors confirm that the data supporting the findings of this study are openly available (Juhász et al. 2023).

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

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