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The impact of beaver dams on distribution of waterborne *Escherichia coli* and turbidity in an agricultural landscape

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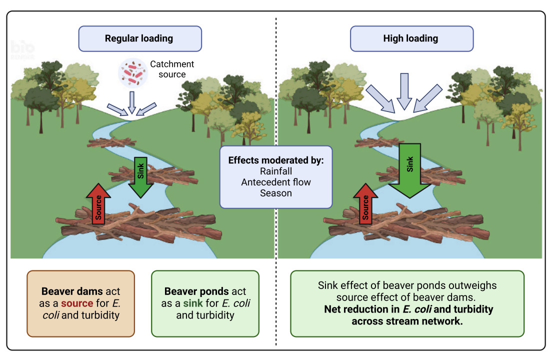
HIGHLIGHTS

- Beaver dams act as source of *E. coli* and turbidity, whereas ponds act as a sink.
- Sink effects of ponds increase with loading to outweigh source effects of dams.
- *E. coli* and turbidity are moderated by season, hydrology and pond-scale attributes.
- Under high loading, beaver dams can reduce pollution reaching downstream receptors.
- Beaver dams or their analogues could support environmental management approaches.

GRAPHICAL ABSTRACT



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ABSTRACT

Globally, freshwater environments are threatened by point source and diffuse pollution, habitat loss, and climate change. Enhancing water quality and reducing microbial pollution are priorities to realise their ecosystem services potential but challenging to achieve and require creative solutions. Beavers are receiving increasing attention as ecosystem engineers, their dams benefitting aquatic ecosystems via improved biodiversity, water quality, and flow regulation. However, effects on microbial water quality remain uncertain. Here, we investigated the influence of engineering by Eurasian beaver (*Castor fiber* L.) on variation in *Escherichia coli* concentrations and turbidity in an agricultural stream. Water samples were collected over a period of two years (2017–2019, encompassing 11 sampling dates), from a sequence of 14 beaver dams and associated ponds to quantify fluxes of turbidity and *E. coli*. On average, dam structures were a source whereas ponds acted as a sink for both turbidity and *E. coli*. The sink effect of ponds strengthened with upstream load, increasingly outweighing the source effect of dams while being moderated by season and antecedent flow and rainfall. To complement these findings, in 2023, an in-situ pollution event was simulated by adding a slurry of livestock manure (25 l) to two nearby closely comparable streams, one beaver-engineered, the other not (control), and tracking the downstream distribution of waterborne *E. coli*. Consistent with our field sampling campaign, *E. coli* was strongly attenuated in beaver ponds, which reduced peak concentrations by >95 % and slowed the flushing of *E. coli*

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compared to the control stream. Our study demonstrates that beaver dams exert a range of effects on microbial and associated pollution but, importantly, under peak loading can significantly decrease pollution reaching downstream receptors. Beaver dams, and potentially their analogues, could therefore support environmental management strategies in agricultural systems as part of a suite of nature-based approaches.

1. Introduction

Fresh water is an essential natural resource; however, globally, freshwater ecosystems are being increasingly degraded through multiple stressors such as land-use change, pollution, climate change, and invasive species (Díaz et al., 2019; Vörösmarty et al., 2010). Most recent data indicates that in Europe, 41 % of monitored rivers achieve 'good' or 'high' ecological status under the Water Framework Directive (EEA, 2018); while in England, this figure is only 16 % (JNCC, 2021), with pollution acting as the primary driver of change (Lemm et al., 2021). Agricultural run-off, urban wastewater discharge, storm overflow events, and septic tanks are all significant sources of pollution (Albini et al., 2023). Agricultural run-off often contains pesticide residues, excess nutrients from fertilisers and livestock manure, fine sediment, and faecal-derived pathogens such as *Escherichia coli*, intestinal Enterococci, and *Salmonella* spp. (Brooks et al., 2009; Schreiber et al., 2015), all of which can have negative impacts on water quality and environmental health.

E. coli is naturally present in the gastrointestinal tracts of livestock and other animals, so is widely used as an indicator of faecal pollution. Once in the environment, it can persist for long periods of time, overwintering in frozen soils and in some incidences becoming naturalised (Ishii et al., 2006). Upon transfer to the aquatic system, it can become rapidly dispersed (Jamieson et al., 2005; Sinton et al., 2007). However, *E. coli* is subject to natural die-off within water, influenced by processes such as exposure to solar irradiance, nutrient limitation, temperature fluctuations, competition with native microbial communities, and consumption by zooplankton and protozoa (Bolster et al., 2009; Wanjugi et al., 2016; Whitman et al., 2004). *E. coli* can also bind to suspended particulate matter and become deposited as sediment (Liang et al., 2017), where it may persist for longer (Baker et al., 2021; Jamieson et al., 2005). Free *E. coli* declines faster than particle associated *E. coli* (Garcia-Armisen and Servais, 2009); for example, Garzio-Hadzick et al. (2010) observed *E. coli* in freshwater stream sediment to survive for at least 120 days, five-fold longer than *E. coli* in the water. Survival was also enhanced at lower temperatures, peaking at 4 °C, realistic of freshwater streams in the northern UK (Garzio-Hadzick et al., 2010). Subsequent disturbances, such as high flow events, can resuspend sediment-bound *E. coli* and induce continued transport downstream (Jamieson et al., 2005; Muirhead et al., 2004). *E. coli* concentration often correlates well with turbidity, also an important water quality indicator (Huey and Meyer, 2010; Smith et al., 2008). Turbidity is generated by suspended particulate matter such as silt, clay, chemical precipitates, and biological material. Whilst not usually a direct risk to aquatic health, it is often associated with algal blooms, soil erosion, chemical spillages, and microbial pollution (Huey and Meyer, 2010; Rome et al., 2021; Yao et al., 2016).

Diffuse pollution sources are typically addressed through adopting best management practices (BMPs). These are practical measures that landowners can implement to reduce pollutant load in run-off. They include practices such as riparian buffer strips (Lim et al., 2022; Prosser et al., 2020), fencing off riverbanks from livestock (McDowell, 2023), and sustainable land management techniques such as winter cover cropping and no tillage (Waring et al., 2024). Nevertheless, low concentrations of pathogens and pollutants can still enter the aquatic system, with currently few widely implemented methods for removing them (Lim et al., 2022; McDowell, 2023; Waring et al., 2024). Alternative, ecosystem-based approaches to pollution control, such as construction of artificial wetlands, fall under a suite of actions known as Nature-based Solutions (NbS), which focus on protecting, restoring, and enhancing both natural and artificial ecosystems by utilising their ecosystem services (van Rees et al., 2023). NbS have become increasingly popular for environmental restoration and are now widely promoted by governments and policy makers in Europe and North America (Seddon et al., 2020; van Rees et al., 2023).

In Europe, and more latterly Britain specifically, there has been a surge in interest in the reestablishment of beaver populations as a tool for the restoration of aquatic ecosystems (Heydon et al., 2021). Beavers (Eurasian - *Castor fiber* L., and North American - *Castor canadensis*) are keystone species renowned for their role as ecosystem engineers. Through felling trees and constructing dams, beavers modify the structure and function of riparian and freshwater ecosystems (Brazier et al., 2021). Dams are typically constructed of felled branches, mud and rocks, and sometimes non-woody vegetation. They significantly alter stream hydromorphology, attenuating peak flows and raising and stabilising the water level to create ponds which extend beaver foraging areas and offer them protection from terrestrial predators (Puttock et al., 2017, 2021; Ronnquist and Westbrook, 2021; Westbrook et al., 2006). Beaver ponds can also represent heterogenous and biodiverse wetland ecosystems (Bylak et al., 2024; Law et al., 2016; Stringer and Gaywood, 2016; Willby et al., 2018).

Beaver wetlands also provide numerous ecosystem services, including reduced downstream flood risk; regulation of flow during dry periods; and provision of recreational activities, such as fishing and nature tourism (Westbrook et al., 2006; Puttock et al., 2017, 2021; Thompson et al., 2021). In addition, retention of water and attenuation of flow by beaver dams creates a depositional environment that favours sedimentation of particulate matter and the transition from lotic to semi-lentic conditions (Larsen et al., 2021; Puttock et al., 2018, 2021). The resultant ponds can store large volumes of sediment and are known to act as pollutant sinks, assimilating nutrients and heavy metals (Murray et al., 2021; Law et al., 2016; Puttock et al., 2018).

Despite evidence for beaver-engineered wetlands having a significant impact on water quality and nutrient fluxes (Bylak et al., 2024; Puttock et al., 2017), understanding of their influence on fluxes of faecal bacterial pathogens and microbial water quality, and hence of their potential value for mitigating such pollution, is very limited. Our aims were therefore to (1) identify the sources of seasonal and spatial variation in *E. coli* concentrations and turbidity in a beaver-engineered agricultural stream under baseline conditions, and (2) quantify the impact of beaver dams and ponds on the downstream transport of *E. coli* following a simulated in-situ livestock faecal pollution event. We hypothesised based on past findings for other indicators and principles of retention and dilution that ponds, as depositional environments, might act as sinks for suspended material and associated *E coli*, while dams could act as a source due to the greater hydraulic stress. However, we had no clear expectations of the magnitude of these effects or the relative influence of hydrology, seasonality or the specific attributes of ponds and dams.

2. Materials and methods

The study took place on a 525-ha agricultural and forestry estate, situated near Alyth in eastern Scotland (56°38′37.9"N 3°16′09.5"W). Agricultural land was mainly improved, or semi-improved grassland used for sheep, cattle, and pig grazing, with small areas under cultivation for fodder crops, and was interspersed with a mix of broad-leaved and coniferous woodland. The estate lies approximately 190 m above sea level, receives approximately 850 mm of rainfall annually, and has a mean annual temperature of 8.7 °C (Met Office, 2020). The geology is dominated by sandstone or mixed sandstone-conglomerate formations overlain by glacial till. In 2002, two Eurasian beavers were introduced to the stream on the west side of the estate, and following breeding and further releases, the estate now supports three family units. As a result of beaver activity, over 50 beaver dams (mean length = 13 m; range 1–50 m) and associated ponds are now distributed along 4 km of water courses.

2.1. Baseline temporal and spatial variation in water quality

Sampling was carried out between August 2017 and July 2019 along a 1.6 km section of the main water course traversing the estate. This is a small (1 m wide channel pre-beaver engineering) first order stream, incised and canalised as is typical of agricultural landscapes regionally, and with an average channel gradient of 18 mkm^{-1}. Samples were collected on 11 dates at each of 14 sequential beaver dams (Fig. 1, Table S1), being taken directly upstream and directly downstream of each dam (i.e. within 0.5 m of the dam crest or base). Henceforth, “beaver pond” refers to the area of impounded water upstream of a beaver dam. All ponds were online and situated on a single thread channel. The influence of dams was derived by comparing paired samples from upstream and downstream of each dam on a given date, while the influence of a beaver pond was derived by comparing paired samples taken downstream of one dam and upstream of the next dam in the sequence. We note that in the stream reach we studied, beaver dams were sufficiently closely spaced relative to the local channel gradient to effectively eliminate free-flowing sections which had existed under a lower dam density.

Samples were stored at 4 °C, for a maximum of 24 h, prior to processing. Water turbidity (NTU) was measured with a bench top turbidity meter (HI-88703-02, Hanna Instruments, UK). *E. coli* concentration was enumerated by membrane vacuum-filtration and plating on selective chromogenic agar. Water samples were passed through 0.45 μm cellulose acetate membranes (Merck, Germany) using a vacuum pump (Microsart E.jet Liquid Transfer Pump, Sartorius, Germany). Membranes were transferred onto the surface of Membrane Lactose Glucoronide Agar (MLGA) (Thermo Scientific, Oxoid, UK), incubated at 37 °C for 18 h, and *E. coli* determined by enumerating colony forming units (CFUs).

2.1.1. Hydrological data

Precipitation (mm) data were collected via a tipping bucket rain gauge linked to an on-site solar powered Davis Vantage Pro2 weather station recording hourly and subsequently aggregated to daily values. The weather station operated continuously throughout the period, apart from a 2-month period coinciding with our sampling in January 2018 when very cold weather caused battery failure which necessitated substituting data from a well correlated weather station 13 km north of the site.

Stream stage was measured using a vented transducer (Seametrics PT2X) within a stilling well sited in the pool of a standard 90° V notch weir installed at the start of the study. Stage was recorded in 15-min intervals and then corrected to height above the notch to enable construction of a rating curve based on the Kindsvater-Shen equation. Discharge derived from this rating curve was calibrated against manual estimates of discharge obtained using a combination of volumetric and dilution gauging which indicated a mean discharge measurement uncertainty of 22 %. Mean discharge of the focal stream over the study period was 20.44 ls^{-1} (Van Biervliet, 2023).

Both weather station and V notch weir were installed in the middle of the study reach, midway between dams 5 and 6 (Fig. 1). Subsequent trials using precipitation and daily flow for either the day of sampling, the day prior to sampling, or the combined rainfall or mean daily flow over the three days prior to sampling indicated that values for the previous day were optimal for use in models.

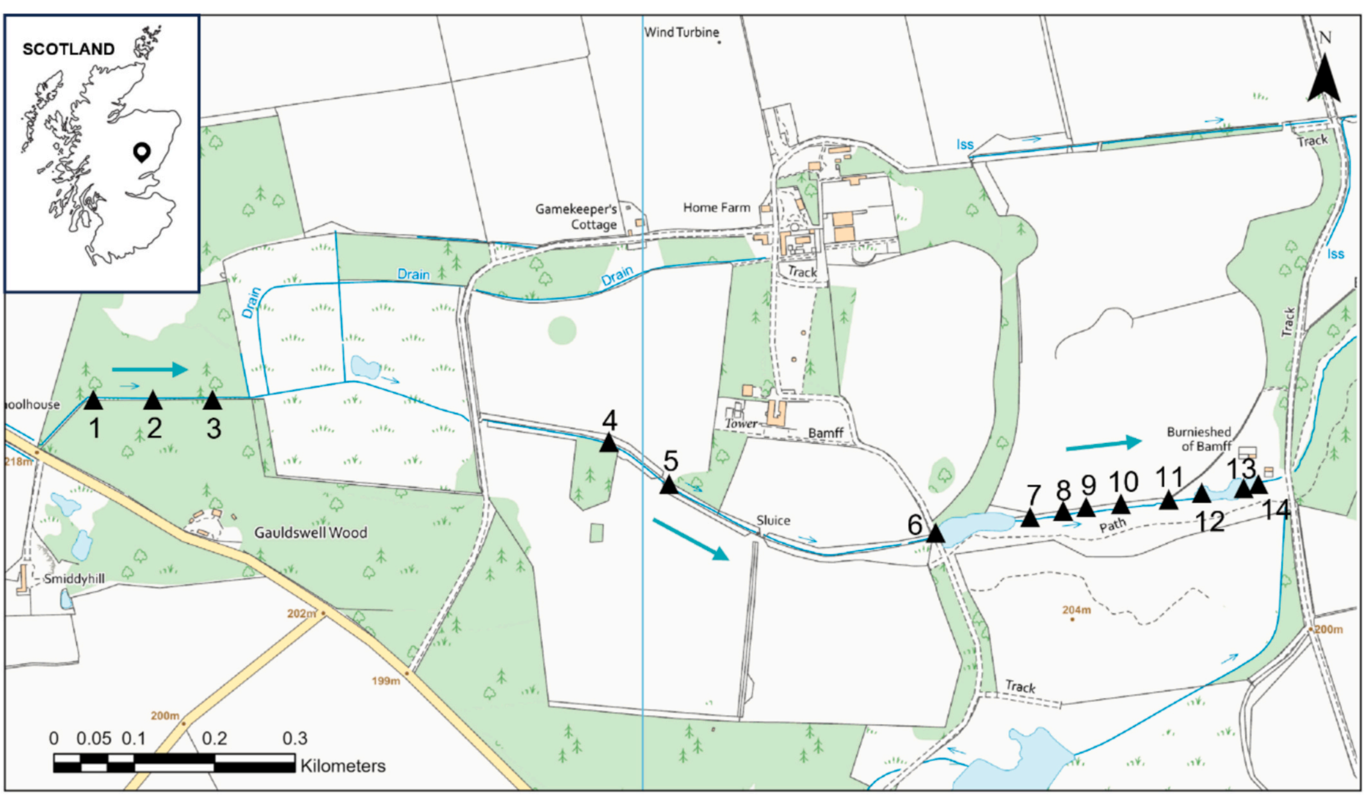

Fig. 1. Location of beaver dams (black triangles) sampled for the analysis of baseline temporal and spatial distribution of *E. coli*.

2.1.2. Morphometric and other attributes of dams and ponds

We measured dam length (median = 10 m, range 1–50 m) along the dam crest from opposite points of bank attachment, and pond area (median = 159 m^2, range 28–1145 m^2) based on recording the pond perimeter in the field with GPS. Average pond depth (median = 50 cm, range = 19–75 cm) was obtained based on replicate measurements from water surface to bed under median flow conditions taken along three transects across the pond positioned perpendicular to its main axis. Pond volume (median = 85 m^3, range 8–781 m^3) was derived from pond area x average depth. To derive an estimate of pond retention time (RT) we divided pond volume (V) by antecedent (day prior to sampling) gauged flow (F) and converted the estimate from seconds to hours (median = 3 h, range = 0.06–233 h):

$$RT = (V/F)/3600$$

All ponds and dams fell within two abutting and well-established beaver territories and experienced regular use by beavers. No dams breached during this study, and all experienced some level of maintenance. However, beaver activity was not evenly dispersed throughout the reach. To allow for this we therefore created a simple three-point index of activity, low (1), medium (2) and high (3), based on our observations of beavers, their feeding signs and pond proximity to the maternal lodge.

2.1.3. Statistical analysis

We used a paired *t*-test to provide a basic comparison of paired values of either turbidity or *E. coli* concentrations measured upstream or upstream of a given dam, or at the upstream and downstream ends of a given pond on a given date. To allow for the underlying spatial and temporal structure of the data we used General Linear Models (GLMs). We reasoned that downstream turbidity or *E. coli* concentrations (i.e. those measured downstream [DS] of a dam or at the downstream end of a pond) would primarily be a function of the upstream [US] load at the time of sampling (i.e. concentration upstream of the equivalent dam or upstream entry to the equivalent pond), but modified by the beaver-engineered feature and any effects of seasonal, hydrological, biological or pond/dam properties. We therefore generated GLMs with downstream turbidity or *E. coli* as the response, one set for dams and another for ponds. For each response we trialled three alternative models. In Model 1 we used the paired upstream load concentration plus rainfall (R) and gauged stream flow (F) on the previous day as covariates, plus season (S) and dam or pond identity (ID) as factors. Thus:

$$\text{Model 1} = [DS] \sim [US] + R + F + S + ID$$

In Model 2 we replaced dam or pond identity with the measured attributes specific to each feature, namely dam length (L), pond volume (V) and pond mean depth (Z), in addition to distance from source (D) to allow for the linear arrangement of sites, alongside beaver activity (BA) as a factor. We excluded pond area from this model as area and volume were highly colinear. Thus:

$$\text{Model 2} = [DS] \sim [US] + R + F + S + L + V + Z + D + BA$$

Model 3 followed the same format as Model 2 but substituted pond volume and flow with their derivative, retention time (RT). Thus:

$$\text{Model 3} = [DS] \sim [US] + R + S + L + Z + D + RT + BA$$

In all cases all responses and covariates were log transformed (i.e. log (x + 1)) prior to analysis and met GLM assumptions. We compared the performance of these three alternative models using AIC. All analyses were constructed in R 4.3.2 (R Core Team, 2023). Forest plots are used to visualise effect sizes of the model predictors and observed downstream relative to upstream concentrations are plotted with the full model predictions overlain.

2.2. Simulated microbial pollution event

In 2023, 80 m reaches of two adjacent first order fishless streams, one beaver-engineered and the other (control) with no beaver activity (Fig. 2), were used to quantify the effect of damming on microbial water quality following a pollution event. These streams were hydrologically independent of the focal stream in section 2.1 but situated on the same site. The beaver-engineered stream included six dams within the study reach (Fig. 3b-g), whilst the control stream (Fig. 3h-l) showed no evidence of beaver activity but was closely representative of its paired beaver-engineered stream prior to animals first being released. Discharge of both streams on the day of the study (April 2023) was 7 ls^{-1}, based on volumetric gauging, and their average channel slope was 70 mkm^{-1}. Continuous monitoring data (N. Willby, unpublished data) indicate that water temperatures in these streams at this time of year are typically 8.5 - 10 °C (beaver-engineered) and 6–8 °C (control). Conductivity is closely comparable between sites (control 169 μScm^{-1}; beaver-engineered stream 186 μScm^{-1}. To determine baseline concentrations of *E. coli* in each stream prior to the event, triplicate water samples were collected from eight sites along each 80 m reach. Samples were stored at 4 °C, for a maximum of 24 h, prior to processing, with *E. coli* enumerated by membrane vacuum-filtration as described above.

Freshly deposited cattle and pig faeces (75:25) were collected from surrounding fields and mixed with stream water in a large bucket to create a homogenous faecal slurry. Twenty-five litres of slurry were added to each stream to simulate a minor organic pollution event (Fig. 2; Fig. 3), and timed grab sampling of water was performed at a series of stations downstream of the point of slurry release (Table S2, Fig. 2). Based on the observed progress of the plume, grab samples were collected over 2.5 h on the beaver-engineered stream and 25 min on the control stream (Table S2). Sampling also occurred with a 7 min lag between sampling at each site on the beaver-engineered stream, (i.e., 14-, 21-, and 28-min post slurry addition at sites A, B, and C, respectively) and without time lag between sampling sites on the control stream. These timings were also informed by a priori estimates of water residence times in each reach (5 h for beaver engineered stream and 0.5 h for control). Water was collected in sterile plastic containers and stored at 4 °C, for a maximum of 24 h, prior to processing (as described above). Triplicate samples of the faecal slurry were serially diluted in sterile phosphate buffered saline (PBS) and *E. coli* expressed as CFU g^{-1} dry weight. Once manual grab sampling had ended automatic water samplers (ISCO 3700 Automatic Water Sampler, RS Hydro, UK) were deployed at sites C and D on the beaver-engineered stream and control stream, respectively (Fig. 2). Samples of 500 ml were collected in sterilised bottles at time intervals as described in Table S2, with sampling continuing for a further 24 h.

3. Results

3.1. Effect of beaver engineering on temporal and spatial variation in E. coli concentration and turbidity

Of the three models we tested, based on AIC, Model 2 was superior to the other models in two responses (turbidity downstream of dams and *E. coli* at the downstream end of ponds). For the remaining two responses (*E. coli* downstream of dams and turbidity at the downstream end of ponds) Model 2 was the second-best model but in both cases differed by <2 AIC units from the best performing model suggesting these models were effectively indistinguishable. Henceforth, we therefore refer exclusively to outputs based on Model 2. The evaluation of all models and model outputs is provided in Supplementary Material, Appendix 1: A-D.

Turbidity and *E. coli* concentrations were generally higher directly downstream of beaver dams (median turbidity 9.57 NTU (10 – 90th percentile = 2.98–62 NTU); median *E.coli* concentration (41 CFU 100 ml^{-1} (10 - 90th percentile = 7–178 CFU 100 ml^{-1}) compared to

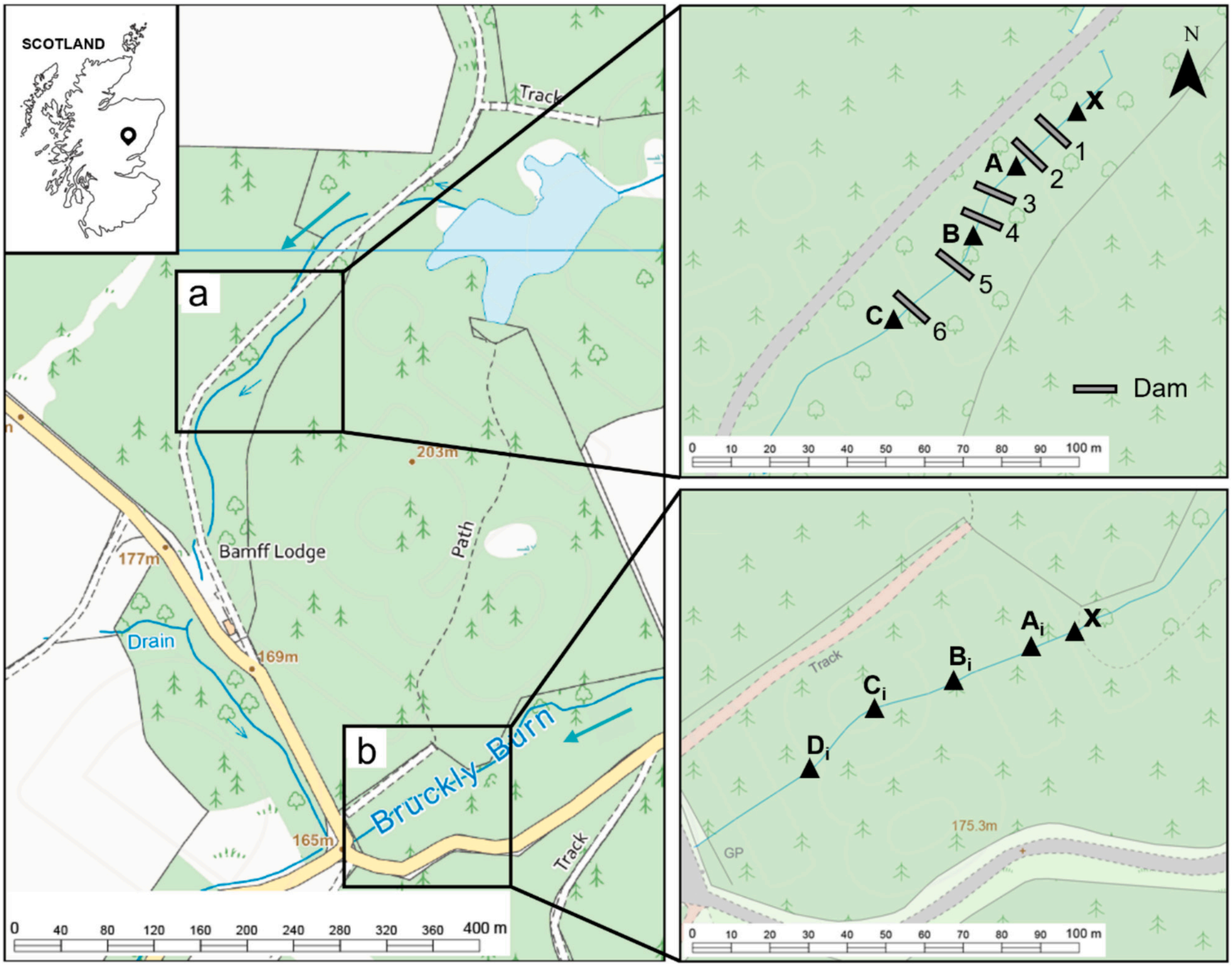

Fig. 2. Beaver engineered stream with locations of dams (a), and the control stream (b) used for the simulated pollution event. Location of slurry input (x) and sampling sites (black triangles).

upstream (median turbidity 6.24 NTU (10 – 90th percentile = 1.94–31.01 NTU); median *E.coli* concentration (32 CFU 100 ml^{-1} (10 - 90th percentile = 4–135 CFU 100 ml^{-1}). Paired *t*-tests ($n = 154$ paired observations) confirmed that these differences were significant (turbidity: $t = 7.78$, $p < 0.001$; *E. coli*: $t = 3.83$, $p < 0.001$). Beaver dam structures were thus an overall weak to moderate source of turbidity and weak source of *E. coli*.

Model 2 indicated that for both turbidity and *E. coli* the upstream load was the dominant driver of concentrations downstream of dams (turbidity: upstream coefficient = 0.723; $p < 0.001$; *E. coli*: upstream coefficient = 0.737; $p < 0.001$; Fig. 5). Model 2 also revealed that the source effect of dams diminished with upstream load, being significant only over the lower quartile of the load (illustrated by overlap at higher loads between confidence limits of fitted response and the no effect line in Fig. 5), with dams shifting towards weak sink behaviour under the highest loading (Fig. 4). There was very limited influence of other factors on downstream values of either response at dams (Fig. 5), with *E. coli* concentrations being lower downstream of longer dams (dam length coefficient = −0.124; $p = 0.003$) but also increasing slightly downstream through the focal reach (distance coefficient = 0.024; $p = 0.045$). Implications for changes in downstream turbidity and *E. coli* concentrations after passage over a dam under contrasting upstream loads are summarised in Table 1 based on the parameter estimates from Model 2.

Turbidity and *E. coli* concentrations were generally lower at the downstream end of beaver ponds (median turbidity 6.20 NTU (10 – 90th percentile = 1.93–11.98 NTU); median *E.coli* concentration (31 CFU 100 ml^{-1} (10 - 90th percentile = 4–135 CFU 100 ml^{-1})) compared to upstream (median turbidity 9.83 NTU (10 – 90th percentile = 2.96–62 NTU); median *E.coli* concentration (42 CFU 100 ml^{-1} (10 - 90th percentile = 8–194 CFU 100 ml^{-1})). Paired t-tests ($n = 143$ paired observations) confirmed that these differences were significant (turbidity: $t = 6.69$, $p < 0.001$; *E. coli*: $t = 2.70$, $p = 0.008$). Beaver ponds overall thus acted as a weak to moderate sink.

As with dams, Model 2 outputs revealed that upstream load to the pond was a key driver of downstream responses (turbidity: upstream coefficient = 0.161, $p = 0.002$; *E. coli*: upstream coefficient = 0.261, $p = 0.001$, Fig. 5). However, unlike dams, there was strong evidence from Model 2 of increasing uncoupling of downstream from upstream concentrations as the latter increased, implying a strengthening sink effect of ponds when upstream turbidity was >3 NTU or *E. coli* concentrations >16 CFU 100 ml^{-1} (Fig. 4). Under high upstream loading, beaver ponds therefore typically functioned as a strong sink for both turbidity and *E. coli* (Table 1). Also, in contrast to dams, there were a range of additional significant seasonal and hydrological influences on turbidity and *E. coli* concentrations at the downstream end of ponds relative to upstream (Fig. 5). Specifically, turbidity was significantly lower in autumn (autumn coefficient = −0.181, $p = 0.03$) or when flows on the previous day were high (flow coefficient = −0.154, $p < 0.001$). In the case of *E. coli,* the seasonal and hydrological influences were largely reversed, being significantly higher in autumn (coefficient = 0.367, $p = 0.014$), and higher when the previous day was wetter (rainfall coefficient =

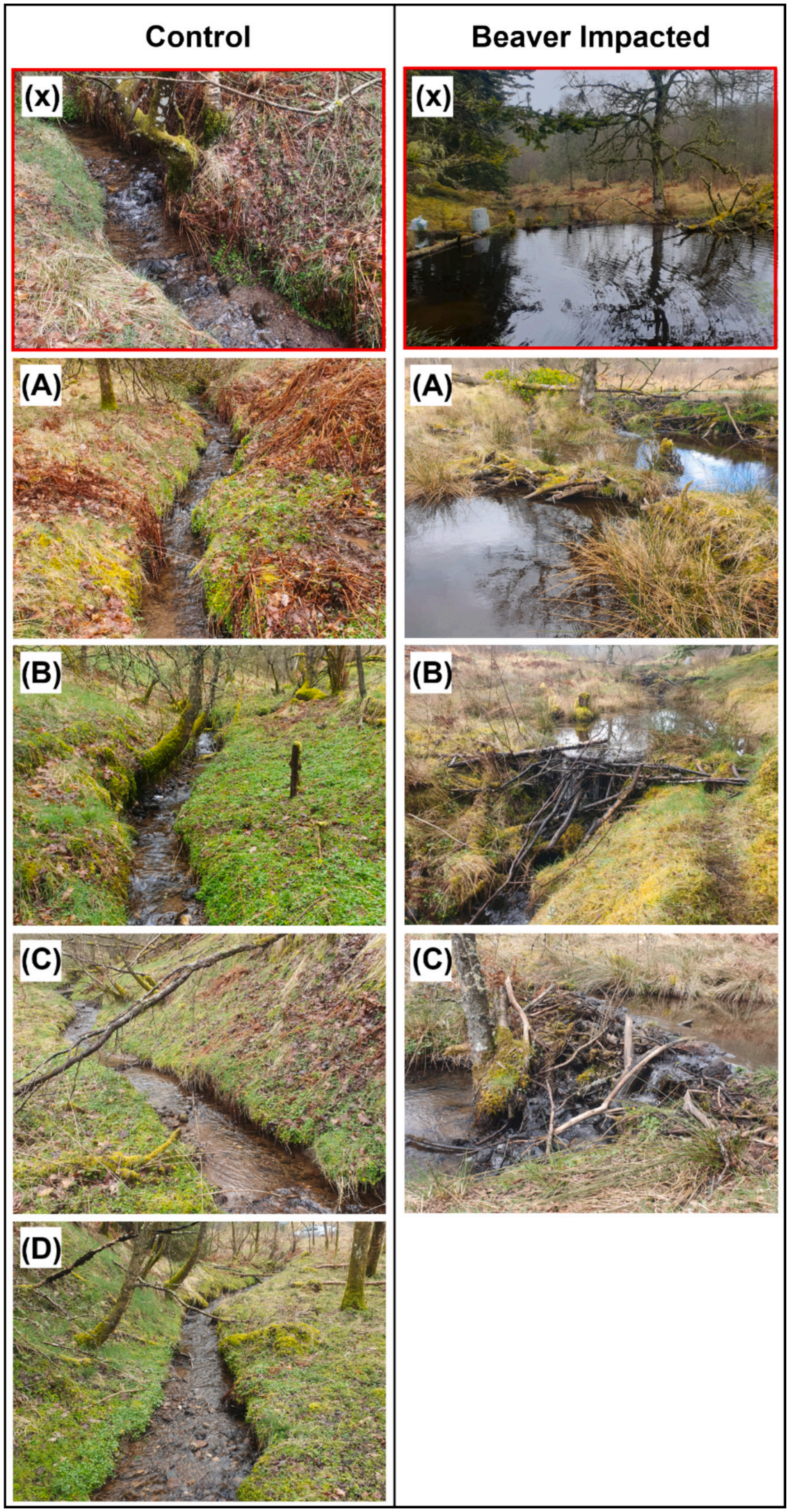

Fig. 3. Sampling sites on the control stream, left, and beaver-engineered stream, right. Slurry release sites (x).

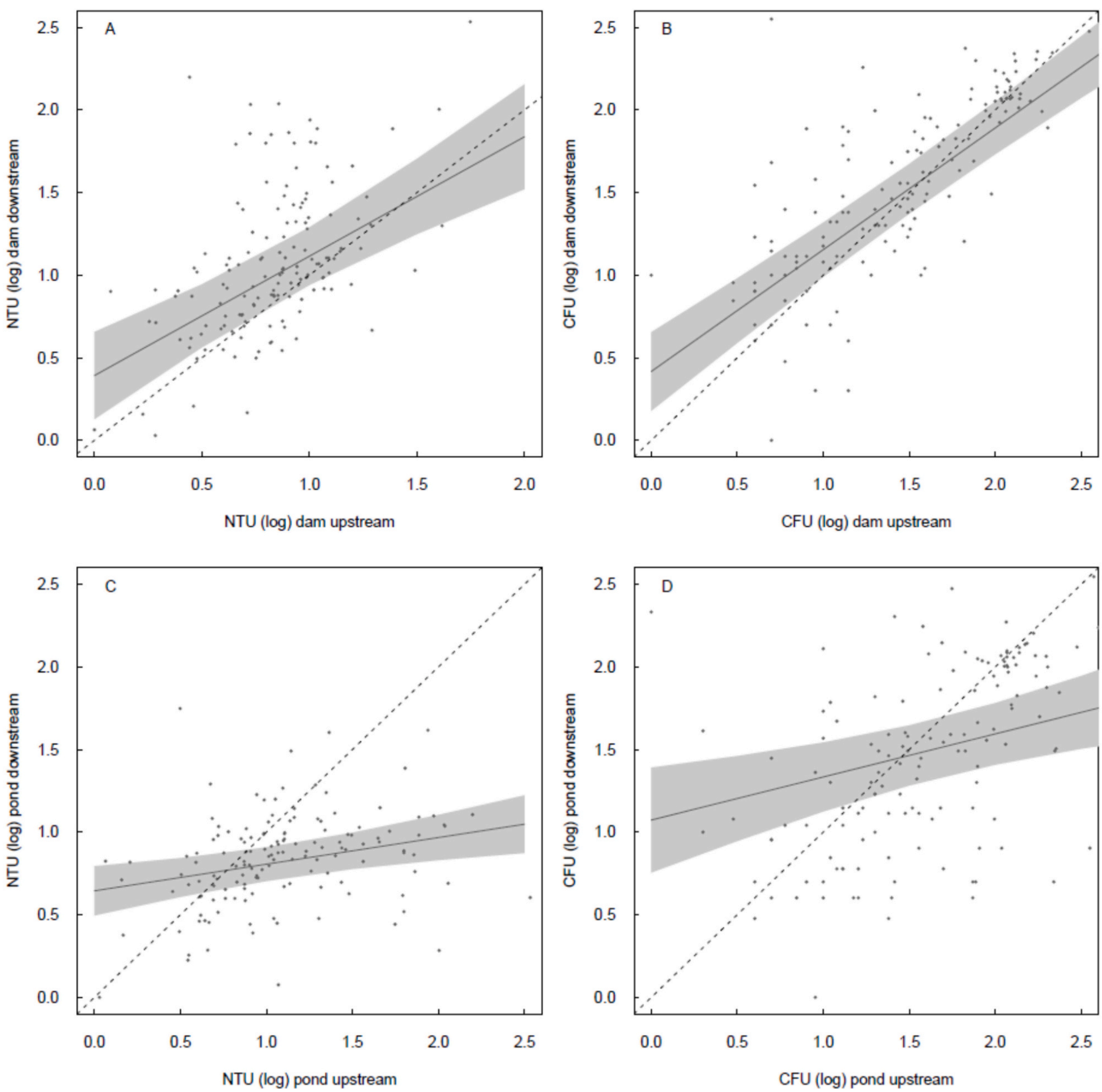

Fig. 4. Downstream versus upstream log concentrations for turbidity (as NTU) and *E. coli* (as CFU 100 ml^{-1}) in relation to beaver dams (A and B) and ponds (C and D). Solid lines show fitted response from Model 2 with the 95 % confidence interval shaded. Dashed lines show 1:1 relationship (no effect line). Points falling below this line indicate a sink effect of the beaver-engineered feature, above the line a source effect.

0.101, $p = 0.023$) or had experienced higher flows (flow coefficient = 0.357, $p < 0.001$). Beaver activity also had some influence on pond *E. coli* concentrations, these being higher in ponds with moderate activity (activity level 2 coefficient = 0.208, $p = 0.026$), although the effect of the highest level of activity was only marginal ($p = 0.085$). We found no significant effect of a range of pond and dam morphometric characteristics (pond volume and depth, dam length).

Taking the modelled effects and their uncertainty for dams and ponds together (Table 1), the typical net effect of a pond + dam combination relative to the upstream inflow to a pond would be to act as a weak source at low inflow concentrations shifting to neutral to weak sink effects under normal flows, and to a strong sink under high inflow concentrations.

A GLM (see Supplementary material, Appendix 1:E-F) revealed that *E. coli* concentrations were significantly ($p < 0.001$) positively correlated with turbidity both upstream (turbidity coefficient = 0.572) and downstream (turbidity coefficient = 0.496) of dams. Antecedent flow exerted a strong positive effect on *E. coli* in both cases (upstream: flow coefficient = 0.548; downstream: flow coefficient = 0.473, both $p < 0.001$), with rainfall (upstream: rainfall coefficient = 0.12; downstream: rainfall coefficient = 0.11, both $p < 0.01$) also significantly shaping these relationships. In both cases *E. coli* concentrations were relatively higher in autumn (upstream: autumn coefficient = 0.586; downstream: autumn coefficient = 0.581, both $p < 0.001$). Additionally, downstream of dams, there was a strong negative effect of dam length (coefficient = −0.221; $p < 0.001$) and a weak but non-significant effect at the highest level of beaver activity (activity level 3 coefficient = 0.356, $p = 0.07$).

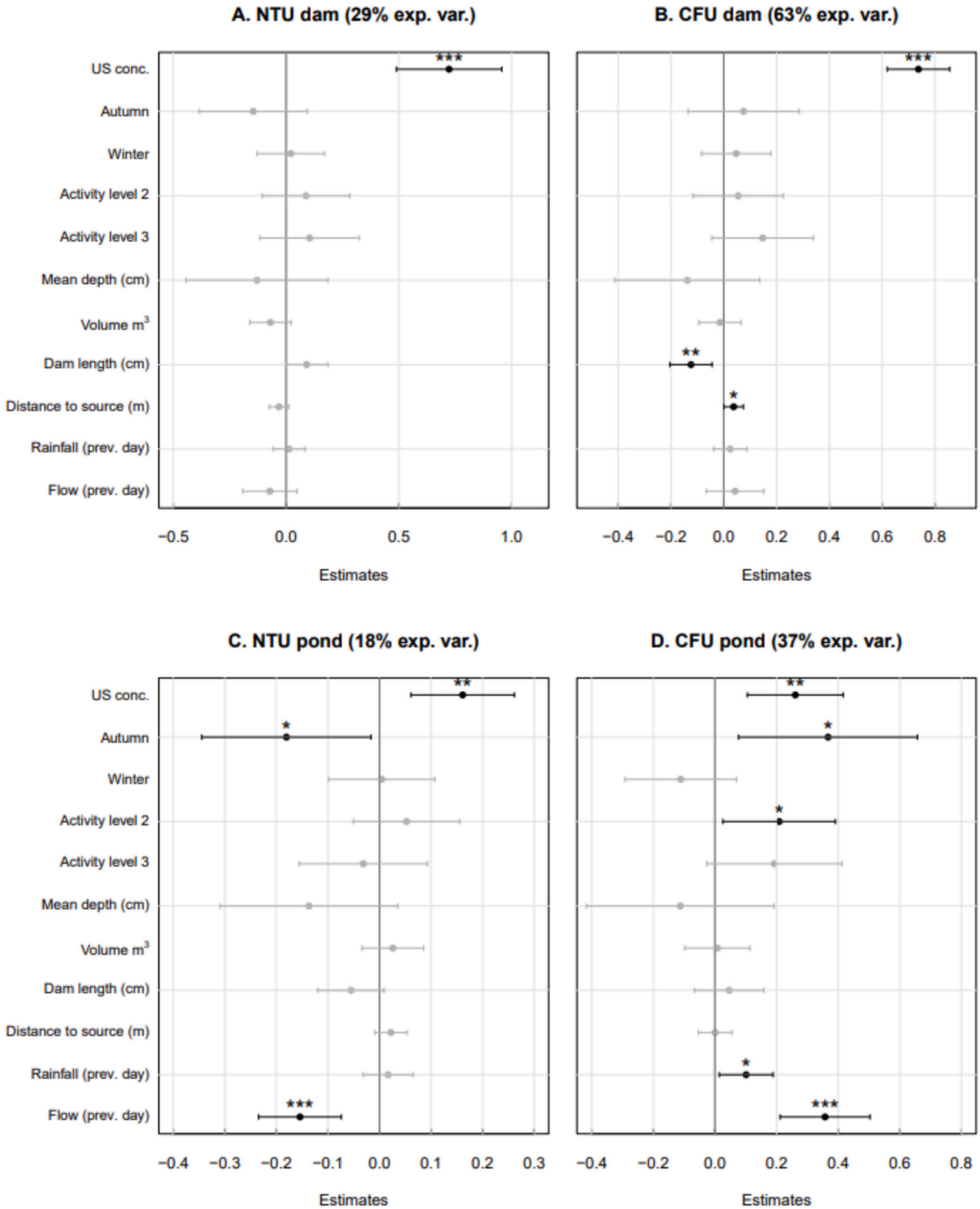

Fig. 5. Forest plots showing effect sizes and their uncertainty for terms in Model 2 for explaining variation in turbidity and *E. coli* concentration downstream of dams (A and B) and at the downstream end of ponds (C and D). *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$. For factorial terms, seasonal effects are arbitrarily expressed relative to summer as the reference value and relative to level 1 (low) for activity.

Table 1
Modelled *changes* in downstream relative to upstream turbidity and *E. coli* concentrations for beaver dams and ponds. Values shown are the model estimates of mean downstream concentrations and their 95 % CL (bracketed) expressed as the change from corresponding upstream concentrations based on the 10th, 50th and 90th percentiles of the observed upstream load. Upper panel refers to change from upstream to downstream of a dam structure, lower panel to change from upstream to downstream end of a pond. Effects are categorised as sink (negative change), source (positive change), or neutral (negligible change) with the magnitude of this effect scaled by the median inflow concentration (weak = change<median; moderate ≤(median*2); strong ≥ (median*2). Asterisks signify significant effects where the 95 % CL does not span zero.

Parameter/Location	Inflow concentration percentile					
	10th		50th		90th	
Dam						
Turbidity (NTU)	2.43	weak source*	2.99	weak source	2.59	weak source
	(0.46 to 5.38)	neutral - weak source	(−0.32 to 7.90)	neutral - moderate source	(−3.05 to 11.11)	weak sink - moderate source
E coli (CFU 100 ml-1)	3.5	weak source*	2.2	neutral	−40.0	moderate sink
	(0.6 to 7.9)	neutral - weak source	(−8.0 to 15.4)	weak source - weak sink	(−69.4 to 5.8)	strong sink - weak source
Pond						
Turbidity (NTU)	1.50	weak source*	−4.31	weak sink*	−54.29	strong sink*
	(0.27 to 3.08)	neutral-weak source	(−5.64 to −2.64)	weak sink	(−56.54 to −51.52)	strong sink
E coli (CFU 100 ml-1)	11.9	weak source*	−11.4	weak sink	−148.2	strong sink*
	(3.9 to 24.9)	weak source	(−22.1 to 4.9)	weak sink - neutral	(−165.5 to −120.9)	strong sink

3.2. *Impact of beaver dams on a simulated microbial pollution event*

To account for naturally occurring waterborne *E. coli*, baseline water samples were collected at each sampling site along the 80 m reach of both streams prior to the addition of the faecal slurry. In all cases, baseline concentrations of naturally occurring *E. coli* were below 10 CFU 100 ml^{-1} in both stream types (Fig. S1); however, turbidity was generally higher in the beaver-engineered stream compared to the control (2.65 ± 0.20 vs. 1.76 ± 0.16 NTU) (Fig. S1).

The concentration of *E. coli* in the faecal slurry added to both experimental streams was 1.05×10^6 and 2.19×10^6 CFU g^{-1} dry weight in the beaver-engineered and control streams respectively, equating to a total input of 2.75×10^9 and 5.33×10^9 CFU. In both streams, the faecal slurry was detectable as a marked rise in the *E. coli* concentration and turbidity of water samples compared to baseline (Fig. 6; Fig. S2).

Both streams showed decreasing peaks in both *E. coli* concentration and turbidity, with distance downstream (Fig. 6; Fig. S2). The concentration of waterborne *E. coli* at each time point was much lower in the beaver-engineered stream compared to the control (Fig. 6; Fig. S2), for example, peak *E. coli* concentration was over 900-fold lower at site A compared to the same site on the control stream. Peak turbidity was also reduced over 100-fold in the beaver-engineered stream compared with the control stream.

The speed of downstream transport of faecal *E. coli* was greatly reduced in the beaver-engineered stream compared to the control

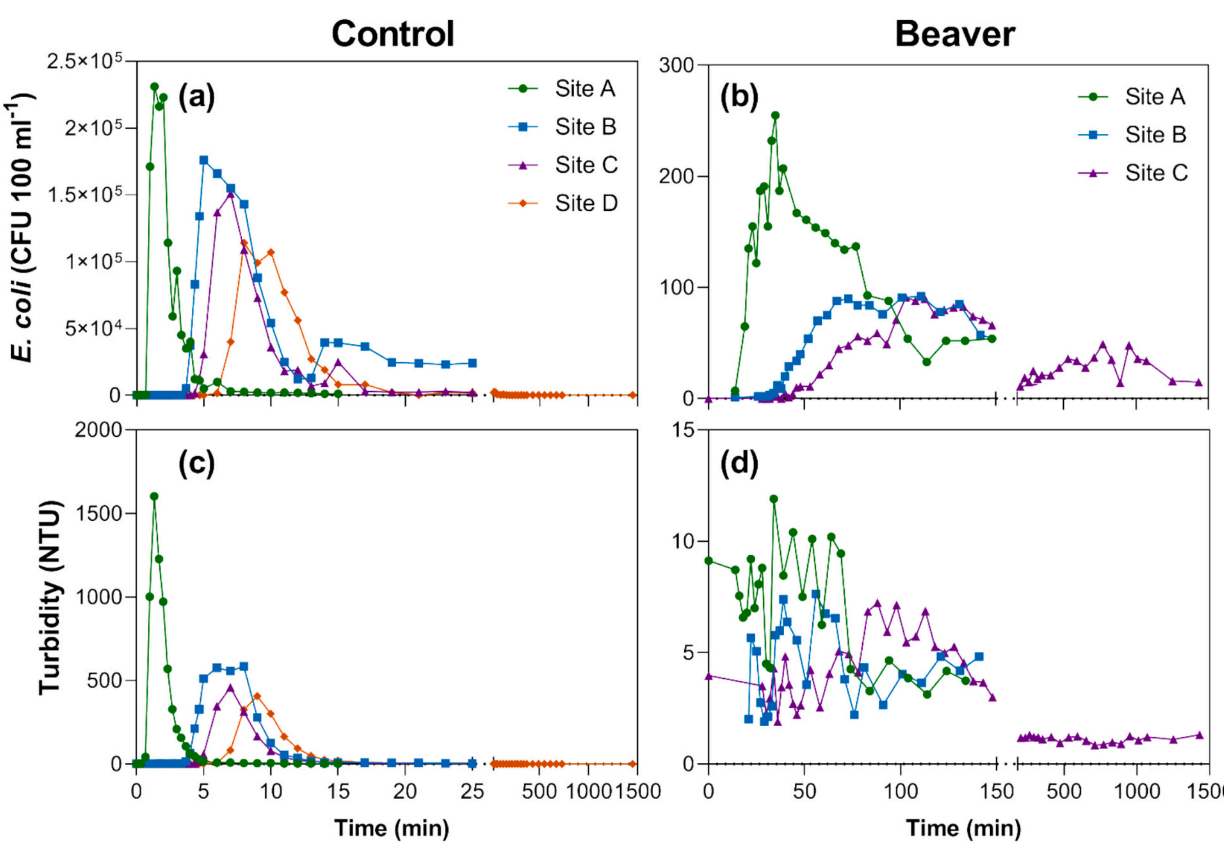

Fig. 6. *E. coli* concentration (a and b) and turbidity (c and d) of water samples taken at time intervals across sites A to D of the control stream (left) and beaver-engineered stream (right), after the addition of faecal slurry. Note differing scales on both x and y axes.

stream (Fig. 6; Fig. S2). There was a delay of 44 min between slurry release and first detection of *E. coli* at the most downstream sampling site (c. 80 m) in the beaver-engineered stream (site C), versus a delay of only 5 min in the control stream (site D) over the same distance, with a similar trend evident for turbidity (Fig. 6). It also took longer to reach peak *E. coli* concentrations in the beaver-engineered stream compared to the control stream (Fig. 6; Fig. S2). For example, peak *E. coli* concentration at site A of the beaver-engineered stream occurred 22-times slower than in the control stream, 30 min versus 1 min 20 s respectively. There was a similar pattern for turbidity, with the peak value occurring 24-times slower in the beaver-engineered stream versus the control stream. However, in both streams, *E. coli* concentrations (but not turbidity) remained elevated above baseline across the 24-h sampling period, indicating that *E. coli* had not been fully flushed through the reach within this time, although by this stage the elevation in concentrations relative to background was biologically trivial.

4. Discussion

This study demonstrates that dam building by Eurasian beavers influences the spatial and temporal dynamics of microbial water quality in a stream environment, with dam structures generally acting as weak sources of *E. coli* and turbidity under low upstream loading, and ponds acting as weak sources or sinks transitioning to strong sinks as upstream loading increases. After a simulated microbial pollution event, the speed of downstream transport of *E. coli* through a beaver-engineered stream reach was substantially reduced, with subsequent order of magnitude reductions in peak *E. coli* concentrations and turbidity downstream. Our data indicate, given the minor absolute changes in turbidity or *E. coli* we mostly observed, that habitat engineering by Eurasian beaver has little biologically relevant impact on waterborne *E. coli* pollution under low to ambient loading, but that damming, or more specifically the ponds formed as a result, may be beneficial under higher loads for mitigating point source microbial pollution.

4.1. Spatial and temporal dynamics of microbial water quality in a beaver-engineered stream

On average beaver dams per se were a weak source of turbidity and *E. coli* and their influence on downstream concentrations was limited. The similar response of turbidity and *E. coli* in relation to dams in our GLMs, points to most *E. coli* being sediment bound. The coupling we observed between turbidity and *E. coli* downstream of dams suggests that the dam matrix could also act as a source of this *E. coli*. Fine sediment is a key component of the structure of beaver dams, whether accumulating passively via deposition or being added actively by beavers, and our findings in relation to turbidity are in line with an earlier reach scale study at this site (Law et al., 2016) and reports from elsewhere (Fracz and Chow-Fraser, 2013). Small mechanical disturbances, such as excavation of sediment by beavers for dam maintenance, or erosion of sediment from the top or matrix of the dam during increased flow, are all likely to mobilise sediment around beaver dams and lead to subsequent fluctuations in turbidity and bound *E. coli* downstream. The absence of a significant hydrological or seasonal influence on the *E. coli* and turbidity signal downstream of dams suggests that any increased loss of sediment and associated *E. coli* from the dam, as might be expected under higher flows, is masked by the effects of mechanical disturbance by beavers under low or ambient flows.

By contrast, ponds exerted relatively strong effects on downstream turbidity and *E. coli* concentrations, increasingly uncoupling these from upstream concentrations as inputs increased. Beaver ponds capture large quantities of sediment due to the rapid reduction in stream velocity as flowing water enters a pond (Puttock et al., 2018; Giriat et al., 2016), making the reduction in turbidity due to settlement of suspended material unsurprising. Whilst *E. coli* can move freely in a planktonic state, cells often adhere to suspended particulate matter and can subsequently become incorporated into the sediment where they persist (Jamieson et al., 2005; Liang et al., 2017). The parallel reductions in concentration of *E. coli* and turbidity we observed across beaver ponds therefore suggest that *E. coli* was commonly bound to suspended particles and consequently precipitated from the water column during extended water transit through a pond.

The contrasting seasonal and hydrological controls on *E. coli* and turbidity in ponds points to generation of turbidity within this system being mainly by local, internal processes with turbidity reducing under higher flows and rainfall, consistent with increased dilution. The major generator of turbidity within ponds is likely to be small scale mechanical disturbances associated with uprooting of macrophytes during feeding by water birds or beavers, or excavation of sediment by beavers for canals or dam maintenance, usually under lower or ambient flows. By contrast, the environmental signature of *E. coli* is more strongly indicative of catchment-based contributions, the increases observed downstream under high flow or heavier rainfall being consistent with lateral inputs of livestock derived *E. coli* delivered via surface run-off from adjacent land (Kay et al., 2010). However, higher flow will also reduce water residence time within ponds, potentially impacting their attenuation effectiveness, particularly under rising flows. Additionally, since freshwater populations of *E. coli* will readily form biofilms (Moreira et al., 2012), such flows might also remobilise internal *E. coli* sources by sloughing biofilms from submerged plant or wood surfaces or by disturbing shallow sediments.

As well as attenuation through reduced water velocity and sedimentation, declines in *E. coli* across beaver ponds may also occur due to increased water temperatures and UV exposure causing higher rates of *E. coli* die-off (Garzio-Hadzick et al., 2010; Whitman et al., 2004). Higher temperatures might also stimulate grazing of *E. coli* by zooplankton (Ismail et al., 2019). Since these influences should be most acute in summer, our finding that *E. coli* was highest at the downstream end of ponds during autumn, with no difference between winter and summer, is unexpected. A combination of extensive macrophyte cover and elevated DOC observed in these and commonly other beaver ponds (Law et al., 2016; Nummi and Holopainen, 2014) might, however, shield bacteria from UV exposure. Enhanced *E. coli* concentrations during the autumn could reflect enhanced faecal loading from livestock during surface runoff, or lower roughness and associated poorer retention of *E. coli* within ponds during macrophyte senescence.

Whilst beaver engineering can have a positive impact on freshwater *E. coli* inputs, animals can also represent a source of *E. coli* and other zoonotic pathogens such as *Salmonella* spp., *Cryptosporidium* spp. and *Giardia* (Girling et al., 2019). *E. coli* is present in the gastrointestinal tracts of beavers (Pratama et al., 2019) and is excreted directly into the environment since beavers preferentially defecate in water (Krojerová-Prokešová et al., 2010). Beavers may also indirectly stimulate *E. coli* concentrations as their engineering activities create wetland ecosystems attractive to waterbirds and mammals (Nummi et al., 2019; Nummi and Holopainen, 2014; Razik and Sagot, 2020), which can be associated with faecal pollution and elevated waterborne *E. coli* concentrations (Chandran and Mazumder, 2015; Somarelli et al., 2007). However, the overall contribution of beavers to environmental *E. coli* remains to be fully quantified. The Beapol01 genetic marker, developed for detection of beaver faeces, shows high host specificity yet does not correlate well with *E. coli* concentrations in environmental samples, indicating a minor direct contribution of beavers to the environmental burden of *E. coli* (Marti et al., 2013). Our study found only limited evidence that *E. coli* concentrations were elevated at sites where beavers were most active, while the hydrological controls on *E. coli* suggest that in agricultural catchments, beaver-specific inputs will be outweighed by livestock-derived inputs from the surrounding catchment.

4.2. Potential role of habitat engineering by beavers in mitigating microbial pollution

During the simulated pollution event, the faecal slurry took substantially longer to transit the beaver engineered stream compared to the control stream, despite the two streams having an equal flow and gradient. Water residence time can be a good predictor of pollutant transport time (Hart et al., 2020), and, although residence time was not calculated in this component of our study, where a beaver dam increases water storage capacity by impounding a greater proportion of inflow, there will inevitably be an increase in water residence time (Hafen et al., 2024; Larsen et al., 2021; Majerova et al., 2015) that will delay pollutant transport and increase the contact time for abiotic and biotic interactions within the system. Therefore, the faecal slurry, introduced as a simulated pollution event, was likely to have spent much longer within the beaver-engineered reach, with more opportunity for *E. coli* to interact with processes such as sedimentation, integration with biofilms, or consumption by zooplankton, leading to a lowering in downstream microbial load and risk of exposure of sensitive receptors to critical concentrations. These findings demonstrate that beaver ponds may have value in mitigating microbial pollution risks in agricultural environments in the same way they could mitigate fine sediment pulses associated with felling activity (Bylak and Kukuła, 2022). As such, they also appear to reproduce some effects of constructed wetlands designed to treat agricultural drainage which can include high removal efficiencies of contaminants such as microbial pathogens (O'Geen et al., 2010).

Beaver dams can also increase the upstream storage of water (Hafen et al., 2024; Puttock et al., 2017; Scamardo et al., 2022), thus increasing dilution capacity. Within our focal beaver-engineered reach there was extensive impoundment of water upstream of each dam and *E. coli* concentrations were 900-fold lower than in the control reach after the addition of faecal slurry, indicating the additional potential role of dilution. Beaver dams can also stabilise the water table and stream discharge, attenuating seasonal declines during periods of low flow (Dewey et al., 2022; Majerova et al., 2015; Westbrook et al., 2006), which ensures dilution capacity is maintained year-round and could potentially minimise the severity of low-flow summer pollution events.

4.3. Limitations

Our study focussed on a single site in Scotland, albeit with multiple dams covering a range of values for attributes including pond area, volume, depth, retention time, and dam length. A wider network of sites across different land use, soil, and hydromorphological contexts would provide a fuller understanding of the transport and fate of *E. coli* in beaver modified systems. Incorporating an analysis of particle size distribution might also further this understanding since *E. coli* is often associated with suspended sediment, and particle size is known to have an influence on the transport dynamics of suspended material and associated pollutants in fluvial systems (Dorrell et al., 2018; Zhang et al., 2011). Similarly, simulating pollution events under different seasons and hydrological conditions would expand understanding of how flow affects transport of peak microbial loads.

Although we sought primarily to understand the spatial and temporal dynamics of turbidity and *E. coli* in a beaver engineered stream system, rather than to constrain the role of individual attributes of ponds or dams, it is surprising, given the expected role of retention and dilution processes, that we could not find a clearer effect of volume, depth or retention time on pond performance. We attribute this to three causes (1) beaver ponds are additionally influenced by varying extents of submerged and emergent vegetation, plus fallen dead or cached wood (Law et al., 20,021) which could significantly distort the effect of volume or retention time, while dams cover a range of composition, size, age, and hydrological integrity (Ronnquist and Westbrook, 2021) that we may not have adequately captured, despite those we studied all being mature and structurally broadly similar; (2) variation in water bird activity influences turbidity and microbial pollution in beaver ponds, or the type and intensity of beaver activity in the period prior to sampling needs to be better resolved and more locally to sampling points; (3) minor diffuse lateral inputs e.g. from tile drainage or local livestock activity, may obscure the role of morphometric attributes in human modified landscapes.

Whether beaver ponds offer a permanent sink for microbial pollutants and suspended matter is unclear since these ponds are known to breach periodically, especially under high flow stress. This can lead to surges of water and the rapid resuspension and transport of large quantities of sediment (Brent et al., 2003; Butler and Malanson, 2005; Westbrook et al., 2020). However, some studies report that most sediment captured by a beaver pond remains in situ after dam failure (Butler and Malanson, 2005). In dam breaches observed at our site post-this study, stored sediment was only mobilised significantly from the former channel bed. Retention in ponds should also allow natural die-off in stored *E. coli,* ultimately reducing the concentration reaching downstream receptors after any dam breach. The impact of beaver dams on legacy *E. coli* pollution is yet to be fully understood, and longer-term monitoring would be required to ascertain any chronic effects on water quality.

5. Conclusions

Microbial pollution is likely to increase in the future due to enhanced pressures on water, food, and waste management systems (E. R. Jones et al., 2023), Thus, there is an urgent demand for sustainable solutions for prevention and remediation. Whilst Eurasian beavers are widely documented to have positive impacts on aquatic ecosystems (Brazier et al., 2021; Heydon et al., 2021; Thompson et al., 2021), their role in aquatic *E. coli* pollution - whether as mitigators or contributors - has received little attention. Our results show that the influence of beaver-engineered habitats varies spatially, temporally, and in relation to upstream inputs, but under high loading can considerably reduce the speed of downstream transport and concentration of *E. coli* and turbidity. Despite the potential for increased microbial loading from beavers themselves, or indirectly via associated wildlife, our findings indicate that habitat engineering by beavers should mostly offer a net reduction in downstream aquatic microbial pollution risk. As such, it could be a valuable tool for increasing the resilience of aquatic ecosystems in agricultural landscapes to microbial pollution as part of wider nature-based solution strategies and the growing shift towards more holistic ecosystem-wide approaches to management.

CRediT authorship contribution statement

Hannah L. White: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Rosie Fellows:** Writing – review & editing, Investigation. **Luke Woodford:** Writing – review & editing, Investigation. **Michael J. Ormsby:** Writing – review & editing, Investigation. **Ollie van Biervliet:** Investigation, Data curation. **Alan Law:** Writing – review & editing, Formal analysis. **Richard S. Quilliam:** Writing – review & editing, Conceptualization. **Nigel J. Willby:** Writing – review & editing, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.178871.

Data availability

Data will be made available on request.

References

Albini, D., Lester, L., Sanders, P., Hughes, J., Jackson, M.C., 2023. The combined effects of treated sewage discharge and land use on rivers. Glob. Chang. Biol. 29 (22), 6415–6422. https://doi.org/10.1111/gcb.16934.

Baker, C.A., Almeida, G., Lee, J.A., Gibson, K.E., 2021. Pathogen and surrogate survival in relation to fecal Indicator Bacteria in freshwater Mesocosms. Appl. Environ. Microbiol. 87 (15). https://doi.org/10.1128/AEM.00558-21.

Bolster, C. H., Haznedaroglu, B. Z., & Walker, S. L. (2009). Diversity in cell properties and transport behaviour among 12 different environmental Escherichia coli isolates. J. Environ. Qual., 38(2), 465–472. http://doi.wiley.com/https://doi.org/10.2134/jeq2008.0137.

Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H., Brown, C.M.L., 2021. Beaver: Nature's ecosystem engineers. Wiley Interdiscip. Rev. Water 8 (1), e1494. https://doi.org/10.1002/WAT2.1494.

Brent, C., Peter, E., Marten, G., 2003. Catastrophic failure of a beaver dam at Chudnuslida lake. East Central British Columbia. https://doi.org/10.13140/2.1.4497.8249.

Brooks, J.P., Adeli, A., Read, J.J., McLaughlin, M.R., 2009. Rainfall simulation in greenhouse microcosms to assess bacterial-associated runoff from land-applied poultry litter. J. Environ. Qual. 38 (1), 218–229. https://doi.org/10.2134/jeq2008.0029.

Butler, D.R., Malanson, G.P., 2005. The geomorphic influences of beaver dams and failures of beaver dams. Geomorphology 71 (1–2), 48–60. https://doi.org/10.1016/j.geomorph.2004.08.016.

Bylak, A., Kochman-Kędziora, N., Kukuła, E., Kukuła, K., 2024. Beaver-related restoration: an opportunity for sandy lowland streams in a human-dominated landscape. J. Environ. Manag. 351, 119799. https://doi.org/10.1016/j.jenvman.2023.119799.

Bylak, A., Kukuła, K., 2022. Impact of fine-grained sediment on mountain stream macroinvertebrate communities: forestry activities and beaver-induced sediment management. Sci. Total Environ. 832, 155079. https://doi.org/10.1016/j.scitotenv.2022.155079.

Chandran, A., Mazumder, A., 2015. Investigation on the temporal variation and source tracking of faecal bacteria in a forest dominated watershed (Comox Lake), British Columbia. Canada. Journal of Applied Microbiology 119 (6), 1718–1728. https://doi.org/10.1111/jam.12969.

Dewey, C., Fox, P.M., Bouskill, N.J., Dwivedi, D., Nico, P., Fendorf, S., 2022. Beaver dams overshadow climate extremes in controlling riparian hydrology and water quality. Nat. Commun. 13 (1), 6509. https://doi.org/10.1038/s41467-022-34022-0.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Zayas, C.N., 2019. Pervasive human-driven decline of life on earth points to the need for transformative change. Science 366 (6471). https://doi.org/10.1126/science.aax3100.

Dorrell, R.M., Amy, L.A., Peakall, J., McCaffrey, W.D., 2018. Particle size distribution controls the threshold between net sediment Erosion and deposition in suspended load dominated flows. Geophys. Res. Lett. 45 (3), 1443–1452. https://doi.org/10.1002/2017GL076489.

EEA. (2018). European waters - Assessment of status and pressures 2018, EEA Report 7/2018. doi:https://doi.org/10.2800/303664.

Fracz, A., Chow-Fraser, P., 2013. Changes in water chemistry associated with beaver-impounded coastal marshes of eastern Georgian bay. Can. J. Fish. Aquat. Sci. 70 (6), 834–840. https://doi.org/10.1139/cjfas-2012-0431.

Garcia-Armisen, T., Servais, P., 2009. Partitioning and fate of particle-Associated E. Coli in river waters. Water Environ. Res. 81 (1), 21–28. https://doi.org/10.2175/106143008X304613.

Garzio-Hadzick, A., Shelton, D.R., Hill, R.L., Pachepsky, Y.A., Guber, A.K., Rowland, R., 2010. Survival of manure-borne E. Coli in streambed sediment: effects of temperature and sediment properties. Water Res. 44 (9), 2753–2762. https://doi.org/10.1016/j.watres.2010.02.011.

Giriat, D., Gorczyca, E., Sobucki, M., 2016. 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.

Girling, S.J., Naylor, A., Fraser, M., Campbell-Palmer, R., 2019. Reintroducing beavers Castor fiber to Britain: a disease risk analysis. Mammal Rev. 49 (4), 300–323. https://doi.org/10.1111/mam.12163.

Hafen, K.C., Wheaton, J.M., Roper, B.B., Bailey, P., Macfarlane, W.W., Neilson, B.T., Tennant, C.J., 2024. Estimating increased transient water storage with increases in beaver dam activity. Water 16 (11), 1515. https://doi.org/10.3390/w16111515.

Hart, J., Rubinato, M., & Lavers, T. (2020). An experimental investigation of the hydraulics and pollutant dispersion characteristics of a model beaver dam. Water, 12 (9), 2320. Doi:https://doi.org/10.3390/w12092320Heydon, M. J., Pouget, D., gray, S., Wagstaff, G., Ashton, M. E. M., & Andison, E. (2021). Beaver reintroductions in England 2000 - 2021. JP036.

Heydon, M.J., Pouget, D., Gray, S., Wagstaff, G., Ashton, M.E.M., Andison, E., 2021. Beaver reintroductions in England: 2000-2021. JP036. Natural England, York, UK. https://publications.naturalengland.org.uk/publication/5363285194178560.

Huey, G.M., Meyer, M.L., 2010. Turbidity as an Indicator of water quality in diverse watersheds of the upper Pecos River basin. Water 2 (2), 273–284. https://doi.org/10.3390/w2020273.

Ishii, S., Ksoll, W.B., Hicks, R.E., Sadowsky, M.J., 2006. Presence and growth of naturalized *Escherichia coli* in temperate soils from Lake Superior watersheds. Appl. Environ. Microbiol. 72. https://doi.org/10.1128/AEM.72.1.612-621.2006.

Ismail, N.S., Blokker, B.M., Feeney, T.R., Kohn, R.H., Liu, J., Nelson, V.E., Ollive, M.C., Price, S.B.L., Underdah, E.J., 2019. Impact of Metazooplankton filter feeding on Escherichia coli under variable environmental conditions. Appl. Environ. Microbiol. 85 (23). https://doi.org/10.1128/AEM.02006-19.

Jamieson, R.C., Joy, D.M., Lee, H., Kostaschuk, R., Gordon, R.J., 2005. Resuspension of sediment-associated Escherichia coli in a natural stream. J. Environ. Qual. 34 (2), 581–589. https://doi.org/10.2134/jeq2005.0581.

JNCC, 2021. UKBI - B7. Surface water status. https://jncc.gov.uk/our-work/ukbi-b7-surface-water-status/#key-results-figure-b7i-status-classification-of-uk-surface-water-bodies-under-the-water-framework-directive-2009-to-2020.

Jones, E.R., Bierkens, M.F.P., van Puijenbroek, P.J.T.M., van Beek, L.P.H., Wanders, N., Sutanudjaja, E.H., van Vliet, M.T.H., 2023. Sub-Saharan Africa will increasingly become the dominant hotspot of surface water pollution. Nature Water 1 (7), 602–613. https://doi.org/10.1038/s44221-023-00105-5.

Kay, D., Anthony, S., Crowther, J., Chambers, B.J., Nicholson, F.A., Chadwick, D., Stapleton, C.M., Wyer, M.D., 2010. Microbial water pollution: a screening tool for initial catchment-scale assessment and source apportionment. Sci. Total Environ. 408 (23), 5649–5656. https://doi.org/10.1016/j.scitotenv.2009.07.033.

Krojerová-Prokešová, J., Barančeková, M., Hamšíková, L., Vorel, A., 2010. Feeding habits of reintroduced Eurasian beaver: spatial and seasonal variation in the use of food resources. J. Zool. 281 (3), 183–193. https://doi.org/10.1111/j.1469-7998.2010.00695.x.

Larsen, A., Larsen, J.R., Lane, S.N., 2021. 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.

Law, A., Mclean, F., Willby, N.J., 2016. Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. Freshw. Biol. 61 (4), 486–499. https://doi.org/10.1111/FWB.12721.

Lemm, J.U., Venohr, M., Globevnik, L., Stefanidis, K., Panagopoulos, Y., van Gils, J., Posthuma, L., Kristensen, P., Feld, C.K., Mahnkopf, J., Hering, D., Birk, S., 2021. Multiple stressors determine river ecological status at the European scale: towards an integrated understanding of river status deterioration. Glob. Chang. Biol. 27 (9), 1962–1975. https://doi.org/10.1111/gcb.15504.

Liang, X., Liao, C., Soupir, M.L., Jarboe, L.R., Thompson, M.L., Dixon, P.M., 2017. Escherichia coli attachment to model particulates: the effects of bacterial cell characteristics and particulate properties. PLoS One 12 (9), e0184664. https://doi.org/10.1371/journal.pone.0184664.

Lim, T.J.Y., Sargent, R., Henry, R., Fletcher, T.D., Coleman, R.A., McCarthy, D.T., Lintern, A., 2022. Riparian buffers: disrupting the transport of E. Coli from rural catchments to streams. Water Res. 222, 118897. https://doi.org/10.1016/j.watres.2022.118897.

Majerova, M., Neilson, B.T., Schmadel, N.M., Wheaton, J.M., Snow, C.J., 2015. Impacts of beaver dams on hydrologic and temperature regimes in a mountain stream. Hydrol. Earth Syst. Sci. 19 (8), 3541–3556. https://doi.org/10.5194/HESS-19-3541-2015.

Marti, R., Zhang, Y., Tien, Y.-C., Lapen, D.R., Topp, E., 2013. Assessment of a new Bacteroidales marker targeting north American beaver (Castor canadensis) fecal pollution by real-time PCR. J. Microbiol. Methods 95 (2), 201–206. https://doi.org/10.1016/j.mimet.2013.08.016.

McDowell, R.W., 2023. The longevity of fencing out livestock as a method of decreasing contaminant concentrations in a headwater stream. J. Environ. Qual. 52 (1), 173–179. https://doi.org/10.1002/jeq2.20417.

Moreira, S., Brown, A., Ha, R., Iserhoff, K., Yim, M., Yang, J., Liao, B., Pszczolko, E., Qin, W., Leung, K.T., 2012. Persistence of Escherichia coli in freshwater periphyton: biofilm-forming capacity as a selective advantage. FEMS Microbiol. Ecol. 79 (3), 608–618. https://doi.org/10.1111/j.1574-6941.2011.01244.x.

Muirhead, R.W., Davies-Colley, R.J., Donnison, A.M., Nagels, J.W., 2004. Faecal bacteria yields in artificial flood events: quantifying in-stream stores. Water Res. 38 (5), 1215–1224. https://doi.org/10.1016/j.watres.2003.12.010.

Murray, D., Neilson, B.T., Brahney, J., 2021. Source or sink? Quantifying beaver pond influence on non-point source pollutant transport in the intermountain west. J. Environ. Manag. 285, 112127. https://doi.org/10.1016/j.jenvman.2021.112127.

Nummi, P., Holopainen, S., 2014. Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. Aquat. Conserv. Mar. Freshwat. Ecosyst. 24 (5), 623–633. https://doi.org/10.1002/aqc.2437.

Nummi, P., Liao, W., Huet, O., Scarpulla, E., Sundell, J., 2019. The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. Global Ecology and Conservation 20, e00701. https://doi.org/10.1016/j.gecco.2019.e00701.

Office, Met, 2020. UK climate averages. HadUK-Grid dataset, Blairgowrie (Perth and Kinross). https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-climate-averages/gfj9gvswj.

O'Geen, A.T., Budd, R., Gan, J., Maynard, J.J., Parikh, S.J., Dahlgren, R.A., 2010. Mitigating Nonpoint Source Pollution in Agriculture with Constructed and Restored Wetlands, pp. 1–76. https://doi.org/10.1016/S0065-2113(10)08001-6.

Pratama, R., Schneider, D., Böer, T., Daniel, R., 2019. First insights into bacterial gastrointestinal tract communities of the Eurasian beaver (Castor fiber). Front. Microbiol. 10. https://doi.org/10.3389/fmicb.2019.01646.

Prosser, R.S., Hoekstra, P.F., Gene, S., Truman, C., White, M., Hanson, M.L., 2020. A review of the effectiveness of vegetated buffers to mitigate pesticide and nutrient transport into surface waters from agricultural areas. J. Environ. Manag. 261, 110210. https://doi.org/10.1016/j.jenvman.2020.110210.

Puttock, A., Graham, H.A., Ashe, J., Luscombe, D.J., Brazier, R.E., 2021. Beaver dams attenuate flow: a multi-site study. Hydrol. Process. 35 (2). https://doi.org/10.1002/hyp.14017.

Puttock, A., Graham, H.A., Carless, D., Brazier, R.E., 2018. Sediment and nutrient storage in a beaver engineered wetland. Earth Surf. Process. Landf. 43 (11), 2358–2370. https://doi.org/10.1002/esp.4398.

Puttock, A., Graham, H.A., Cunliffe, A.M., Elliott, M., Brazier, R.E., 2017. Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. Sci. Total Environ. 576, 430–443. https://doi.org/10.1016/J.SCITOTENV.2016.10.122.

R Core Team, 2023. _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Razik, I., Sagot, M., 2020. Vertebrate species richness at Littoral beaver lodges in a temperate artificial pond. J. Fish Wildl. Manag. 11 (2), 422–429. https://doi.org/10.3996/092019-JFWM-078.

Rome, M., Beighley, R.E., Faber, T., 2021. Sensor-based detection of algal blooms for public health advisories and long-term monitoring. Sci. Total Environ. 767, 144984. https://doi.org/10.1016/j.scitotenv.2021.144984.

Ronnquist, A.L., Westbrook, C.J., 2021. Beaver dams: how structure, flow state, and landscape setting regulate water storage and release. Sci. Total Environ. 785, 147333. https://doi.org/10.1016/j.scitotenv.2021.147333.

Scamardo, J.E., Marshall, S., Wohl, E., Julianne Scamardo, C.E., Peters, C., D. P., 2022. Estimating widespread beaver dam loss: habitat decline and surface storage loss at a regional scale. Ecosphere 13 (3), e3962. https://doi.org/10.1002/ECS2.3962.

Schreiber, C., Rechenburg, A., Rind, E., Kistemann, T., 2015. The impact of land use on microbial surface water pollution. Int. J. Hyg. Environ. Health 218 (2), 181–187. https://doi.org/10.1016/j.ijheh.2014.09.006.

Seddon, N., Daniels, E., Davis, R., Chausson, A., Harris, R., Hou-Jones, X., Huq, S., Kapos, V., Mace, G.M., Rizvi, A.R., Reid, H., Roe, D., Turner, B., Wicander, S., 2020. Global recognition of the importance of nature-based solutions to the impacts of climate change. Global Sustainability 3, e15. https://doi.org/10.1017/sus.2020.8.

Sinton, L.W., Braithwaite, R.R., Hall, C.H., Mackenzie, M.L., 2007. Survival of Indicator and pathogenic Bacteria in bovine feces on pasture. Appl. Environ. Microbiol. 73 (24), 7917–7925. https://doi.org/10.1128/AEM.01620-07.

Smith, R.P., Paiba, G.A., Ellis-Iversen, J., 2008. Short communication: turbidity as an Indicator of Escherichia coli presence in water troughs on cattle farms. J. Dairy Sci. 91 (5), 2082–2085. https://doi.org/10.3168/jds.2007-0597.

Somarelli, J.A., Makarewicz, J.C., Sia, R., Simon, R., 2007. Wildlife identified as major source of Escherichia coli in agriculturally dominated watersheds by BOX A1R-derived genetic fingerprints. J. Environ. Manag. 82 (1), 60–65. https://doi.org/10.1016/j.jenvman.2005.12.013.

Stringer, A.P., Gaywood, M.J., 2016. The impacts of beavers Castor spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. Mammal Rev. 46 (4), 270–283. https://doi.org/10.1111/mam.12068.

Thompson, S., Vehkaoja, M., Pellikka, J., Nummi, P., 2021. Ecosystem services provided by beavers *Castor* spp. Mammal Rev. 51, 25–39. https://doi.org/10.1111/mam.12220.

Van Biervliet, O., 2023. The Hydrological Effects of the Eurasian Beaver (*Castor fiber*) in a UK Headwater Catchment. University College London.

van Rees, C.B., Jumani, S., Abera, L., Rack, L., McKay, S.K., Wenger, S.J., 2023. The potential for nature-based solutions to combat the freshwater biodiversity crisis. PLOS Water 2 (6), e0000126. https://doi.org/10.1371/journal.pwat.0000126.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature 467 (7315), 555–561. https://doi.org/10.1038/nature09440.

Wanjugi, P., Fox, G.A., Harwood, V.J., 2016. The interplay between predation, competition, and nutrient levels influences the survival of Escherichia coli in aquatic environments. Microb. Ecol. 72 (3), 526–537. https://doi.org/10.1007/s00248-016-0825-6.

Waring, E.R., Pederson, C., Lagzdins, A., Clifford, C., Helmers, M.J., 2024. Water and soil quality respond to no-tillage and cover crops differently through 10 years of implementation. Agric. Ecosyst. Environ. 360, 108791. https://doi.org/10.1016/j.agee.2023.108791.

Westbrook, C.J., Cooper, D.J., Baker, B.W., 2006. Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. Water Resour. Res. 42 (6). https://doi.org/10.1029/2005WR004560.

Westbrook, C.J., Ronnquist, A., Bedard-Haughn, A., 2020. Hydrological functioning of a beaver dam sequence and regional dam persistence during an extreme rainstorm. Hydrol. Process. 34 (18), 3726–3737. https://doi.org/10.1002/hyp.13828.

Whitman, R.L., Nevers, M.B., Korinek, G.C., Byappanahalli, M.N., 2004. Solar and temporal effects on Escherichia coli concentration at a Lake Michigan Swimming Beach. Appl. Environ. Microbiol. 70 (7), 4276–4285. https://doi.org/10.1128/AEM.70.7.4276-4285.2004.

Willby, N.J., Law, A., Levanoni, O., Foster, G., Ecke, F., 2018. Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. Philos. Trans. R. Soc. B 373 (1761), 20170444. https://doi.org/10.1098/rstb.2017.0444.

Yao, H., Zhuang, W., Qian, Y., Xia, B., Yang, Y., Qian, X., 2016. Estimating and predicting metal concentration using online turbidity values and water quality models in two Rivers of the Taihu Basin. Eastern China. PloS One 11 (3), e0152491. https://doi.org/10.1371/journal.pone.0152491.

Zhang, G.H., Wang, L.L., Tang, K.M., Luo, R.T., Zhang, X.C., 2011. Effects of sediment size on transport capacity of overland flow on steep slopes. Hydrol. Sci. J. 56 (7), 1289–1299. https://doi.org/10.1080/02626667.2011.609172.