

The effect of beaver dams on physico-chemical properties of stream water in the Carpathians (Poland and Slovakia)

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Abstract. In recent decades, the population of the Eurasian beaver (*Castor fiber*) has undergone a rapid recovery from near extinction to abundance across vast areas of Europe. The ability of this species to build dams has a significant impact on ecological processes making beaver reintroduction an important environmental factor in recolonised areas. Although the effects of beaver dams on stream water chemistry have been studied extensively, general conclusions are often limited by site specific conditions. Therefore, the aim of this study was to assess the impact of a geomorphic type and an age of beaver pond sequences on physico-chemical water properties in and below beaver ponds compared to upstream channel sections throughout the seasons.

This study was conducted on nine beaver-inhabited streams distributed across the Western Carpathians (Poland and Slovakia). The beaver ponds were classified into two geomorphic categories: overflowing river banks or confined to the river channel. The age of the ponds ranged from <2 years to >10 years. Water samples were collected above, within, and below beaver pond sequences under baseflow conditions during four seasons in 2022-2023.

In general, a greater decrease in NO_3^- and SO_4^{2-} concentrations within and below the ponds was observed during the warm seasons than during the cold seasons. The age of beaver pond sequences was found to be a more significant factor than the pond type. It was positively related to decrease in dissolved oxygen, SO_4^{2-} and pH in the ponds and decrease in SO_4^{2-} in downstream channel sections. A comparison between two geomorphic types of beaver ponds revealed that there was a greater decrease in NO_3^- and Ca^{2+} concentrations within overflowing ponds and a greater decrease in pH downstream of these ponds compared to in-channel ponds. Biogeochemical processes involving organic matter accumulated in beaver ponds, that include its decomposition and aerobic/anaerobic oxidation, as well as CaCO_3 precipitation might be responsible for the observed differences. The long residence time of water in overflowing beaver ponds fuels the dynamics of these processes.

The role of the age of beaver ponds suggest that their long-term persistence may be important for sustaining water purification processes. However, further research based on a larger dataset and a more frequent sampling strategy is needed to identify the

30 biogeochemical processes occurring in beaver ponds under specific hydro-meteorological conditions: during low flow periods,
snowmelt and rainfall events.

1 Introduction

Beavers, the two semi-aquatic species of the genus *Castor*, significantly alter riverine ecosystems through foraging activity and the construction of dams, canals, burrows and lodges (Rosell et al., 2005; Brazier et al., 2021). Their influence on
35 hydrological, geomorphological and ecological processes makes them perfect examples of environmental engineers and
keystone species (Jones, 1994; Holtmeier, 2015). Their ability to build dams is particularly important because of the strong
impact their structures have on the hydrogeomorphological system (Gurnell, 1998). The physical features of the created ponds
and their influence on biogeochemical cycles affect habitat availability for other organisms and lead to increased biodiversity
(Wright et al., 2002; Larsen et al., 2021). In addition, beavers are recognised as providers of important ecosystem services,
40 e.g. through their support of water retention and purification (Puttock et al., 2017; Thompson et al., 2021).

The Eurasian beaver (*Castor fiber*) was once widespread across both continents until excessive hunting resulted in the
disappearance of the species from most of its former range. Only eight remnant populations were left at the beginning of the
20th century (Nolet and Rosell, 1998). Their subsequent reintroductions, hunting restrictions and natural dispersal led to a
substantial population increase and the near re-establishment of the species distribution (Halley et al., 2020). According to the
45 data collected by Wróbel (2020), the highest beaver population density among the six Carpathian countries is currently found
in Poland, followed by Slovakia. A few centuries before the species disappeared from the lowest parts of the Polish Carpathians
in the 19th century, it was extirpated from more elevated catchments (Żurowski, 1986). Beaver releases in Poland, conducted
since the 1940s, have mainly focused on the lowlands (Dzięciołowski and Gozdziwski, 1999). The first reintroduction
program aimed at re-establishing Carpathian populations was successfully carried out between 1980 and 1985 (Żurowski and
50 Kasperczyk, 1990). Beavers in the northern part of Slovakia originated solely from the Polish reintroduction (Pachinger and
Hulik, 1999) and were first documented along the Ondava river in 1981 (Valachovič, 2012). Since then, both countries have
observed substantial increases in the range and abundance of recovering beaver populations (Čanádý et al., 2016; Wróbel and
Krzysztofiak-Kaniewska, 2020).

In recent decades, there has been increasing interest in studying the impact of beavers on river water chemistry. Understanding
55 the implications for water resource management and nature conservation (Bason et al., 2017; Čiuldienė et al., 2020; Stevenson
et al., 2022; Bylak et al., 2024) is particularly important in the face of contemporary environmental crises. Most beaver-related
studies have focused on the areas inhabited by the Canadian beaver (*Castor canadensis*) (Halley et al., 2020; Larsen et al.,
2021). It's commonly assumed that both species exert similar influences on the environment even though the Eurasian beaver
expresses less advanced building activity in terms of the number and size of created structures (Gurnell, 1998; Rosell et al.,
60 2005) and inhabits different ecosystems. Thus, the impacts of the Eurasian beaver are still relatively understudied even as its

significance for shaping fluvial processes is growing due to the increasing population. Moreover, to our knowledge, most of the studies on the impact of the Eurasian beaver on water properties have been focused on the lowlands (Puttock et al., 2018; Čiuldienė et al., 2020; Kalvīte et al., 2021; Bylak et al., 2024) despite the high activity rates of the species and its influence on hydrogeomorphological processes in the mountains (Giriati et al., 2016; Gorczyca et al., 2018). The species recently became a prominent environmental factor across the Carpathian mountains after centuries of absence, therefore understanding its impact on this area is particularly important.

Beaver dams decrease water flow velocity, which promotes the sedimentation of suspended solids and increases nutrient retention (Maret et al., 1987; Puttock et al., 2018). Therefore, beaver ponds may act as substantial catchment-scale sinks for nitrogen (Lazar et al., 2015). The accumulation of organic carbon and phosphorus is also commonly observed (Lizarralde et al., 1996; Wohl et al., 2012; Čiuldienė et al., 2020). Moreover, the filtration capacity of beaver dams results in the attenuation of heavy metal concentrations downstream of beaver ponds compared to upstream river sections (Čiuldienė et al., 2020; Murray, 2021). The influence of beavers on river water quality is often recognised as positive because they enhance self-purification processes. Consequently, they have the potential to be considered as a restoration tool for degraded streams (Bason et al., 2017; Puttock et al., 2017; Bylak et al., 2024). However, most studies highlight the role of seasonal changes in source and sink transitions, depending on flow rate and ecosystem productivity (Maret et al., 1987; Wegener et al., 2017; Murray, 2021).

The impact of a particular beaver dam on the physico-chemical stream water parameters may not reflect generally recognised trends due to the influence of local site-specific characteristics (Kalvīte et al., 2021). Brazier et al. (2021) also pointed out the potential differences in the impacts of a single pond compared to a sequence of multiple ponds. These may hinder deriving general conclusions regarding the impact of complex beaver-mediated modifications to river channels, especially when contradictory patterns are observed (Majerova et al., 2015; Weber et al., 2017). The identification of factors reflecting the diversity of beaver ponds and their effects on water chemistry, would improve the understanding of the effects of beaver presence in river systems. The age of beaver ponds was commonly proposed as a such feature in previous studies on upstream-downstream gradients of physico-chemical parameters in beaver-occupied streams. For example, Bason et al. (2017) found a greater reduction of suspended solids in older dam sequences compared to younger ones. Metal sequestration rates and a sediment organic matter content inside beaver ponds also rise with the pond age according to the study of Murray et al. (2021). Hydrological and thermal differences were observed between various geomorphic units within beaver ponds, representing e.g. main channel, its margins and backwater areas (Majerova et al., 2020). The share of such units, especially related to the floodplain inundation, was then suggested as a potential geomorphic factor that could explain differences between study sites (Murray et al., 2021). Spatially expansive beaver ponds are expected to facilitate a higher proportion of low velocity areas, increase in water residence time, extent of a hyporheic zone, overbank sedimentation and growth of aquatic vegetation, compared to the ponds constrained to the river channel. Both beaver pond age and its geomorphic type may correspond with the prolonged sediment-water interactions resulting in the enhanced biogeochemical processes.

The objective of this study was to determine the effects of beaver dams on physico-chemical water properties in mountain streams of the Western Carpathians (Poland and Slovakia), with regard to seasonality and pond characteristics. The paper focuses on answering the following three questions:

- 1) How do physico-chemical water parameters change between river sections located upstream of, within, and downstream of beaver ponds, and what biogeochemical processes might be responsible for these differences?
- 2) How do these differences vary seasonally?
- 3) How are these differences affected by the geomorphic type and age of beaver ponds?

2 Methods

2.1 Study area

The study was conducted on nine beaver-inhabited streams in the Outer Western Carpathians (Fig. 1). The region consists mainly of alternating series of sandstones, conglomerates, mudstones and shales that make up the sedimentary deposits of Carpathian flysch (Ślaczka et al., 2006; Łajczak et al., 2014). Generally, in the northern, lower-lying foothills of the study area (sites 1, 2, 4-6), easily weathered, soluble shales comprise a large portion of the geological structure (Burtan et al., 1994, Kopciowski et al., 1997; Jankowski, 2014). In the southern part of the study area (sites 7-9), less weathered sandstones predominate (Kopciowski, 2000). The stream at site 3, despite its location in the northern foothills of the mountains, drains one of the highest foothill ranges, the Brzanka Range, which is largely composed of sandstone (Marciniec and Zimnal, 2009). Streams draining areas underlain by shales and mudstones are typically characterised by higher concentrations of bicarbonates, calcium and magnesium ions due to increased weathering of carbonates and clay minerals, while streams in areas composed mainly of sandstone are usually more diluted and characterised by lower specific conductivity (e.g. Siwek, 2021; Solár and Tomaškovič, 2023).

The geomorphologically diverse terrain in the study area ranges from foothills to medium mountains (Gilewska et al., 1982; Borzuchowski and Olędzki, 2011). The highest parts of the Outer Western Carpathians are classified as medium mountains. These areas are characterised by steep slopes that often exceed 30% and significant relative relief ranging from 400 to 800 m. Low mountains can be found at the margins of these ranges and in isolated ridges. They feature steep slopes and smaller relative relief ranging from 200 to 400 m. The foothill zone is primarily located in the northern part of the study area. It reaches elevations of approximately 500 m above sea level. This zone is mainly characterised by wide, gently sloping ridges that rise 40 to 300 m above the flat valley floors (Starkel, 1990). The mean annual temperature in all selected catchments ranges from 5.1 to 9.1°C and the average precipitation is 770-1140 mm (based on the 2000-2010 period; Szalai et al., 2013; CARPATCLIM, 2013). Rivers in this area are mainly characterised by a nival-pluvial hydrological regime (Wrzesiński, 2017).

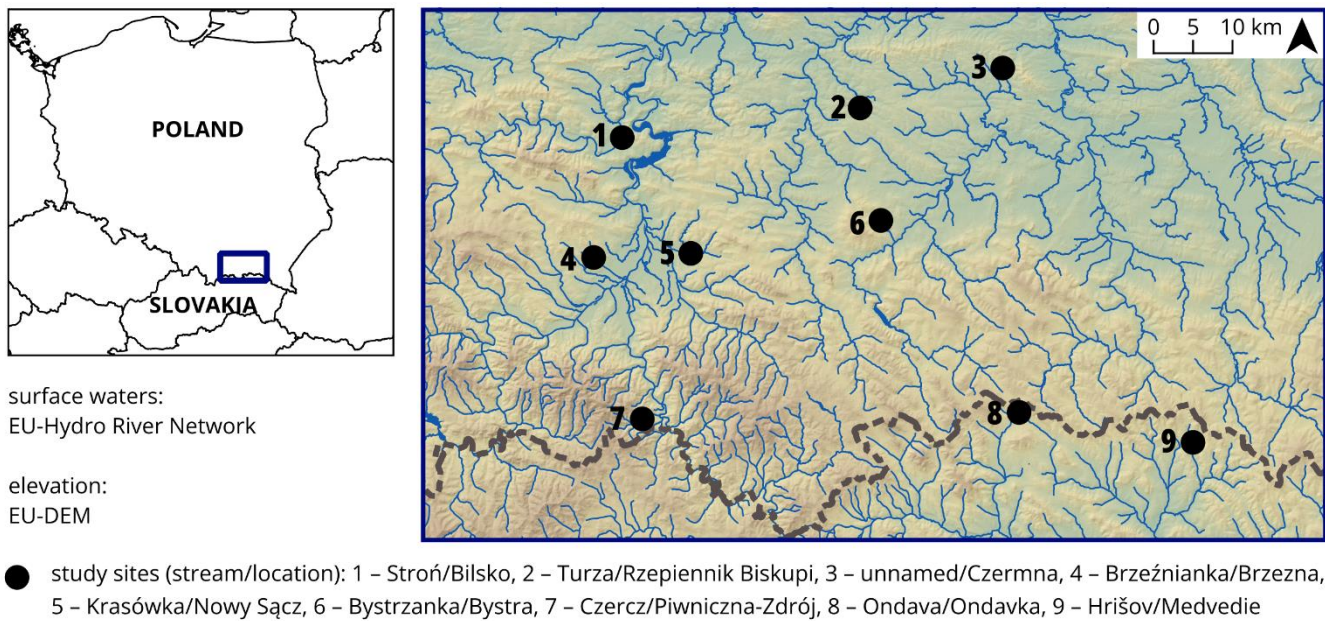


Figure 1: Study area.

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All of the catchments consisted of a mixture of forest and agricultural areas, i.e. arable lands and meadows. Despite the
widespread abandonment of agricultural land and the generally low-to-moderate intensity of agricultural practices in the
130 mountainous catchments (Pazúr et al., 2014; Koleccka et al., 2017), the impact of these activities may be significant locally, as
evidenced by the increase in nitrate concentrations observed in the Ondava catchment due to the use of fertilisers (Pekarova et
al., 2006; Balejčíková et al., 2020). Overall, agricultural practices in the Polish and Slovakian Carpathians are mostly extensive,
characterised by low–input management and mowing and grazing on a small-scale (Pazúr et al., 2014; Koleccka et al., 2017;
Affek et al., 2023). According to national agricultural statistics (Central Statistical Office of Poland, 2025), the average
135 consumption of mineral fertilisers (NPK) in the Małopolskie and Podkarpackie Voivodeships remains one of the lowest in the
country (80–95 kg NPK ha⁻¹ year⁻¹ compared to the national average of ~125 kg ha⁻¹) and has shown little change over the last
two decades. Similar situation is observed in the northern part of Slovakia where the average use of industrial fertilisers is less
than 60 kg NPK ha⁻¹ year⁻¹ (Siman and Velísková, 2018). Consequently, the direct inflow of nutrients from fertilisers into
watercourses is minimal, although local enrichment may occur near farms or areas of intensive grazing. In contrast, domestic
140 wastewater was identified as the main source of stream water pollution in the rural areas of the Polish Carpathians (Siwek,
2021). The intensity of housing development across the study area ranged from negligible levels to artificial surfaces covering
up to 4% of the area and containing a few hundred buildings.

The Slovak part of the Carpathians is characterised by large plots of agricultural land and small, dispersed settlements that are mainly concentrated in the valleys. This pattern is due to the impact of the post-1990 land reforms on land use and farm structure, both of which are characterised by large corporate farms and agricultural cooperatives (Lazikova et al., 2017). Despite the privatisation of land in Slovakia, land continues to be managed by large holdings and production companies (Bański, 2017) and the average size of an arable land parcel is 21.0 ha (Lieskovský et al., 2015). In the Polish Western Carpathians, settlements are more dispersed throughout slopes, and the land reform led to a progressive fragmentation of agricultural land (arable land and grassland) due to the constant division of land between successive owners (Krocak et al., 2018). In the Polish Carpathians, the average agricultural parcel size is 0.5 ha (Kolecka and Kozak, 2019).

The primary criterion for the selection of streams for the study was the presence of beaver dams that span the entire riverbed. The study sites were distributed randomly through the transect of the relatively low-elevation areas in the north to the southern slopes of the ridgeline close to the Poland–Slovakia border. In addition to varying topography, the sites differed in terms of human activity, such as catchment land use and presence of river control structures. The height of the beaver dams studied did not exceed 1.5 m. In most dam sequences, the ponds were directly connected. The only exception was site 7, where short sections of free-flowing reaches were observed between the ponds. For further analyses, the study sites were classified based on the beaver pond characteristics. Two geomorphic types were distinguished considering the extent of a beaver dam: in-channel (dams within river banks) or overflowing (dams extending over river banks and leading to inundation of adjacent parts of river valley). The area covered by the overflowing ponds was two to seven times larger than their respective river channels which indicates a substantial proportion of flooded riparian areas. The age of beaver ponds was assessed based on the archival orthophotos and classified into three categories: young (≤ 3 years old), moderate (4-9 years old), and old (≥ 10 years old) (Table 1).

Table 1: Characteristics of the study sites.

Characteristics		Study sites (number refers to the Fig. 1)								
Subject	Parameter	1	2	3	4	5	6	7	8	9
Catchment	Area [km ²]	2.6	7.7	2.2	7.1	2.0	5.2	16.9	1.1	9.8
	Outlet altitude [m a.s.l.] ^a	245	271	294	348	343	364	457	487	368
	Dominating land cover category: ^b B - broadleaved forest; C - coniferous forest; H - permanent herbaceous	B	H	B	H	C	H	C	H	B
	Share of sealed artificial surfaces [%] ^b	2.1	1.8	1.1	3.1	2.3	4.1	1.0	0.2	0.1
	Approximate number of buildings ^c	250	300	90	530	150	590	650	20	30
	Share of forests [%] ^b	51.2	46.9	59.0	40.4	55.3	37.9	85.4	38.8	86.8

Stream section	Channel gradient [%] ^a	1.9	0.8	1.1	2.1	1.8	1.8	3.1	2.6	2.0
	Length [km]	0.4	0.6	1.3	0.2	0.5	0.1	0.3	0.6	0.3
	Pond sequence area [ha] ^d	0.14	0.24	1.70	0.22	0.42	0.01	0.18	0.57	0.68
	The biggest pond area [ha] ^d	0.04	0.03	0.38	0.07	0.05	0.01	0.02	0.12	0.36
	Approximate age of the beaver pond sequence [years] ^d	4-9	4-9	≥10	≤3	≥10	≤3	≤3	≥10	≥10
	Beaver pond type: I - in-channel; O - overflowing	I	I	O	O	O	I	I	O	O
	Ratio of the pond sequence area to the area of the river channel	1:1	1:1	7:1	2:1	4:1	1:1	1:1	5:1	4:1
	Number of ponds in the sequence	6-10	6-10	>10	3-5	6-10	1-2	3-5	>10	3-5
	River regulation structures: + presence, - absence	+	-	-	+	-	+	-	-	+

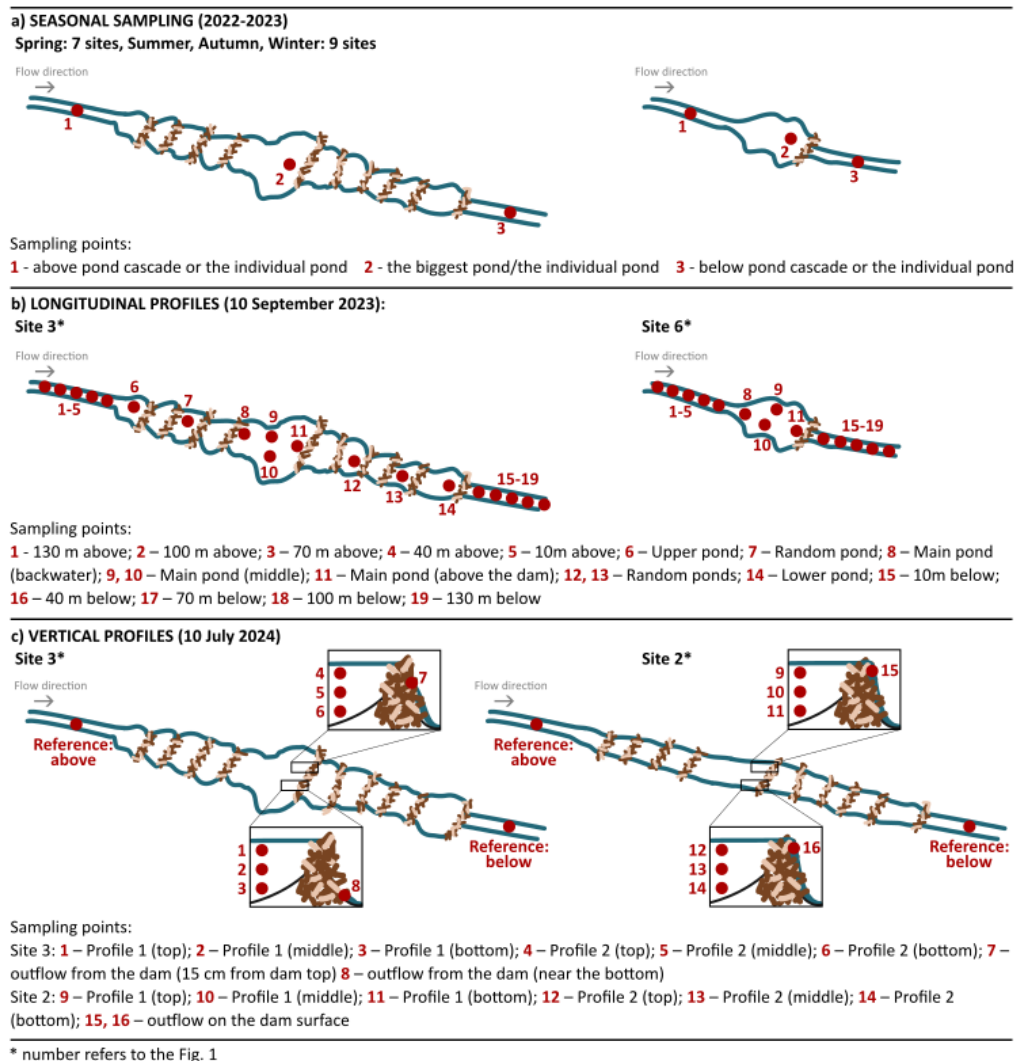
The catchment characteristics refer to the catchments closed at the sampling sites below the beaver pond sequences.

165 Data sources:

- a - digital elevation models (1x1m) obtained from Polish Office of Geodesy and Cartography, and Geodesy Cartography and Cadastre Authority of the Slovak Republic
- b – dataset CLCplus Backbone 2018 (10x10m) obtained from Copernicus Land Monitoring Service
- c - dataset based on Open Street Map obtained through QuickOSM plugin (QGIS)
- d - orthophotos obtained from Polish Office of Geodesy and Cartography (PZGiK) and available in Google Earth Pro

170 **2.2 Water sampling and chemical analysis**

The research followed a three-dimensional sampling scheme: seasonal sampling, longitudinal and vertical profile sampling (Fig. 2). The following water parameters were measured: temperature (T), dissolved oxygen (DO), specific conductivity (SEC), pH and the ionic composition (Ca²⁺, Mg²⁺, Na⁺, K⁺, NO₃⁻, NH₄⁺, HCO₃⁻, SO₄²⁻, Cl⁻).



175 **Figure 2: Study schemes.**

Although both geological variability and human pressure affect the chemical composition of stream water, the sampling design based on comparisons along the longitudinal gradients, helps to minimise the impact of differences between catchments. Three samples were collected at each site in late spring (June), summer (July-September), autumn (October-November) and winter (February) during baseflow conditions (i.e., excluding periods of rainfall events or snowmelts) in 2022–2023 (Fig. 2a). The section ‘above’ the beaver pond or pond sequence that reflected baseline conditions was defined as 50–100 m upstream from a backwater, and the section ‘below’ was 50–100 m downstream from the last dam. The ‘pond’ sample was taken from the main channel section of the pond, i.e. excluding channel margins and backwaters. It was collected approximately 1m above the dam, from the middle of a water column. For sequences of multiple ponds, the representative ‘pond’ sample was collected

180

from the biggest reservoir in the system. Samples were collected between late morning and afternoon, with sampling at each
185 site completed within about an hour. A total of 102 samples were collected from nine sites during the seasonal sampling.

Two sites were selected for additional measurements to create longitudinal stream profiles (Fig. 2b). The sampling was
conducted on 10 September 2023 at site 6 (a single beaver pond created < 2 years ago) and at site 3 (an old beaver pond
sequence created > 10 years ago). Measurements in the ‘above’ and ‘below’ sections were taken every 30 m, starting at a
distance of 130 m from the ponds. Moreover, 4 locations within the ‘ponds’ were sampled to represent the front, middle and
190 periphery of the water body.

To analyse the variation of physico-chemical characteristics in a pond’s vertical profile, water samples were collected on 10
July 2024 at two beaver pond sequences, site 2 and 3, which represented different pond types (Fig. 2c). Solely in-channel
ponds were observed at site 2. By contrast, overflowing stream banks were common at site 3. Measurements were taken from
various depths (near the bottom, in the middle and from the surface of the water column) and from dam outlets. At site 3, outlet
195 measurements were taken from leaks in the upper part of the dam and near its bottom, while at site 2 they were taken from
water overflowing the dam.

Sampling and in situ measurements were conducted without disturbing turbidity. Basic physico-chemical parameters – T (°C),
DO (mg·L⁻¹), SEC (μS·cm⁻¹) and pH – were determined on-site using an ELMETRON CX-401 multifunction meter with the
GXZ-3tk multiparameter immersion head. All pH, SEC and DO probes were calibrated using certified standards before each
200 field study at the laboratory of the Institute of Geography and Spatial Organization Polish Academy of Sciences. Calibration
was performed according to the manufacturer’s guidelines using certified analytical standards: pH probe: three-point
calibration (pH 4.0, 7.0, and 9.0 buffers); SEC probe: calibration with a 1,41mS·cm⁻¹ standard solution, selected according to
anticipated conductivity of the sampled waters; DO probe: air-saturation calibration (100%) followed by zero-oxygen
verification using sodium sulfite solution. Additionally, 250 ml water samples were collected at each site for laboratory
205 analyses.

The HCO₃⁻ (mg·L⁻¹) concentration was determined by titrating the water with a standard solution of hydrochloric acid. The
ionic composition (mg·L⁻¹) was analysed in the Dionex ICS3000 ion chromatograph with analytical columns: IonPac CS16
3×250 mm and IonPac AS18 2×250 mm. Each sample was previously filtered through a glass microfiber filter Whatman GF-
D. The calibration curve was based on the certificate reference standard (CRM) Dionex Combined Six Cation Standard II and
210 Seven Anion Standard II. All solutions were prepared with 1% nitric acid (Suprapur). The following concentrations were
prepared for calibration: 0 (blank), 1, 10, 50, 100 and 1000 μg·dm⁻³. The percent relative error, as determined by the data
quality assessment based on CRM (KEIJM-02, GAW/WMO) was less than 5.0% for all parameters except K⁺ and NH₄⁺. The
respective values were 5.8% for K⁺ and 7.0% for NH₄⁺. The detection limits were 0.4 mg·L⁻¹ for Ca and 0.1 mg·L⁻¹ for the
other ions. Any ion concentrations below the detection limit were replaced with 75% of the detection limit, which is a common

215 procedure in chemistry (Palarea-Albaladejo and Martín-Fernández, 2013). Concentrations below the detection limit were found only for the NO_3^- and NH_4^+ ions. Of all the analysed water samples ($n=102$), the NO_3^- and NH_4^+ concentrations were below the detection limit in 17 and 20 samples, respectively.

2.3 Statistical analysis

220 Principal component analysis (PCA) was performed on the percentage change (Dc) in the values of individual physico-chemical parameters of water in ponds and streams below the beaver dams relative to their values above the ponds, which was calculated using the following formula:

$$Dc = \frac{(Bx - Ax)}{Ax} \cdot 100\%, \quad (1)$$

where:

225 Bx is the value of the physico-chemical parameter x in the pond or stream below the dam, while Ax is the value of the physico-chemical parameter x in the stream above the dam during a particular sampling session.

For the purpose of percentage change calculation, temperature values were converted from $^\circ\text{C}$ to K , to account for potential disruptive impacts of values close to 0°C on the percentage change in winter. Physico-chemical water parameters were included in the PCA if their mean absolute difference $|Dc|$ (for all sampling sites combined) exceeded 5%. This procedure was used to account for the accuracy of analytical measurements defined as percent relative errors. The differences in parameters, which 230 relative percent errors slightly exceeded 5% (i.e. NH_4^+ and K^+), were many times greater than their respective errors, which allowed for their inclusion in the analysis. The calculation of $|Dc|$ used the following formula (N is the total number of sampling sessions):

$$|Dc| = \frac{\sum \left| \frac{Bx - Ax}{Ax} \right|}{N} \cdot 100\%, \quad (2)$$

The variables that fulfilled the aforementioned assumption were: DO , H^+ , Ca^{2+} , K^+ , HCO_3^- , SO_4^{2-} , Cl^- , NO_3^- , and NH_4^+ (Table 235 A1). The H^+ concentration was used instead of the pH value to avoid the analysis involving logarithmic variables. The aim of using Dc in the PCA analysis was to identify the factors that determine changes in the physico-chemical parameters of water caused by the presence of beaver dams. The PCA method reduces the complexity of a large data set to a smaller set of easily interpretable factors that can be associated with specific processes (Drever, 1997). A matrix of factor scores, one of the most important parts of the PCA output, was also analysed. Factor scores provide a measure of the relation between each observation 240 (i.e., each sample) and the identified factors (Shaw and Wheeler, 1997). The Kolmogorov–Smirnov and Lilliefors tests were used to determine the normality of the distributions of the variables. The Kaiser criterion was used to separate factors (the eigenvalues >1).

Seasonal and site-to-site variations in *Dc* were also assessed for T and parameters that met the same criteria as those used for PCA. To compare the study sites, they were first classified according to the age and type of each beaver pond sequence (Table 1). After applying the Shapiro–Wilk test for normality, either a one-way ANOVA or its non-parametric equivalent (the Mann–Whitney U test for two-group comparisons or the Kruskal–Wallis test for multiple-group comparisons) was conducted for each parameter. In addition to the analysis of the entire data set, a separate analysis was performed on the parameters obtained during the spring–summer period (hereafter: warm season). In addition, correlations between physico-chemical parameters and land use cover, catchment area, channel slope and channel width were analysed. Results characterised by $r>0.6$ were considered as demonstrating a strong correlation. All analyses were performed in STATISTICA 12.0. The significance level of $p<0.05$ was used for all the calculations. Additionally, to reduce the risk of family-wise error for multiple comparisons based on the same dataset, we applied a Bonferroni correction to the significance threshold ($p<0.017$) (Armstrong, 2014). The statistical distribution of the data obtained in this study was described by medians and quartile deviation.

3 Results

3.1 Physico-chemical background of the studied streams

The physico-chemical properties of stream water at baseline conditions varied between the catchments studied (Table 2). Significantly higher SEC and concentrations of major ions were found in streams that drained areas with a high proportion of shales in the bedrock (sites 1, 2, 4, and 6). Lower SEC and concentrations of major ions were found in streams draining catchments dominated by sandstones (sites 3, 7–9). Concentrations of Cl^- , Na^+ and K^+ showed high correlations with the share of artificial surfaces in the studied catchments ($r=0.85$, 0.78 and 0.61 respectively). Additionally, concentration of Cl^- correlated with the number of buildings in the catchments ($r=0.61$).

Table 2: Input physico-chemical water parameters, measured above beaver ponds (median values).

Study site*	pH	SEC [$\mu\text{S}\cdot\text{cm}^{-1}$]	DO	Ca^{2+}	Mg^{2+}	Na^+	K^+	NO_3^-	NH_4^+	HCO_3^-	SO_4^{2-}	Cl^-
							[$\text{mg}\cdot\text{L}^{-1}$]					
1	8.2	537.3	9.7	77.5	18.6	18.5	2.7	2.6	0.1	249.2	64.1	14.7
2	8.1	562.7	8.7	76.2	23.0	18.6	1.2	1.3	0.1	266.4	35.2	13.5
3	7.4	272.6	7.9	40.8	7.9	7.6	1.3	1.4	0.2	155.3	28.5	4.0
4	8.3	486.0	9.0	70.6	15.7	28.5	2.9	2.5	0.1	269.1	31.5	34.6
5	8.5	376.2	11.0	61.0	11.5	12.1	0.8	2.8	0.2	205.0	27.8	8.9
6	8.0	410.7	8.4	58.9	7.8	28.5	5.5	4.4	0.1	239.8	27.0	14.7
7	8.4	285.7	10.2	51.2	10.5	5.3	0.9	3.4	0.2	183.7	17.9	4.3
8	7.9	350.0	8.3	67.2	6.3	9.6	0.8	0.3	0.1	251.3	10.3	0.8
9	8.1	303.9	10.2	59.4	6.1	9.5	1.2	0.6	0.2	207.5	24.2	3.5

* number refers to the Fig. 1

3.2 The effect of seasonal and site-specific variability of beaver dams on physico-chemical water parameters

265 There were clear differences in the values of most physico-chemical parameters in and below the beaver ponds compared to
the streams above (Fig. 3, A1 and A2). Those differences were greater in the pond water than in the stream water below the
dams (Fig. 3, Table A1). There were no strong correlations between the percentage change in the physico-chemical parameters
and the catchment and stream characteristics (e.g. land use, catchment area, stream width) or the water parameters above
beaver ponds. Larger differences were observed in streams with older beaver dams than in streams with younger ones (Fig. 3,
270 A1 and A2). The largest changes in the physico-chemical water parameters obtained within beaver ponds ($|Dc| > 20\%$) were
found in H^+ (pH), NO_3^- , NH_4^+ , and DO (in consecutive order). Intermediate changes ($|Dc| = 5-20\%$) occurred in K^+ , SO_4^{2-} , Cl^- ,
 HCO_3^- , and Ca^{2+} , while the smallest changes ($|Dc| < 5\%$) were observed in SEC, Mg^{2+} and Na^+ (Table A1).

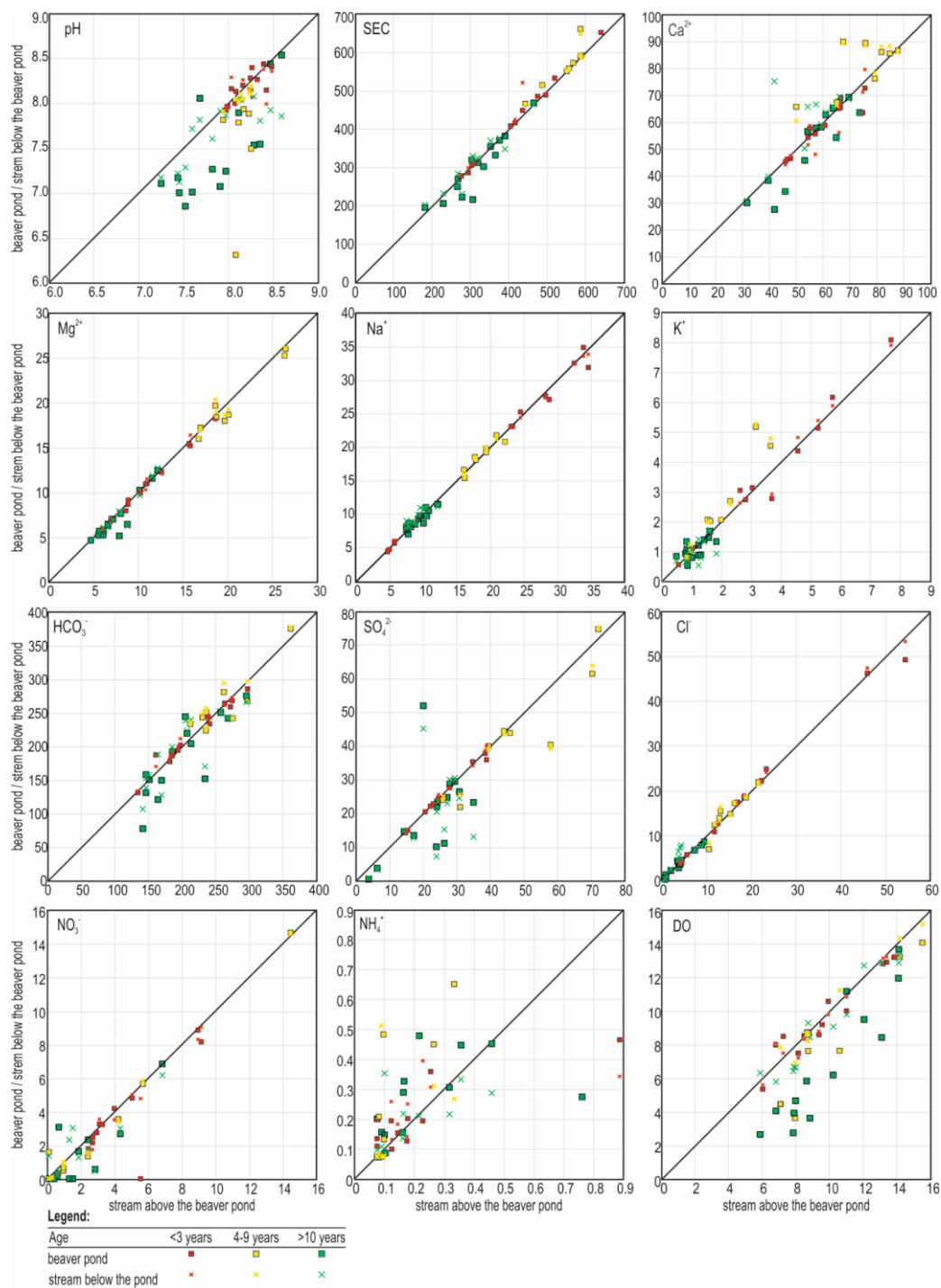


Figure 3: The physico-chemical water parameters, such as pH, SEC [$\mu\text{S}\cdot\text{cm}^{-1}$], major ions, NH_4^+ , NO_3^- , and DO concentrations [$\text{mg}\cdot\text{L}^{-1}$] within and below beaver ponds of different ages in relation to the inlet values.

For streams below the dams, the largest changes in the physico-chemical parameters relative to streams above the ponds ($|Dc| > 20\%$) were found in NO_3^- , H^+ (pH), and NH_4^+ . Intermediate changes ($|Dc| = 5\text{--}20\%$) occurred in Cl^- , SO_4^{2-} , K^+ , Ca^{2+} , HCO_3^- , and DO, while the smallest changes ($|Dc| < 5\%$) were observed in SEC, Mg^{2+} and Na^+ (Table A1). Despite large absolute differences in the values of some parameters ($|Dc|$), the direction of the changes were not strongly consistent across seasons or study sites (Fig. 4, A1, and A2). However, distinctly lower pH values and DO concentrations within and below the beaver ponds, compared to the upstream channels, were observed at most study sites during all seasons. Moreover, several patterns in physico-chemical parameter changes were consistently observed for the majority of the study sites during particular seasons. For example, significant decreases in NO_3^- and SO_4^{2-} concentrations within and below the beaver ponds in comparison to the upstream channels occurred during the spring and summer at most study sites (Fig. 4, A1 and A2).

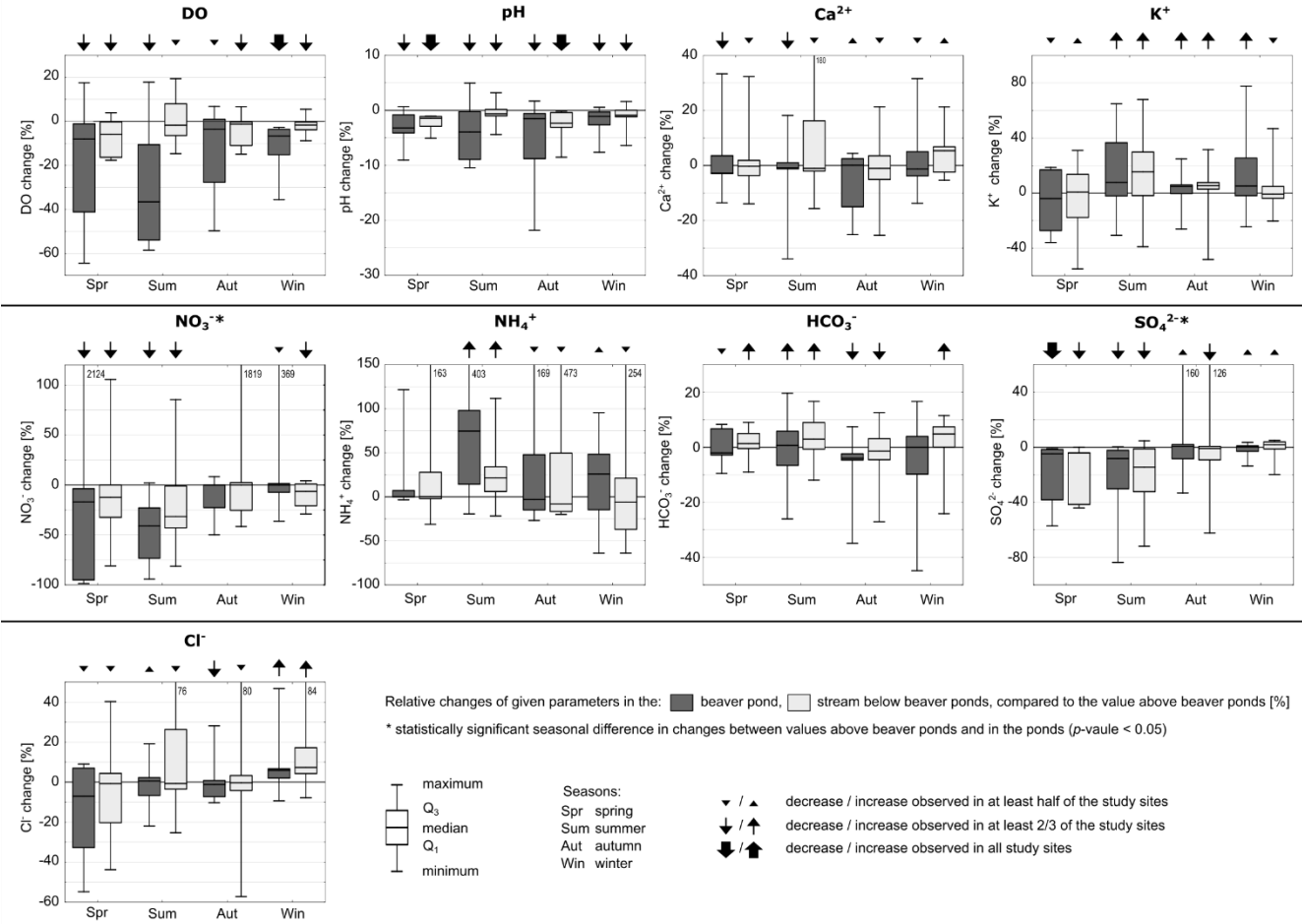


Figure 4: Percentage change (Dc), in the physico-chemical water parameters within and below beaver ponds in relation to stream water above beaver ponds. Only the parameters for which $|Dc| > 5\%$ are shown.

The observed variability in responses to beaver damming was attributed to both the season and the pond type (Table 3, Fig. A1 and A2). In general, a greater decrease in pH was observed downstream of overflowing ponds than in-channel ponds, which had a median value of change of -2.4% ($\pm 1.7\%$) vs. -0.7% ($\pm 0.3\%$), respectively. In addition, greater increases in T and greater decreases in NO_3^- and Ca^{2+} were noted in overflowing ponds (T: $1.0 \pm 0.5\%$; NO_3^- : $-75.3 \pm 22.4\%$; Ca^{2+} : $-2.4 \pm 7.4\%$) compared to in-channel ponds (T: $0.2 \pm 0.2\%$; NO_3^- : $-9.6 \pm 20.1\%$; Ca^{2+} : $0.6 \pm 3.5\%$) during the spring–summer period.

Table 3: Results of group comparisons (ANOVA/Mann–Whitney U/Kruskal–Wallis tests) of the differences (Dc) between inlet values and beaver pond/below the pond in relation to the pond type (i.e., in-channel or overflowing), the age of ponds (i.e., less than 3 years, 4–9 years and 10 years or more) and aggregated seasons (i.e., spring–summer and autumn–winter). Statistical significance thresholds are explained in the footnote.

			Parameter									
			DO	pH	T	Ca ²⁺	K ⁺	NO ₃ ⁻	NH ₄ ⁺	HCO ₃ ⁻	SO ₄ ²⁻	Cl ⁻
Pond type	all seasons	pond				**						
		below		*								
		pond			*			*				
		below										
Age of the pond cascade	all seasons	pond	**	***		*						
		below					**					
	spring and summer	pond	***			*		*				**
		below										**
Spring-summer/ autumn-winter		pond			***			**				**
		below			**							**

*** $p < 0.001$; ** $p < 0.017$ (Bonferroni correction); * $p < 0.05$

Grouping the study sites by the age of the dams yielded a greater number of statistically significant differences, although only changes in DO, pH and SO_4^{2-} showed a clear upward or downward trend (Table 3). There were more significant differences within the ponds than in the streams below the ponds compared to the upstream sections. While pH was barely modified in the youngest (< 3 years old) ponds ($0.1 \pm 0.7\%$), decreases were observed in moderately old ponds (3–9 years old; $-3.4 \pm 2.6\%$) and in ponds older than 10 years ($-6.5 \pm 3.5\%$). A similar trend was observed in DO, with changes of $-3.6 \pm 5.7\%$ in the youngest ponds, $-10.8 \pm 14.1\%$ in moderately old ponds and $-6.5 \pm 3.5\%$ in the oldest ponds. The downward trend of the relative amount of DO with increasing pond age (≤ 3 , 4–9, and ≥ 10 years old) was more prominent during the spring–summer period, where changes of $-3.5 \pm 12.8\%$, $-24.4 \pm 19.3\%$ and $-47.6 \pm 9.3\%$ were observed, respectively.

A decrease in SO_4^{2-} during the spring–summer period was observed both within beaver ponds and in downstream channel sections compared to the upstream sections. Young beaver ponds and the streams below them were characterised by the lowest

changes in SO_4^{2-} concentrations, -1.3% ($\pm 1.0\%$) and -0.6% ($\pm 2.1\%$), respectively. A moderate decrease of SO_4^{2-} was observed in the moderately old sites ($-17.9 \pm 12.0\%$ within the ponds and $-10.7 \pm 10.5\%$ below), and the highest decrease was noted in ≥ 10 years old sites ($-47.7 \pm 18.3\%$ within ponds and $-42.8 \pm 21.9\%$ below).

The importance of beaver dam age in modifying physico-chemical parameters in beaver ponds was also indicated by the PCA, which identified three factors that explain 61% of the variation in physico-chemical parameters between beaver ponds and the upstream channels (Table A2). Factor 1 (F1) determines the concentration differences in most major ions: K^+ , Ca^{2+} , HCO_3^- , and Cl^- , and demonstrates their positive relationships. Factor 2 (F2) is responsible for the negative relationship between the differences in DO and SO_4^{2-} concentration and NH_4^+ , while factor 3 is responsible for the negative relationship between the concentration differences in Cl^- and SO_4^{2-} to NO_3^- . Two clusters of samples were clearly separated by the factor scores of F2 (Fig. 5). The first cluster includes samples from the young beaver ponds in all seasons and moderate beaver ponds in the winter (positive factor scores), and the second cluster includes samples from old beaver ponds in all seasons and moderate beaver ponds in warm seasons: spring, summer and autumn (most have negative factor scores). The samples in the first cluster are more strongly correlated with F1 and F2, as indicated by their concentration near the value of 0 on both the X and Y axes. In contrast, the samples in the second cluster are more dispersed and farther from 0 on both axes.

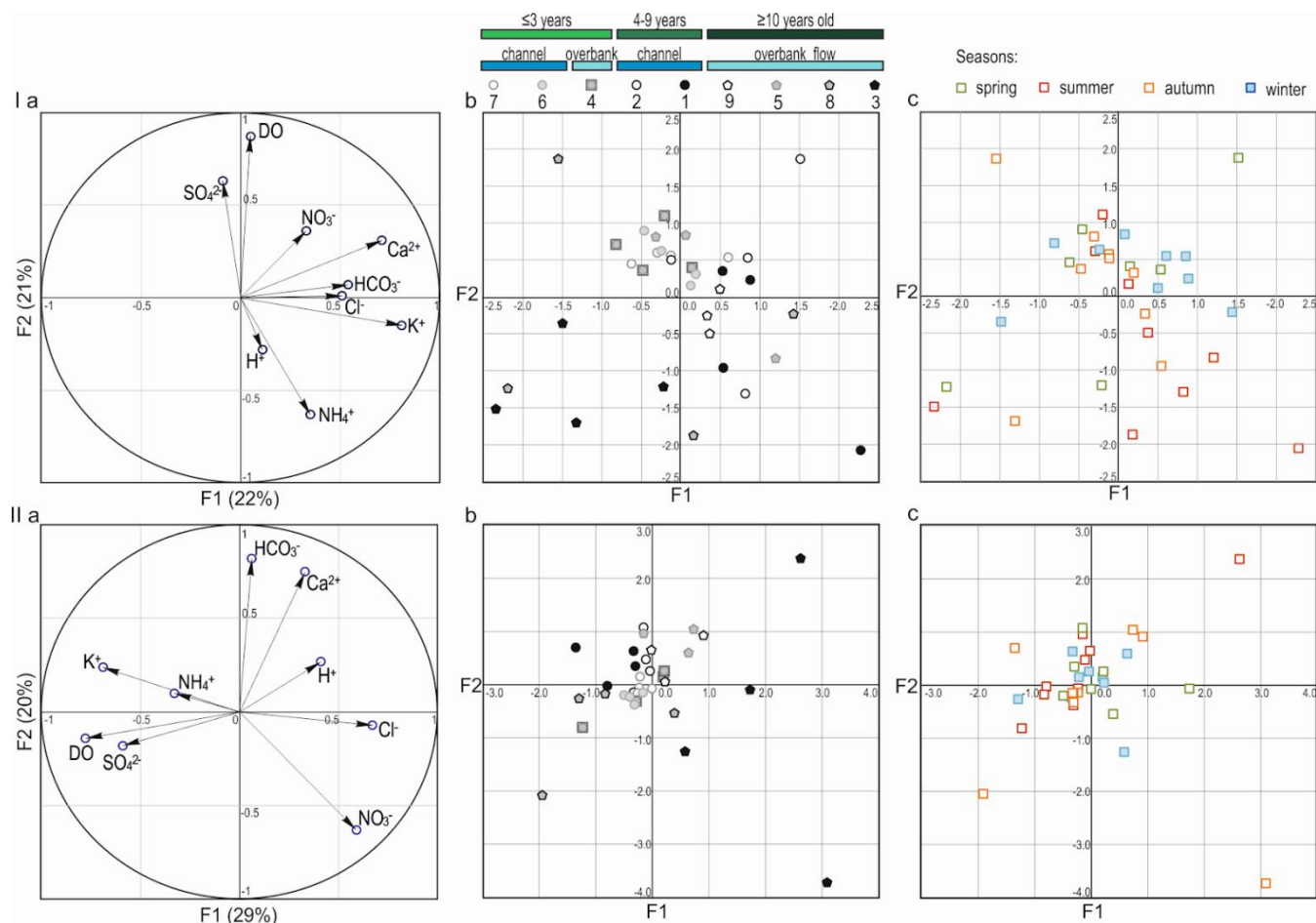


Figure 5: Results of factor analysis for the differences (D_c) between inlet values and beaver ponds (I) or streams below beaver ponds (II): factor loadings (a), factor scores for the water samples classified according to study site (numbers 1-9) (b) and season (c).

3.3 Variation of physico-chemical parameters in the longitudinal and vertical stream profiles

As demonstrated by the longitudinal profiles (Fig. 6 and B1), the older overflowing beaver pond sequence (site 3) has a greater influence on the physico-chemical parameters of water than the young in-channel single pond (site 6). The greatest differences in the physico-chemical parameters at site 3 were seen between the free-flowing upper sections and the inside of the ponds; these changes tended to be partially neutralised in the stream below the beaver dam. The largest differences observed at site 3 were a decrease in NO_3^- within the ponds (-95.4%) and a decrease in SO_4^{2-} both within (-64.5%) and downstream (-71.5%) of the ponds.

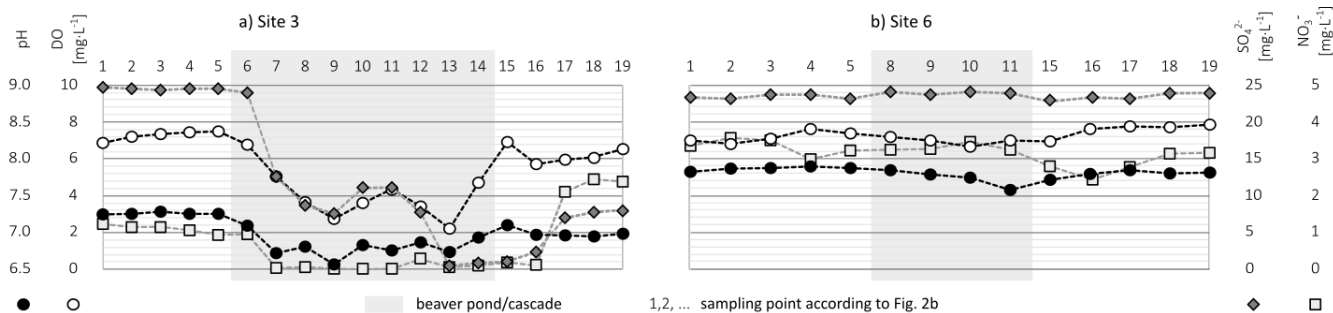


Figure 6: A longitudinal profile of the selected physico-chemical parameters at study sites 3 (a) and 6 (b) on 10 September 2023.

There were significantly greater vertical variations in physico-chemical parameters in the old overflowing beaver pond (site 3) than in the young in-channel beaver pond (site 2). DO, pH and T were found to decrease with pond depth in both studied beaver ponds; however, the range of variation was greater at site 3 than at site 2 (Fig. 7 and B2). The outflow water parameters measured near the base of the dam were notably different from the top of the dam at site 3.

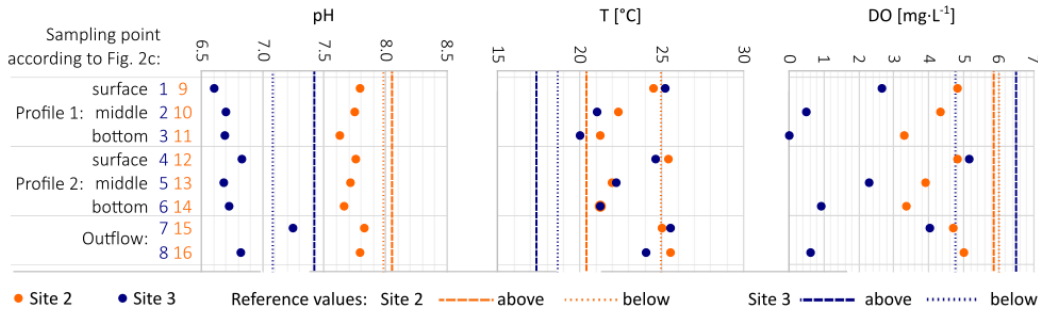


Figure 7: Differentiation of the selected physico-chemical parameters in the vertical profiles of study sites 2 and 3 on 10 July 2024.

4. Discussion

4.1 Biogeochemical processes that control physico-chemical water parameters triggered by the presence of beaver dams

The extensive distribution of the study sites resulted in a diverse initial physico-chemical water properties, which corresponded mainly to the geological structure. Higher SEC and higher concentrations of most of the major ions were found in streams that drain catchments dominated by shales in their bedrock, and they were lower in streams that drain catchments dominated by sandstones. This pattern is characteristic of the Outer Carpathians and it is likely associated with a different resistance to weathering (Siwek et al., 2011; Siwek, 2021; Solár and Tomaškovič, 2023). The relation between Cl^- , Na^+ , K^+ and anthropogenic modification of the catchment suggests human activity as an important factor for concentration of these ions in the study area. Despite the diversity of the selected Carpathian streams, since we based further analysis mainly on concentration

differences of physico-chemical parameters rather than raw concentrations, our results indicated that there are several patterns
350 in physico-chemical water parameters triggered by the presence of beaver dams in stream channels.

The clear decrease in DO concentrations within the beaver ponds compared to the DO concentrations above the ponds (at all study sites) suggests that DO is consumed in the oxidation processes of organic matter under aerobic conditions in the ponds. A beaver-driven decrease in stream DO concentrations was also found by Błędzki et al. (2011) and Stevenson et al. (2022). Detailed investigations carried out in July 2024 at sites 3 and 6 showed that beaver pond water contains high concentrations
355 of total organic carbon (TOC) compared to the stream water upstream. For example, the TOC concentration in the beaver pond at site 3 was found to be more than $13 \text{ mg}\cdot\text{L}^{-1}$, which was almost three times higher than in the stream flowing into the pond (data not shown). This indicates the deposition of organic matter supplied from upstream and/or the in situ production of organic matter via the growth of vegetation in the beaver ponds. Increased organic matter deposition in beaver ponds due to reduced stream flow velocity is often reported in the literature (e.g., Pollock et al., 2003; Green and Westbrook, 2009). Briggs
360 et al. (2012, 2013) found that the accumulation of organic matter in beaver ponds generates specific streambed morphologies, which enhance the exchange of stream water and groundwater within the hyporheic zone behind beaver dams. Furthermore, the high water pressure at the bottom of the ponds causes a downwelling flow over the dam structures. This promotes the transport of organic carbon and DO from the water column to the hyporheic zone, fuelling biogeochemical processes.

The oxidation of organic matter in ponds may also have caused the decrease in SO_4^{2-} concentrations at most of the study sites.
365 Under the anoxic conditions that prevail at the bottom of ponds (as measured at site 3 in July 2024; see Fig. 7), as well as in the hyporheic zone, SO_4^{2-} ions are likely to be reduced to H_2S . These reactions are carried out by microorganisms through the microbial sulphate reduction process, where SO_4^{2-} acts as a specific electron acceptor in the anaerobic oxidation of organic matter under relatively low redox potential (Sutton-Grier et al., 2011). The decrease in SO_4^{2-} concentrations in streams with beaver dams has previously been identified and attributed to the expansion of anoxic conditions (Larsen et al., 2021).
370 According to Naiman et al. (1986; 1994), large accumulations of detritus, in combination with decomposition in expanded wetted areas, result in the development of anaerobic biogeochemical processes.

The decomposition and mineralization of organic matter in the process of ammonification, under both aerobic and anaerobic conditions, leads to the production of NH_4^+ ions in water (Stefanakis et al., 2014). In our study, the ammonification process was indicated by the marked increase in NH_4^+ concentrations in most of the beaver ponds studied in summer. The increase in
375 NH_4^+ concentrations in ponds may also partly be explained by the production of this ion during the denitrification process, as indicated by a marked decrease in NO_3^- concentrations in the studied ponds. Denitrification reduces NO_3^- to NH_4^+ or gaseous N_2 under anoxic conditions in water (Drever 1997). Decreased DO concentrations in the studied ponds could positively influence the denitrification processes in beaver impoundments, as suggested in previous studies by Lazar et al. (2015), Wegener et al. (2017) and Dewey et al. (2022). According to Lazar et al. (2015), denitrification in beaver ponds can remove
380 5–45% of NO_3^- loads at the catchment scale.

The decomposition of organic matter results in the formation of organic acids, which appears to be the cause of the marked decrease in water pH in the studied beaver ponds. According to David and Vance (1991), organic acids constitute most of the dissolved organic carbon in streams and lakes. Strong organic acids with high dissociation capacities significantly decrease water pH (Driscoll et al., 1989). The decrease in stream pH caused by the presence of beaver dams is rarely reported in the literature. In fact, beaver dams most often cause an increase in the stream water pH. For example, in the Appalachian Mountains, USA (Smith et al., 1991; Cirimo and Driscoll, 1993; Cirimo and Driscoll, 1996; Margolis et al., 2001) and the lowlands of Devon, England (Puttock et al., 2017), the pH of stream water increased below beaver dams due to decreased concentrations of acidic ions such as NO_3^- and SO_4^{2-} . According to Margolis et al. (2001), the decrease in NO_3^- and SO_4^{2-} concentrations is one of the largest contributors to the acid neutralising capacity of beaver ponds. In the streams we studied, pH decreased despite the decrease in acid ion concentrations (i.e., NO_3^- and SO_4^{2-}) in the ponds and streams below the beaver dams. Furthermore, the streams and beaver ponds studied in the USA and England (Smith et al., 1991; Cirimo and Driscoll, 1993; Cirimo and Driscoll, 1996; Margolis et al., 2001; Puttock et al., 2017) had similar organic carbon concentrations to the streams and ponds in our study. However, the streams that fed the beaver ponds in the USA and England were more acidic (<7 pH) than the streams we studied (>7 pH). The difference in baseline water pH is likely a key factor in explaining the difference in results because the intensity of organic matter decomposition increases with increasing pH, which is also associated with better conditions for the growth of the bacteria involved in decomposition (Walse et al., 1998). Higher pH values in the streams that feed the studied beaver ponds likely facilitate the greater decomposition of organic matter, which explains the increased production of organic acids in the ponds. Organic acids play an important role as a source of acidity in beaver ponds (Cirimo and Driscoll, 1993).

Our studies indicate that the processes of denitrification, decomposition and oxidation of organic matter, which modify the physico-chemical properties of the beaver pond water, determine the physico-chemical properties of the water below the beaver ponds. The water that flows out of the ponds takes on the physico-chemical properties of the pond water. This is evidenced by the similar directions of changes in physico-chemical parameters within and below the beaver ponds compared to the streams above the ponds. However, the downstream effect of beaver impoundment depends on the structural properties of the dam and, thus, the type of outflow. Due to the vertical complexity of the water column in the ponds, the water flowing out of the ponds through the bottom of the dams has different physico-chemical properties than the water flowing out through the top of the dams. For instance, the oxygen concentrations in the water flowing out from the bottom of the dams are lower than in the water flowing out through the top. Decreasing DO with beaver pond depth is consistent with the results reported by Stevenson et al. (2020). Nevertheless, the changes in the physico-chemical parameters in the water below the ponds, regardless of the type of outflows, are smaller than the changes in the ponds compared to the upstream sections. This is the result of processes specific to running water that cause the physico-chemical properties of pond water to return to the original properties of the stream water. For example, deoxygenated water flowing out of the ponds is slowly reoxygenated, facilitated by the turbulent water flow in the mountainous stream channels. DO concentrations in the streams below the beaver ponds are still lower than in the

streams above the ponds, but it is higher than the DO concentrations in the ponds. Similar decreases in DO within beaver ponds
415 and the subsequent reoxygenation of downstream waters have been observed in previous studies (Smith et al., 1991; Harthun,
2000; Błędzki et al., 2011; Ecke et al., 2017). The return of the stream water to oxic conditions results in the intensification of
the nitrification processes, as evidenced by increased NO_3^- concentrations and decreased NH_4^+ downstream of the beaver ponds
in our study. NO_3^- concentrations below the beaver ponds were still lower than upstream of the ponds, and the NH_4^+
concentrations were still higher, but the differences between the streams above and below the beaver ponds were smaller than
420 the differences between the streams above the ponds and within the ponds. The increased DO concentrations in streams below
ponds favour the aerobic oxidation of organic matter, including the oxidation of organic acids. This increases the pH of stream
water compared to pond water. The reoxygenation of the water in the streams below the beaver ponds involves a series of
biogeochemical processes, such as the aerobic oxidation of organic matter and nitrification, which counterbalance the effects
of the ponds. Our longitudinal study showed that the changes in the physico-chemical properties of the water were partially
425 neutralised within a relatively short downstream distance from the ponds (<100 m).

In the studied streams, the effect of beaver dams on changes in the concentrations of major ions (with the exception of SO_4^{2-}),
was negligible (i.e., their effect on Na^+ and Mg^{2+}) or moderate (i.e., Ca^{2+} , K^+ , HCO_3^- and Cl^-). Observed changes in these ions
were generally not statistically significant. The non-significant effect of beaver dams on Cl^- is similar to the results reported
by Margolis et al. (2001). No clear trends were observed for HCO_3^- concentrations, despite their connection to SO_4^{2-} reduction
430 and NH_4^+ production under anaerobic conditions in other studies (Cirimo and Driscoll, 1993; Larsen et al., 2021).

4.2 Role of seasonality in the beaver dams impact on the physico-chemical water parameters

The greatest changes in most of the physico-chemical parameters within and below the beaver ponds compared to the streams
above the ponds were observed during the warm season (spring and summer). This result can be explained by the higher
intensity of the biogeochemical processes that modify the chemical composition of water at higher temperatures. In the winter,
435 the water temperature in the streams and the surface of the ponds was low; it did not exceed 1.5°C. Winter water temperatures
in ponds are generally not expected to exceed 4°C, the temperature at which water has the highest density (Vega and Abascal,
2005). The situation is different in the warm season, especially in the summer, when water temperatures in the studied streams
and the near-surface layer of the ponds generally exceed 15°C and sometimes rise above 20°C. Biogeochemical processes in
beaver pond water and sediments of the hyporheic zone, such as organic matter decomposition, denitrification and microbial
440 sulphate reduction, are very slow at low temperatures compared to the warm conditions (Qu et al., 2022). As a result, there are
intensive physico-chemical transformations in the stream water flowing into the ponds in the warm seasons. The increase in
 NH_4^+ concentrations and the decrease in NO_3^- concentrations in the studied beaver ponds were particularly prominent in the
warm period of the year due to the intensive ammonification (NH_4^+ production) and denitrification processes (NO_3^- depletion).
This is consistent with the findings of Margolis et al. (2001) and Law et al. (2016): the greatest NO_3^- decrease downstream of
445 beaver ponds occurs in the summer. NO_3^- ion is one of the most effective electron acceptors (oxidants) in the process of

anaerobic oxidation of organic matter; therefore, NO_3^- is the preferred oxidising agent for anaerobic microbes. The process of NO_3^- reduction (denitrification) under anaerobic oxidation of organic matter occurs at a relatively high redox potential level (Anderson and Fidel, 2025). However, it should be noted that the decrease in NO_3^- concentrations in the beaver ponds and streams below the ponds in the summer is partly related to the nitrogen fixation process, which is associated with increased microbial activity in sediments mediated by anaerobic conditions, as well as uptake by aquatic vegetation (Naiman and Melillo, 1984; Maret et al., 1987; Songster-Alpin and Klotz, 1995). Furthermore, the decrease in SO_4^{2-} concentrations in the studied ponds and downstream of the beaver dams was mainly observed during the warm period. This is also likely due to the high rate of anaerobic oxidation of organic matter during that time. According to Smith et al. (1991), Cirimo and Driscoll (1993), and Margolis et al. (2001), the intensive anaerobic oxidation of organic matter can occur despite the relatively low redox potential of the water during the low-flow conditions of summer. During that time anaerobic microbes used even relatively inefficient oxidants, such as SO_4^{2-} , in the anaerobic oxidation of organic matter due to the low concentration of NO_3^- (a more effective oxidant) in the studied waters. The average concentration of NO_3^- in ponds and streams below them was very low during the summer, the average was up to $1.5 \text{ mg}\cdot\text{L}^{-1}$.

Our study showed low seasonality in terms of the changes in major ion concentrations (with the exception of SO_4^{2-}) in the upstream-pond-downstream gradient. However, a slight decrease in the concentrations of Ca^{2+} within and below the beaver ponds was observed during the summer at most of the studied sites. These results may be related to the H^+ ion exchange processes in the sediments, which were indicated by a decrease in water pH. However, based on the small changes in the concentrations of these ions, this process likely plays a minor role in modifying the chemical composition of beaver ponds. According to Cirimo and Driscoll (1993), beaver pond sediments and vegetation act as temporal sinks for Ca^{2+} in the summer, presumably as a result of H^+ exchange and their enhanced biological uptake during the growing season. The slight increase in K^+ concentrations within and below the studied beaver ponds in the summer and autumn may indicate the decomposition and mineralisation of organic matter as a source of K^+ . Lizarralde et al. (1996) found that the net K^+ export in beaver-occupied streams was attributed to the decomposition of leaf litter inputs.

4.3 The effects of beaver dam age and beaver pond geomorphic type on the physico-chemical water parameters

Our research suggests that the age of beaver dams and the geomorphic type of beaver ponds (i.e., overflowing vs. in-channel) play important roles in altering the chemical composition of stream water (Fig. 8). Previously, the impact of beaver dams on various physico-chemical water parameters was commonly found to be inconsistent across different study sites. For example, different directions of change in pH were documented by Lizarralde et al. (1996), Harthun (2000) and Čiuldienė et al. (2020). The beaver pond characteristic proposed in our study may to some extent explain those site-to-site differences. For instance, the magnitudes of the decrease in pH, DO and SO_4^{2-} concentrations in the studied beaver ponds were found to be positively related to the age of the beaver pond sequences. These water parameters are influenced mainly by the decomposition and aerobic/anaerobic oxidation of organic matter. According to Gurnell et al. (1998), Meentemeyer and Butler (1999), Bason et

al. (2017) and Puttock et al. (2018), older ponds have greater pools of organic matter deposited on their bottoms. Although the pond age does not cause the difference directly, it can be used as a proxy for the accumulation of organic-rich sediments over time and the enhancement of respective biogeochemical processes. For example, it facilitates the natural removal of pollutants in beaver-occupied streams through metal sequestration (Murray et al., 2021). Our study shows that the long-term durability of beaver ponds increases the extent to which SO_4^{2-} is reduced. The difference may be linked to anaerobic oxidation of organic matter, as indicated by the corresponding differences in DO. The effect of the pond age on SO_4^{2-} persists downstream of the beaver dam, suggesting that it may be an important factor in the stream water purification process.

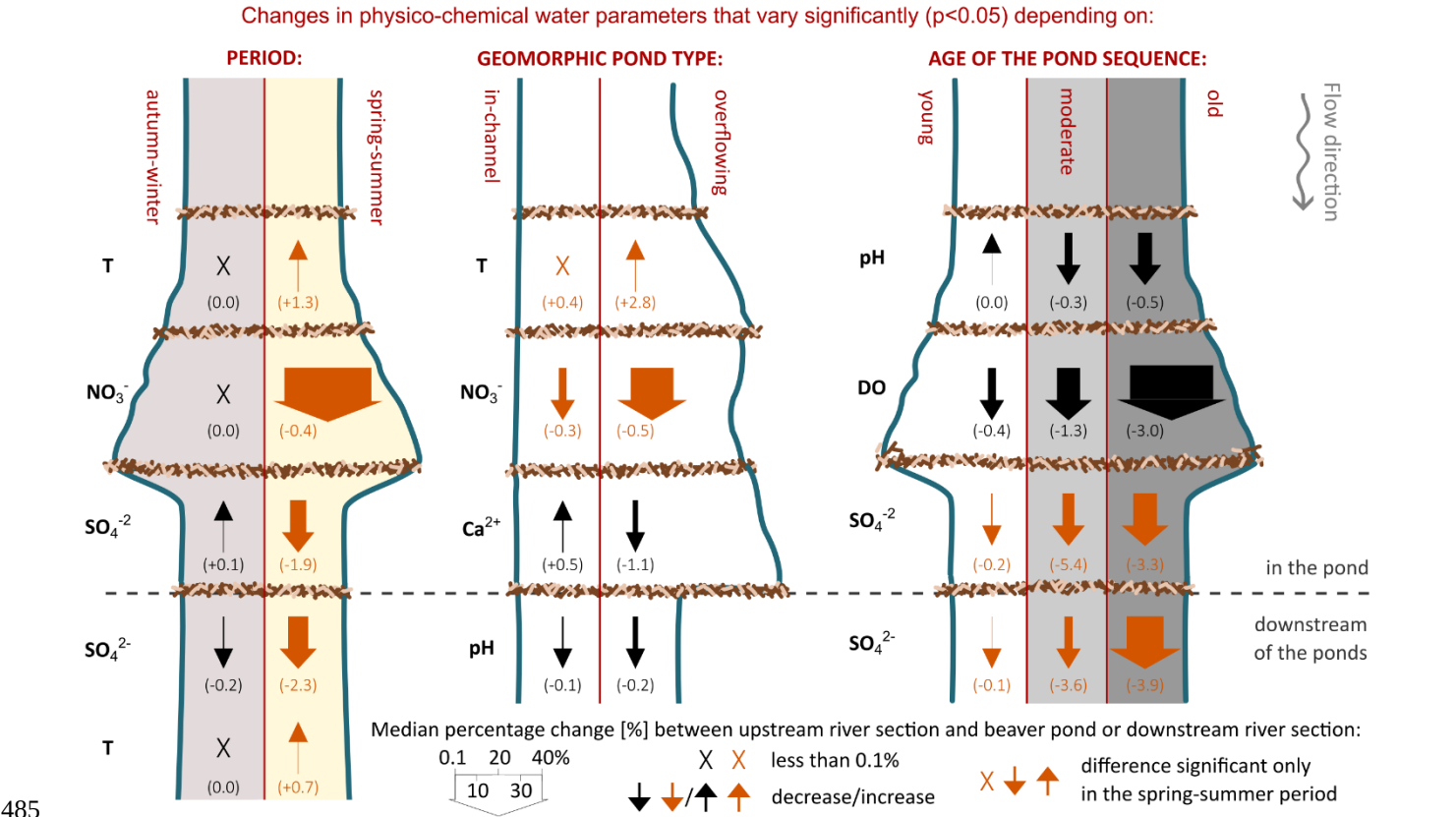


Figure 8: The role of seasons and characteristics of a beaver pond sequence in changes to physico-chemical water properties within and downstream of the beaver ponds. Median changes in measurement units (T in °C, DO and ion concentrations in mg·L⁻¹) are given in brackets.

Although the significance of pond type was generally lower than that of pond age, the geomorphological context appears to be important in terms of changes in NO_3^- concentration. The decrease in NO_3^- concentration was greater in overflowing ponds than in the ponds restricted to river channels. This difference is in line with the higher temperature increase observed in such ponds, since denitrification rates in aquatic ecosystems generally increase with temperature and DO depletion (de Klein et al., 2017). The observed thermal difference is most likely due to the larger area of open water created by overflowing ponds, as

opposed to the more shaded in-channel impoundments. It may also be attributed to the higher proportion of shallow, slow-
495 flowing water at the pond margins, which enhances warming (Majerova et al., 2020). The longer residence time of water in
the overflowing ponds may also explain the higher denitrification rates in the water of both the pond and the hyporheic zone
where the bottom pond water and groundwater mix (Merrill and Tonjes, 2014). The rate of biogeochemical processes is
controlled by residence time, as it determines the duration of contact between solutes and microbial communities (Briggs et
al., 2012). Extended hyporheic zones, which are associated with the formation of overflowing ponds, are likely areas of NO_3^-
500 removal due to denitrification. Furthermore, as demonstrated by Puttock et al. (2018), total nitrogen storage per unit area in
beaver pond sediments increases with pond size. It may suggest that the relationship between an overflowing pond type and
the decrease in water NO_3^- concentrations is indicative of the enhanced mineral nitrogen uptake by vegetation and the
accumulation of nitrogen-rich organic sediment at the bottom of territorially expansive ponds. The inundation of the area
surrounding the river channel (the riparian zone) reduces flow velocity and increases water residence time (Larsen et al., 2021).
505 This in turn supports the development of aquatic vegetation which facilitates the attenuation of nitrogen (Murray et al., 2021).
Maret et al. (1987) also attributed the greater extent of NO_3^- decrease in pond water to higher sediment loads and seasonal
expansion of the beaver pond area.

The geomorphic type of beaver ponds also plays an important role in altering the concentration of Ca^{2+} . The decrease in Ca^{2+}
concentrations was observed in the overflowing ponds, as opposed to the in-channel ponds. The decrease in Ca^{2+} concentration
510 in those ponds is probably related to calcium carbonate (CaCO_3) precipitation from the aqueous solution. The precipitation of
 CaCO_3 is favoured by the removal of CO_2 from the pond water due to an increase in water temperature (Korchef and Touaibi,
2020, Escoffier et al., 2023). Our study shows that the temperature increase in overflowing ponds is higher than in in-channel
ponds during warm seasons. Furthermore, Escoffier et al. (2023) pointed out that the precipitation of calcium carbonate causes
a decrease in the alkalinity (decrease in pH) of water, as the bicarbonate concentration in the water is reduced. Such pH
515 decrease, coinciding with Ca^{2+} concentration decrease, occurred in the overflowing beaver ponds that we studied.

4.4 Study limitations

The wide spatial scope of the study and the high diversity of beaver-influenced streams introduced certain limitations. The
spread of the study sites across a vast area restricted the number of samples collected to one sample per site each season, due
to the time and cost constraints. In addition, dam failures resulting from floods and their targeted elimination during the
520 research period decreased the planned sample size by half. The remaining study sites may have been affected by continuous
dam maintenance by beavers. In the most extreme cases, temporal breaches of the dam may have been overlooked after its
reconstruction. Moreover, since the study focused on the base flow conditions, early spring high flows have been omitted,
which likely explains the similarities between the results from the late spring and the summer.

Although a Before–After–Control–Impact (BACI) model would be the most appropriate approach for studying the impact of beavers on the chemical composition of water, it was not possible to use this method in this area due to the lack of investigations prior to dam construction. Instead, the study focused on spatial and temporal contrasts throughout the year and used a comparative ‘upper-lower river’ method, where upstream sections were used as reference sections. This research approach is commonly used in field studies to assess hydrochemical gradients generated by beaver dams when it is logistically or environmentally impossible to obtain ‘before’ data on dam construction (Green and Westbrook, 2009; Klotz, 2010; Fuller and Peckarsky, 2011; Puttock et al., 2017; Stevenson et al., 2022). It enables the identification of local hydrological and chemical effects caused by beaver damming while minimising the confounding influence of catchment heterogeneity. Although this approach lacks independent control sections, as in a full BACI model, it provides robust comparative evidence for evaluating the magnitude and spatial extent of changes induced by beaver activity under natural field conditions. Future research should be more detailed and extensive to enable the application of the BACI model.

As there was no identified relationship between the initial values and the percentage change in the physico-chemical parameters, it was assumed that the observed changes would not differ significantly based on upstream conditions. This allowed various catchments with different land uses and levels of anthropogenic influence to be included in the study. However, it should be noted that the inclusion of the streams characterised by particularly high concentrations of certain components, e.g. highly anthropogenically modified, may have resulted in different observations.

Although the sample locations were standardised to a certain extent, they may not reflect typical stream or pond conditions. Stream samples are more likely to be well-mixed and representative due to turbulent flow conditions. This is also evidenced by the homogeneity of most longitudinal profiles upstream and downstream of beaver ponds. However, the spatial distribution of the pond samples may be more biased as it did not cover the full spectrum of hydrological units observed within the ponds (Majerova et al., 2020). Additionally, as the samples were taken from the middle of the water column, they do not represent the surface and bottom water layers, which according to the vertical sampling scheme could substantially affect observed physico-chemical parameters. One of the greatest limitations of the study was the absence of field measurements of redox potential in streams and vertical profiles of beaver ponds. Such measurements would have enabled the direct identification of redox conditions in the studied waters rather than relying on speculation based on the concentration of key redox reaction ions. Direct measurements of redox potential, microbial activity and vegetation cover in the future studies would enable empirical assessment of the role of the discussed processes.

The assessment of the impact of individual characteristics of beaver dam sequences may be constrained by the interconnections between some variables. Beaver ponds tend to be more persistent in smaller streams, and the length of the beaver occupancy seems to be related, to some extent, to the longitudinal and lateral development of the pond sequences. However, the estimation of mutual correlations was limited by the use of categorical values. Continuous values for the factors representing beaver pond

555 age could not be obtained from the available sources, and the categorisation of the number of ponds was carried out because of the dynamics of this variable during the study period.

5 Conclusions

560 This study addressed the relatively new ecosystem role of beavers in the mountainous environment of the Western Carpathians, where beaver populations have recently recovered after more than a century of absence. We found that beaver dams had a strong impact on the physico-chemical water properties inside the ponds during warm seasons, including an increase in water temperature and decreases in pH, DO, NO_3^- and SO_4^{2-} concentrations. These changes were the result of specific biogeochemical processes occurring in the newly formed aquatic environments of beaver ponds. Although these processes affect the downstream sections of the streams, in general, they were partially attenuated within a short distance of the dam.

565 The processes involving NO_3^- and SO_4^{2-} decrease were found to be more effective during the warm period of the year than during the cold period. Moreover, a larger decrease in NO_3^- and Ca^{2+} concentrations occurred in ponds that overflow river banks, and higher pH decrease was identified below overflowing ponds, compared to the ponds restricted to the banks. The denitrification process, which is responsible for the decrease in NO_3^- concentration, requires anoxic conditions in the pond water, which are favoured in overflowing ponds due to greater temperature increases and longer water residence time than in in-channel ponds during warm seasons. Furthermore, the higher temperature in overflowing ponds leads to the removal of CO_2 570 from the pond water and the precipitation of CaCO_3 , which is probably responsible for the decrease in Ca^{2+} concentration in the overflowing ponds. The age of the dams was identified as an important factor affecting the decrease in dissolved oxygen and pH in beaver ponds and the decrease in sulphate within and below the ponds. These changes were regulated by the decomposition and aerobic/anaerobic oxidation of organic matter, which was more abundant in older ponds. Although much is known about the contribution of beavers to water purification through nitrogen fixation, their less recognised role in sulphate 575 reduction may be equally important from a water management perspective. Finally, the extensiveness and persistence of beaver pond complexes may be critical for the effectiveness of these processes.

Although most of the processes identified in the present study are consistent with previous research, our results are complemented by additional insights. Attention should be drawn to newly emerging issues, such as the widespread decrease in water pH as a result of beaver dams. These results indicate that there is still much to address in future research on the effects 580 of beaver presence. A larger dataset would improve our understanding of the effects of beaver impoundments, especially in streams with varying inlet conditions, outflow types and topographic characteristics. Likewise, more data from representative mountain streams (including side-channel and main-channel ponds and various levels of geomorphic beaver activity), as well as comparative data from lowland streams, would be useful. Lastly, further research is needed to identify the spatial and temporal durability of the influence of beaver dams and elucidate the thresholds that determine their impact on the ecological 585 stream properties.

Author contributions (CRediT)

JW: Conceptualization, Project administration, Methodology, Investigation, Formal analysis, Visualization, Writing – original draft, Writing – review and editing

JPS: Methodology, Investigation, Formal analysis, Visualization, Writing – original draft, Writing – review and editing

590 MKS: Conceptualization, Funding acquisition, Project administration, Methodology, Investigation, Writing – review and editing, Supervision

EG: Investigation, Writing – review and editing, Supervision

Data availability

595 The data that support the findings of this study are available at Zenodo open access data repository (doi: 10.5281/zenodo.17937225).

Competing interests

The authors declare that they have no conflict of interest.

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References

- Affek, A. N., Jabs-Sobocińska, Z., Wolski, J., Radeloff, V. C.: Pockets of persistence of agricultural land use during the socioeconomic shock of forced post-WWII displacements in the Carpathians, *Land Use Policy*, 131, 106678, <https://doi.org/10.1016/j.landusepol.2023.106678>, 2023.
- Anderson, A., Fidel, R.: *Introduction to soil science*, 2nd edition, Iowa State University Digital Press, Ames-Iowa, 366 pp., <https://doi.org/10.31274/isudp.2025.201>, 2025.
- Armstrong, R. A.: When to use the Bonferroni correction, *Ophthalmic and Physiol. Optics*, 34, 502-508, <https://doi.org/10.1111/opo.12131>, 2014.
- Balejčíková, L., Tall, A., Kandra, B., Pavelková, D.: Relationship of nitrates and nitrites in the water environment with humans and their activity, *Acta Hydrol. Slovaca*, 21, 74-81, <https://doi.org/10.31577/ahs-2020-0021.01.0009>, 2020.
- Bański, J.: The consequences of changes of ownership for agricultural land use in Central European countries following the collapse of the Eastern Bloc, *Land Use Policy*, 66, 120-130, <https://doi.org/10.1016/j.landusepol.2017.04.045>, 2017.
- Bason, C. W., Kroes, D. E., Brinson, M. M.: The effect of beaver ponds on water quality in rural coastal plain streams, *Southeast. Nat.*, 16, 584-602, <https://doi.org/10.1656/058.016.0408>, 2017.
- Błędzki, L. A., Bubier, J. L., Moulton, L. A., Kyker-Snowman, T. D.: Downstream effects of beaver ponds on the water quality of New England first- and second-order streams, *Ecohydrology*, 4, 698-707, <https://doi.org/10.1002/eco.163>, 2011.
- Borzuchowski, J., Olędzki, J. R.: Cyfrowa mapa geomorfologiczna Karpat, *Teledetekcja Środowiska*, 46, 52-71, 2011.
- Brazier, R. E., Puttock, A., Graham, H. A., Auster, R. E., Davies, K. H., Brown, C. M. L.: Beaver: Nature's ecosystem engineers, *WIREs Water*, 8, e1494, <https://doi.org/10.1002/wat2.1494>, 2021.
- Briggs, M. A., Lautz, L. K., McKenzie, J. M., Gordon, R. P., Hare, D. K.: Using high-resolution distributed temperature sensing to quantify spatial and temporal variability in vertical hyporheic flux, *Water Resour. Res.*, 48, W02527, <https://doi.org/10.1029/2011WR011227>, 2012.
- Briggs, M. A., Lautz, L. K., Hare, D. K., González-Pinzón, R.: Relating hyporheic fluxes, residence times, and redox-sensitive biogeochemical processes upstream of beaver dams, *Freshwater Science*, 32 (2), 622-641, <https://doi.org/10.1899/12-110.1>, 2013.
- Burtan, J., Cieszkowski, M., Ślaczka, A., Zuchiewicz, W.: *Szczegółowa mapa geologiczna Polski 1:50 000, arkusz Męcina (1018, M-34-78-C)*, Państwowy Instytut Geologiczny, Warszawa, 1994.
- Bylak, A., Kochman-Kędziora, N., Kukuła, E., Kukuła, K.: Beaver-related restoration: An opportunity for sandy lowland streams in a human-dominated landscape, *J. Environ. Manage.*, 351, 119799, <https://doi.org/10.1016/j.jenvman.2023.119799>, 2024.
- CARPATCLIM Database © European Commission - JRC, 2013.

- Čanády, A., Krišovský, P., Bajomi, B., Huber, A., Czabán, D., Olekšák, M.: Is new spread of the European beaver in Pannonian basin an evidence of the species recovery?, *European Journal of Ecology*, 2, 44-63, <https://doi.org/10.1515/eje-2016-0015>, 2016.
- Central Statistical Office of Poland, Statistical Yearbook of Agriculture, www.stat.gov.pl, 2025.
- Cirmo, C. P., Driscoll, C. T.: Beaver pond biogeochemistry: acid neutralizing capacity generation in a headwater wetland, *Wetlands*, 13, 277-292, 1993.
- Cirmo, C. P., Driscoll, C. T.: The impacts of a watershed CaCO₃ treatment on stream and wetland biogeochemistry in the Adirondack Mountains, *Biogeochemistry*, 32, 265-297, 1996.
- Čiuldienė, D., Vigricas, E., Belova, O., Aleinikovas, M., Armolaitis, K.: The effect of beaver dams on organic carbon, nutrients and methyl mercury distribution in impounded waterbodies, *Wildlife Biol.*, 2020, 1-8, <https://doi.org/10.1111/wlb.00678>, 2020.
- David, M. B., Vance, G. F.: Chemical character and origin of organic acids in streams and seepage lakes of central Maine, *Biogeochemistry*, 12, 17-41, 1991.
- de Klein, J. J., Overbeek, C. C., Juncher Jørgensen, C., Veraart, A. J.: Effect of temperature on oxygen profiles and denitrification rates in freshwater sediments, *Wetlands*, 37, 975-983, <https://doi.org/10.1007/s13157-017-0933-1>, 2017.
- Dewey, C., Fox, P. M., Bouskill, N. J., Dwivedi D., Nico P., Fendorf, S.: Beaver dams overshadow climate extremes in controlling riparian hydrology and water quality, *Nat. Commun.*, 13, 6509, <https://doi.org/10.1038/s41467-022-34022-0>, 2022.
- Drever, J. I.: *The Geochemistry of Natural Waters: Surface and Groundwater Environments*, 3rd Edition, Prentice Hall, Upper Saddle River, New Jersey, 436 pp., ISBN 9780132727907, 1997.
- Driscoll, C. T., Fuller, R. D., Schecher, W. D.: The role of organic acids in the acidification of surface waters in the eastern U.S., *Water Air Soil. Poll.*, 43, 21-40, 1989.
- Dzięciołowski, R., Gozdziwski, J.: The reintroduction of European beaver, *Castor fiber*, in Poland: a Success Story, in: *Beaver protection, management, and utilization in Europe and North America*, edited by: Busher, P. E., Dzięciołowski, R., Kluwer Academic/Plenum Publishers, New York, 31-35, 1999.
- Ecke, F., Levanoni, O., Audet, J., Carlson, P., Eklöf, K., Hartman, G., McKie, B., Ledesma, J., Segersten, J., Truchy, A., Futter, M.: Meta-analysis of environmental effects of beaver in relation to artificial dams, *Environ. Res. Lett.*, 12, 113002, <https://doi.org/10.1088/1748-9326/aa8979>, 2017.
- Escoffier, N., Perolo, P., Many, G., Pasche, N. T., Perga, M.-E.: Fine-scale dynamics of calcite precipitation in a large hardwater lake, *Sci. Total. Environ.*, 864, 160699, <https://doi.org/10.1016/j.scitotenv.2022.160699>, 2023.
- Fuller, M. R., Peckarsky, B. L.: Does the morphology of beaver ponds alter downstream ecosystems? *Hydrobiol.*, 668, 35-48, <https://doi.org/10.1007/s10750-011-0611-x>, 2011.
- Gilewska, S., Klimkowa, M., Starkel, L.: The 1:500 000 Geomorphological Map of Poland, *Geographia Polonica*, 48, 7-24, 1982.

- Giriati, D., Gorczyca, E., Sobucki, M.: Beaver ponds' impact on fluvial processes (Beskid Niski Mts., SE Poland), *Sci. Total. Environ.*, 544, 339-353, <https://doi.org/10.1016/j.scitotenv.2015.11.103>, 2016.
- Gorczyca, E., Krzemień, K., Sobucki, M., Jarzyna, K.: Can beaver impact promote river renaturalization? The example of the Raba River, southern Poland, *Sci. Total. Environ.*, 615, 1048-1060, 2018.
- 675 Green, K. C., Westbrook, C. J.: Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams, *BC Journal of Ecosystems and Management*, 10, 68-79, <https://doi.org/10.22230/jem.2009v10n1a412>, 2009.
- Gurnell, A. M.: The hydrogeomorphological effects of beaver dam-building activity, *Prog. Phys. Geog.*, 22, 167-189, <https://doi.org/10.1177/030913339802200202>, 1998.
- Halley, D. J., Saveljev, A. P., Rosell, F.: Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia, *Mammal Rev.* 51, 1-24, <https://doi.org/10.1111/mam.12216>, 2021.
- 680 Harthun, M.: Influence of the Damming-up by Beavers (*Castor fiber albus*) on Physical and Chemical Parameters of Highland Brooks (Hesse, Germany), *Limnologica*, 30, 21-35, 2000.
- Holtmeier, F. K.: Keystone Species, in: *Animals' Influence on the Landscape and Ecological Importance: Natives, Newcomers, Homecomers*, Springer, Dordrecht, 295–331 pp., https://doi.org/10.1007/978-94-017-9294-3_4, 2015.
- 685 Jankowski, L. S.: Szczegółowa mapa geologiczna Polski 1:50 000, arkusz Rzepiennik (1020, M-34-79-C), Państwowy Instytut Geologiczny, Warszawa, 1994.
- Jones, C. G., Lawton, J. H., Shachak, M.: Organisms as ecosystem engineers, *OIKOS*, 69, 373–386, <https://doi.org/10.2307/3545850>, 1994.
- Kalvīte, Z., Lībiete, Z., Kļaviņš, I., Bārdule, A., Bičkovskis, K.: The impact of beaver dam removal on the chemical properties of water in drainage ditches in peatland forests, *Scand. J. Forest. Res.*, 36, 1-14, <https://doi.org/10.1080/02827581.2020.1855364>, 2021.
- 690 Klotz, R. L.: Reduction of high nitrate concentrations in a Central New York State stream impounded by beaver, *Northeast. Nat.*, 17, 349-356, <https://www.jstor.org/stable/40959749>, 2010.
- Kolecka, N., Kozak, J., Kaim, D., Dobosz, M., Ostafin, K., Ostapowicz, K., Wężyk, P., Price, B.: Understanding farmland abandonment in the Polish Carpathians, *Appl. Geogr.*, 88, 62-72, <https://doi.org/10.1016/j.apgeog.2017.09.002>, 2017.
- 695 Kozak, J.: Wall-to-wall parcel-level mapping of agricultural land abandonment in the Polish Carpathians, *Land*, 8, 129, <https://doi.org/10.3390/land8090129>, 2019.
- Kopciowski R., Zimnal Z., Chrzastowski., Jankowski L., Szymakowska F.: Szczegółowa mapa geologiczna Polski 1:50 000, arkusz Gorlice (1037, M-34-91-A), Państwowy Instytut Geologiczny, Warszawa, 1997.
- 700 Kopciowski R.: Szczegółowa mapa geologiczna Polski 1:50 000, arkusz Zborów (1054, M-34-91-D), Państwowy Instytut Geologiczny, Warszawa, 2000.
- Korchef, A., Touaibi, M.: Effect of pH and temperature on calcium carbonate precipitation by CO₂ removal from iron-rich water, *Water Environ. J.*, 34, 331-341, <https://doi.org/10.1111/wej.12467>, 2020.

- Krocak, R., Fidelus-Orzechowska, J., Bucala-Hrabia, A., Bryndal, T.: Land use and land cover changes in small Carpathian catchments between the mid-19th and early 21st centuries and their record on the land surface, *J. Mt. Sci.*, 15, 2561-2578. <https://doi.org/10.1007/s11629-018-5095-y>, 2018.
- Larsen, A., Larsen, J. R., Lane, S. N.: Dam builders and their works: Beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems, *Earth-Sci. Rev.*, 218, 103623, <https://doi.org/10.1016/j.earscirev.2021.103623>, 2021.
- Law, A., McLean, F., Willby, N.J.: Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams, *Freshwater Biol.* 61, 486–499, <https://doi.org/10.1111/fwb.12721>, 2016.
- Lazar, J. G., Addy, K., Gold, A. J., Groffman, P. M., McKinney, R. A., Kellogg, D. Q.: Beaver ponds: Resurgent nitrogen sinks for rural watersheds in the northeastern United States, *J. Environ. Qual.*, 44, 1684–1693. <https://doi.org/10.2134/jeq2014.12.0540>, 2015.
- Lazikova, J., Rumanovska, L., Takac, I., Lazikova, Z.: Land fragmentation and efforts to prevent it in Slovak legislation, *Agr. Econ.-Czech.*, 63, 559-568, <https://doi.org/10.17221/180/2016-AGRICECON>, 2017.
- Lieskovský, J., Bezák, P., Špulerová, J., Lieskovský, T., Koleda, P., Dobrovodská, M., Bürgi, M., Gimmi, U.: The abandonment of traditional agricultural landscape in Slovakia - Analysis of extent and driving forces, *J. Rural. Stud.*, 37, 75-84, <https://doi.org/10.1016/j.jrurstud.2014.12.007>, 2015.
- Lizarralde, M. S., Deferrari, G. A., Alvarez, S. E., Escobar, J. M.: Effects of beaver (*Castor canadensis*) on the nutrient dynamics of the southern beech forests of Tierra del Fuego (Argentina), *Ecología Austral*, 6, 101–105, 1996.
- Łajczak, A., Margielewski, W., Rączkowska, Z., Świąchowicz, J.: Contemporary geomorphic processes in the Polish Carpathians under changing human impact, *Episodes Journal of International Geoscience*, 37, 21-32, <https://doi.org/10.18814/epiiugs/2014/v37i1/003>, 2014.
- Majerova, M., Neilson, B. T., Schmadel, N. M., Wheaton, J. M., Snow, C. J.: Impacts of beaver dams on hydrologic and temperature regimes in a mountain stream, *Hydrol. Earth Syst. Sc.*, 19, 3541–3556, <https://doi.org/10.5194/hess-19-3541-2015>, 2015.
- Marciniec, P., Zimnal, Z.: Szczegółowa mapa geologiczna Polski 1:50 000, arkusz Tuchów (1001, M-34-79-A), Państwowy Instytut Geologiczny, Warszawa, 2009.
- Maret, T. J., Parker, M., Fannin, T. E.: The effect of beaver ponds on the nonpoint source water quality of a stream in southwestern Wyoming, *Water R.*, 21, 263-268, 1987.
- Margolis, B. E., Castro, M. S., Raesly, R. L.: The impact of beaver impoundments on the water chemistry of two Appalachian streams, *Can. J. Fish. Aquat. Sci.*, 58, 2271-2283, <https://doi.org/10.1139/cjfas-58-11-2271>, 2001.
- Meentemeyer, R. K., Butler, D. R.: Hydrogeomorphic effects of beaver dams in Glacier National Park, Montana, *Phys. Geogr.*, 20, 436–446, <https://doi.org/10.1080/02723646.1999.10642688>, 1999.
- Merill, L., Tonjes, D. J.: A review of the hyporheic zone, stream restoration, and means to enhance denitrification, *Technology and Society Faculty Publications*, 5, 2014.

- Murray, D., Neilson, B. T., Brahney, J.: Source or sink? Quantifying beaver pond influence on non-point source pollutant transport in the Intermountain West, *J. Environ. Manage.*, 285, 112127, <https://doi.org/10.1016/j.jenvman.2021.112127>, 2021.
- 740 Naiman, R. J., Melillo, J. M.: Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*), *Oecologia*, 62, 150-155, 1984.
- Naiman, R. J., Melillo, J. M., Hobbie, J. E.: Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*), *Ecology*, 67, 1254-1269, <https://doi.org/10.2307/1938681>, 1986.
- Naiman, R. J., Pinay, G., Johnston, C. A., Pastor, J.: Beaver influences on the long-term biogeochemical characteristics of
745 boreal forest drainage networks, *Ecology*, 75, 905-921, <https://doi.org/10.2307/1939415>, 1994.
- Nolet, B. A., Rosell, F.: Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems, *Biol. Conserv.*, 83, 165-173, [https://doi.org/10.1016/S0006-3207\(97\)00066-9](https://doi.org/10.1016/S0006-3207(97)00066-9), 1998.
- Pachinger, K., Hulik, T.: Origin, present conditions, and future prospects of the Slovakian beaver population, in: *Beaver protection, management, and utilization in Europe and North America*, edited by: Busher, P. E., Dzięciołowski, R., Kluwer
750 Academic/Plenum Publishers, New York, 43-51, 1999.
- Palarea-Albaladejo, J., Martín-Fernández, J. A.: Values below detection limit in compositional chemical data, *Anal. Chim. Acta.*, 764, 32-43, <https://doi.org/10.1016/j.aca.2012.12.029>, 2013.
- Pazúr, R., Lieskovský, J., Feranec, J., O'rahel', J.: Spatial determinants of abandonment of large-scale arable lands and managed grasslands in Slovakia during the periods of post-socialist transition and European Union accession, *Appl. Geogr.*, 54, 118-
755 128, <https://doi.org/10.1016/j.apgeog.2014.07.014>, 2014.
- Pekárová, P., Pekár, J., Miklánek, P.: Impact of water sampling frequency on estimating water quality status in the Ondava River, *Ecohydrol. and Hydrobiol.*, 6, 105-113, [https://doi.org/10.1016/S1642-3593\(06\)70132-X](https://doi.org/10.1016/S1642-3593(06)70132-X), 2006. Pollock, M. M., Heim, M., Werner, D.: Hydrologic and geomorphic effects of beaver dams and their influence on fishes, *American Fisheries Society Symposium* 37 , 213–234, 2003.
- 760 Puttock, A., Graham, H. A., Cunliffe, A. M., Elliott, M., Brazier, R. E.: Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands, *Sci. Total. Environ.*, 576, 430-443, <http://dx.doi.org/10.1016/j.scitotenv.2016.10.122>, 2017.
- Puttock, A., Graham, H. A., Carless, D., Brazier, R. E.: Sediment and nutrient storage in a beaver engineered wetland, *Earth. Surf. Proc. Land.*, 43, 2358-2370, <https://doi.org/10.1002/esp.4398>, 2018.
- 765 Qu, W., Suo, L., Liu R., Liu, M., Zhao, Y., Xia, L., Fan, Y., Zhang, Q., Gao, Z.: Influence of Temperature on Denitrification and Microbial Community Structure and Diversity: A Laboratory Study on Nitrate Removal from Groundwater, *Water*, 14, 436, <https://doi.org/10.3390/w14030436>, 2022.
- Rosell, F., Bozsér, O., Collen, P., Parker, H.: Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems, *Mammal Rev.*, 35, 248-276, <https://doi.org/10.1111/j.1365-2907.2005.00067.x>, 2005.
- 770 Shaw, G., Wheeler, D.: *Statistical techniques in geographical analysis*, 2nd Edition, David Fulton Publishers, London, 368 pp., ISBN 1853462292, 1994.

- Smith, M. E., Driscoll, C. T., Wyskowski, B. J., Brooks, C. M., Cosentini, C. C.: Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, *Can. J. Zool.*, 69, 55-61, <https://doi.org/10.1139/z91-009>, 1991.
- 775 Siman, C., Velísková, Y.: Consumption of fertilizers in districts of Slovakia in the period 2006–2015, *Acta Agrar. Debreceniensis*, 150, 389-398, <https://doi.org/10.34101/actaagrar/150/1735>, 2018. Siwek, J. P.: Environmental and anthropogenic determinants of water chemistry in the Carpathians, in: *Quality of water resources in Poland*, edited by: Zeleňáková, M., Kubiak-Wójcicka, K., Negm A.M., Springer Water, Cham, Switzerland, 297-319, https://doi.org/10.1007/978-3-030-64892-3_13, 2021.
- 780 Solár, J., Tomaškovič, J.: Physicochemical properties of mountain streams in the High and Western Tatras, *Environ. Monit. and Assess.*, 195, 1543, <https://doi.org/10.1007/s10661-023-12158-w>, 2023.
- Songster-Alpin, M.S., Klotz, R.L.: A comparison of electron transport system activity in stream and beaver pond sediments, *Can. J. Fish. Aquat. Sci.*, 52, 1318-1326, <https://doi.org/10.1139/f95-128>, 1995.
- Starkel, L.: Ewolucja środowiska przyrodniczego Karpat w okresie działalności człowieka, *Problemy Zagospodarowania Ziemi Górskich*, 29, 34-46, 1990.
- 785 Stefanakis, A., Akratos, Ch.S., Tsihrintzis V.A.: *Vertical Flow Constructed Wetlands. Eco-engineering Systems for Wastewater and Sludge Treatment*, 1st Edition, Elsevier, Amsterdam-Oxford-Waltham, 392 pp., ISBN 978-0-12-404612-2, 2014.
- Stevenson, J. R., Dunham, J. B., Wondzell, S. M., Taylor, J.: Dammed water quality—Longitudinal stream responses below beaver ponds in the Umpqua River Basin, Oregon, *Ecohydrology*, 15, e2430, <https://doi.org/10.1002/eco.2430>, 2022.
- 790 Sutton-Grier, A. E., Keller, J. K., Koch, R., Gilmour, C., Megonigal, J. P.: Electron donors and acceptors influence anaerobic soil organic matter mineralization in tidal marshes, *Soil Biol. Biochem.*, 43, 1576-1583, <https://doi.org/10.1016/j.soilbio.2011.04.008>, 2011.
- Szalai, S., Auer, I., Hiebl, J., Milkovich, J., Radim, T., Stepanek, P., Zahradnicek, P., Bihari, Z., Lakatos, M., Szentimrey, T.,
- 795 Limanowka, D., Kilar, P., Cheval, S., Deak, Gy., Mihic, D., Antolovic, I., Mihajlovic, V., Nejedlik, P., Stastny, P., Mikulova, K., Nabyvanets, I., Skyryk, O., Krakovskaya, S. Vogt, J., Antofie, T., Spinoni, J.: *Climate of the Greater Carpathian Region, Final Technical Report*, www.carpatclim-eu.org, 2023.
- Ślęczka, A., Kruglov, S., Golonka, J., Oszczytko, N., Popadyuk, I.: Geology and hydrocarbon resources of the Outer Carpathians, Poland, Slovakia, and Ukraine: general geology, in: *AAPG Memoir 84, The Carpathians and their foreland: Geology and hydrocarbon resources*, edited by: Golonka, J., Picha, F., American Association of Petroleum Geologists, 221-258. <https://doi.org/10.1306/985610M843070>, 2006.
- 800 Thompson, S., Vehkaoja, M., Pellikka, J., Nummi, P.: Ecosystem services provided by beavers *Castor* spp., *Mammal Rev.*, 51, 25-39, <https://doi.org/10.1111/mam.12220>, 2021.

- Valachovič, D.: European beaver (*Castor fiber*), in: *Mammals of Slovakia: Distribution, Bionomy and Protection*, edited by: Krištofik, J., Danko, Š., VEDA–Slovak Academy of Sciences Publishing House, Bratislava, 81–85, ISBN: 978-80-224-1264-3, 2012.
- Vega, C., Abascal, J. L. F.: Relation between the melting temperature and the temperature of maximum density for the most common models of water, *J. Chem. Phys.*, 123, 144504, <https://doi.org/10.1063/1.2056539>
- Walse, C., Berg, B., Sverdrup, H.: Review and synthesis of experimental data on organic matter decomposition with respect to the effect of temperature, moisture, and acidity, *Environ. Rev.*, 6, 25-40, <https://doi.org/10.1139/a98-001>, 1998.
- Weber, N., Bouwes, N., Pollock, M. M., Volk, C., Wheaton, J. M., Wathen, G., Wirtz, J., Jordan, C. E.: Alteration of stream temperature by natural and artificial beaver dams, *PLoS ONE*, 12, e0176313, <https://doi.org/10.1371/journal.pone.0176313>, 2017.
- Wegener, P., Covino, T., Wohl, E.: Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism, *Water Resour. Res.*, 53, 4606-4623, <https://doi.org/10.1002/2016WR019790>, 2017.
- Wohl, E., Dwire, K., Sutfin, N., Polvi, L., Bazan, R.: Mechanisms of carbon storage in mountainous headwater rivers, *Nat. Commun.*, 3, 1263, <https://doi.org/10.1038/ncomms2274>, 2012
- Wright, J. P., Jones, C. G., Flecker, A. S.: An ecosystem engineer, the beaver, increases species richness at the landscape scale, *Oecologia*, 132, 96-101, <https://doi.org/10.1007/s00442-002-0929-1>, 2002.
- Wróbel, M.: Population of Eurasian beaver (*Castor fiber*) in Europe, *Global Ecology and Conservation*, 23, e01046, <https://doi.org/10.1016/j.gecco.2020.e01046>, 2020.
- Wróbel, M., Krysztofiak-Kaniewska, A.: Long-term dynamics of and potential management strategies for the beaver (*Castor fiber*) population in Poland, *The European Zoological Journal*, 87, 116-121, <https://doi.org/10.1080/24750263.2020.1727969>, 2020
- Wrzesiński, D.: Identyfikacja cech reżimu odpływu rzek w Polsce na różnych poziomach grupowania, *Badania Fizjograficzne*, 68, 265-278, 2017.
- Żurowski, W.: Bobry w górach, *Przyroda Polska*, 6, 10-11, 1986.
- Żurowski, W., Kasperczyk, B.: Results of beaver reintroduction in some Carpathian mountain streams, *Ochrona Przyrody, Zakład Ochrony Przyrody i Zasobów Naturalnych PAN*, 47, 201-213, 1990.

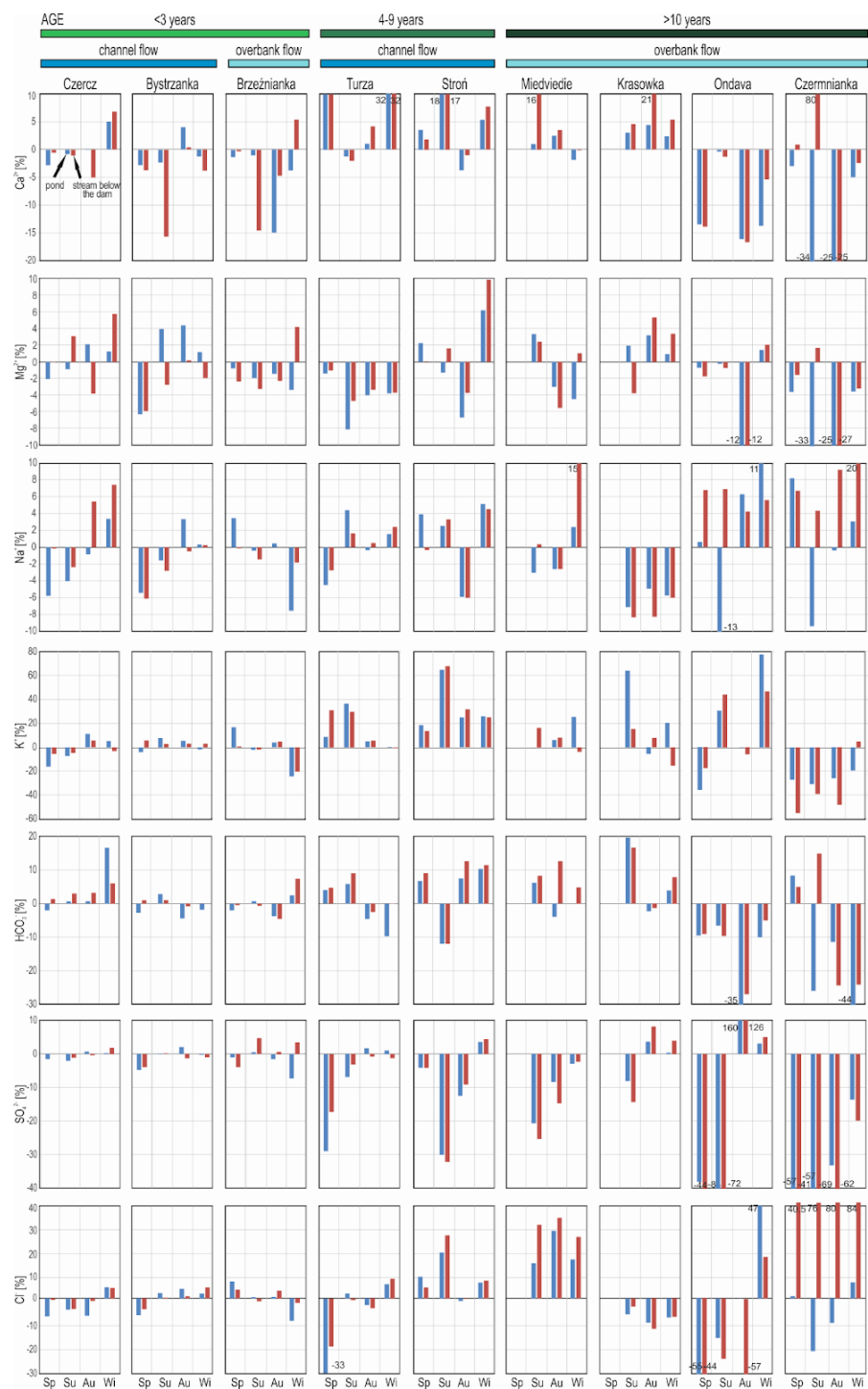
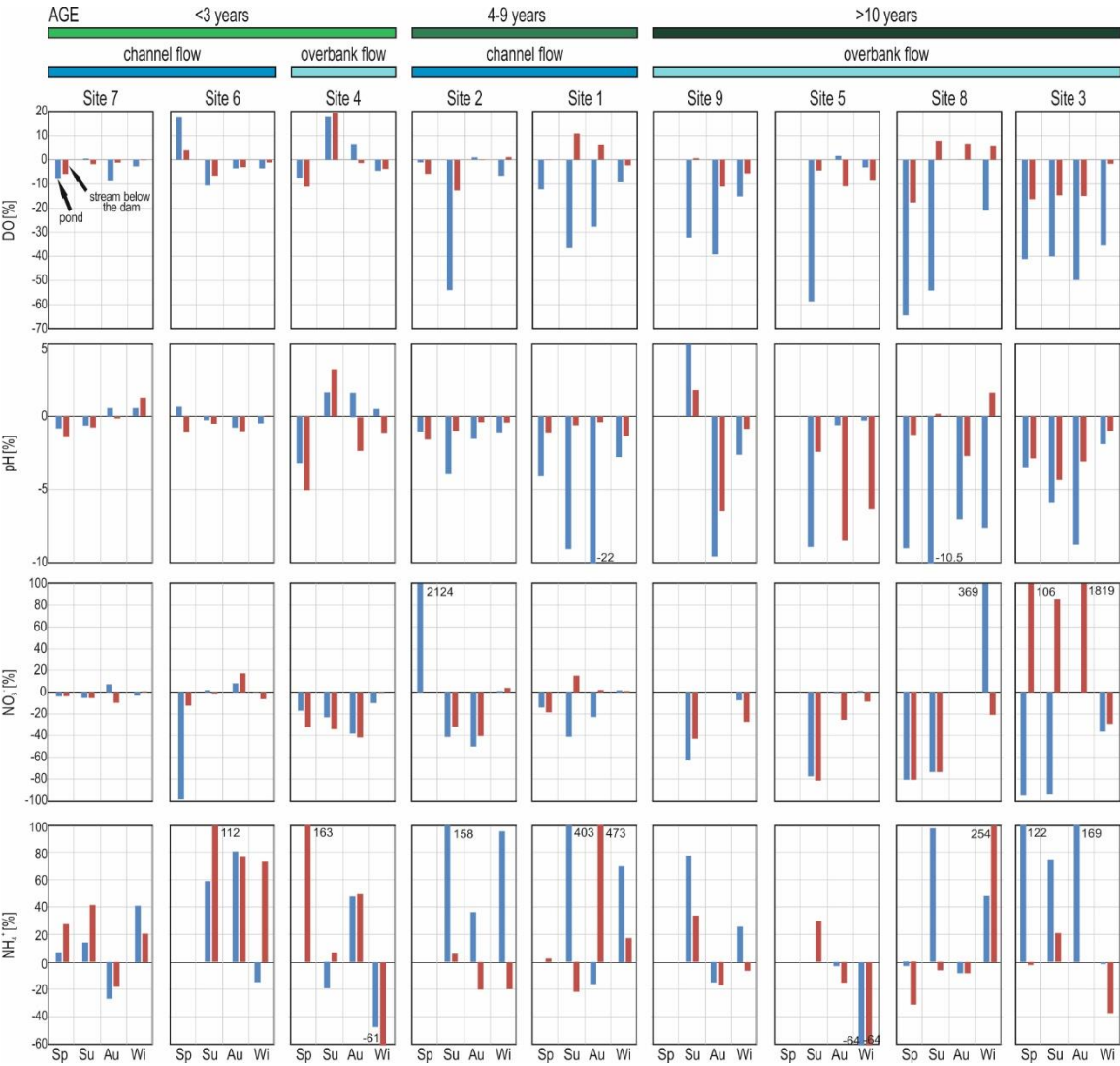


Figure A1: Percentage changes (D_c) in main ion concentrations in and below beaver ponds compared to their upstream values (Sp – spring, Su – summer, Au – autumn, Wi – winter).



835 **Figure A2: Percentage changes (D_c) in pH, and DO, NH_4^+ and NO_3^- concentrations in and below beaver ponds compared to their upstream values (Sp – spring, Su – summer, Au – autumn, Wi – winter).**

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Table A1: Statistical characteristics of absolute changes (|Dc|) of physico-chemical parameters values in ponds and streams below beaver dams in relation to values in streams before beaver dams (n=34). Average absolute changes >5% are marked in bold.

Parameters	Beaver ponds		Streams below the beaver dams	
	Average value	Standard deviation	Average value	Standard deviation
DO	20.5	19.7	6.6	5.6
SEC	4.4	6.2	4.3	5.0
HCO ₃ ⁻	8.5	9.9	7.7	7.2
Cl ⁻	11.1	12.7	18.8	24.1
SO ₄ ²⁻	17.7	32.1	17.8	28.0
Ca ²⁺	7.8	9.9	10.2	14.8
Mg ²⁺	4.7	6.8	4.0	4.8
Na ⁺	4.2	3.2	4.6	4.4
K ⁺	19.4	19.2	17.5	18.1
NO ₃ ⁻	100.3	363.7	78.8	308.9
NH ₄ ⁺	54.4	76.4	51.1	90.5
H ⁺	294.9	962.6	57.8	90.2

Table A2: Results of the PCA analyses of the differences between inlet values and beaver ponds/streams below beaver ponds (Dc). Factor loadings that exceed 0.5 are marked in bold.

Parameters	PCA factor loadings					
	Beaver pond			Stream below beaver ponds		
	1	2	3	1	2	3
DO	0.05	0.87	-0.12	-0.78	-0.14	0.33
HCO ₃ ⁻	0.54	0.07	0.36	0.06	0.82	0.07
Cl ⁻	0.51	0.01	-0.73	0.67	-0.07	0.54
SO ₄ ²⁻	-0.09	0.63	-0.58	-0.59	-0.18	-0.58
Ca ²⁺	0.71	0.31	0.36	0.33	0.75	0.13
K ⁺	0.81	-0.15	-0.31	-0.69	0.24	0.32
NO ₃ ⁻	0.33	0.36	0.58	0.59	-0.63	0.21
NH ₄ ⁺	0.35	-0.63	-0.14	-0.33	0.10	0.46
H ⁺	0.11	-0.28	0.01	0.41	0.27	-0.60
Eigenvalue	1.97	1.88	1.60	2.60	1.84	1.47
% of expl. variance	0.22	0.21	0.18	0.29	0.20	0.16

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Appendix B – Concentrations of the chemical components in the longitudinal and vertical profiles

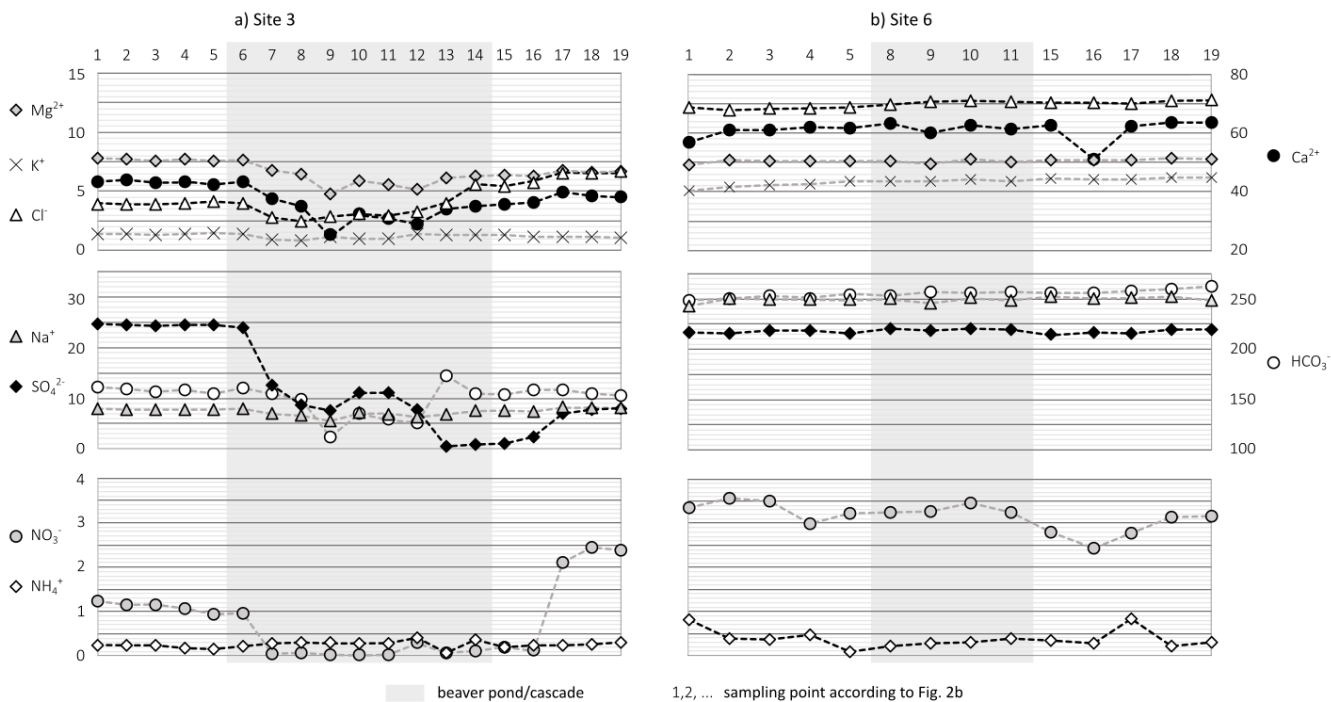


Figure B1: Concentrations of the chemical components of water [mg·L⁻¹] in the longitudinal stream profiles at study sites 3 (a) and 6 (b) on 10 September 2023.

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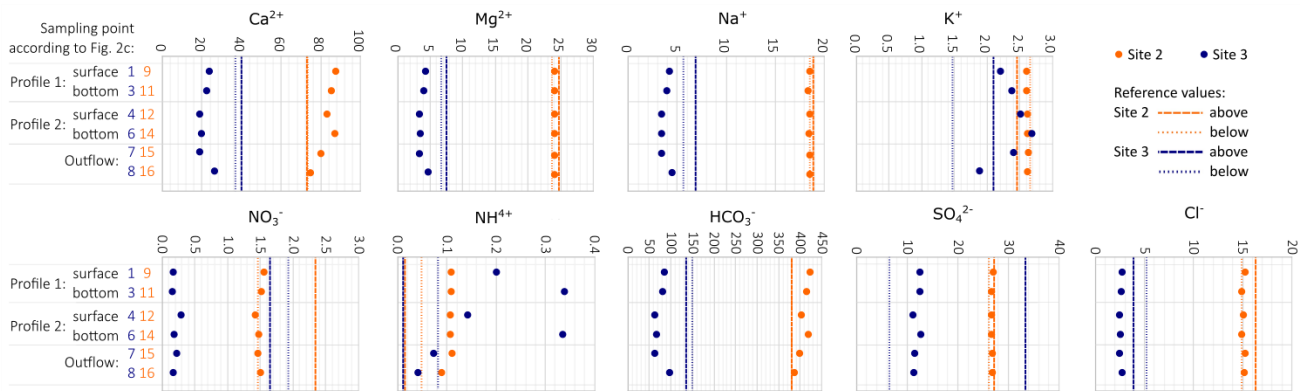


Figure B2: Concentration of the chemical components of water [mg·L⁻¹] in the vertical profiles of study sites 2 and 3 on 10 July 2024.