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Whole System Ecohydrological Change Following Natural Flood Management and a Five-Year Beaver Reintroduction Trial

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ABSTRACT

Once-common beavers have been absent from the British landscape for centuries, but wild beaver populations have returned in recent years as part of reintroduction schemes, including releases into monitored enclosures. In North Yorkshire, such a release of Eurasian beavers took place in 2019. Using an interdisciplinary combination of traditional (e.g., species surveys, repeat fixed-point photography) and cutting-edge (e.g., mobile LiDAR and eDNA sampling) monitoring and modelling, we report on the effect of those beavers on the hydrology, geomorphology and ecology over a 5-year period, including their interaction with existing natural flood management infrastructure. The beavers constructed six dams after which the hydrological response became less flashy with lower peak flows than in the pre-beaver period. Compared with an upstream gauge, there was a 46.6% reduction in median peak flows, a 417% increase in baseflow (Q95), a 31% median reduction in turbidity and general improvement in other water quality metrics. Beavers did not initially incorporate existing in-stream infrastructure into their dams, which degraded and lost over half of their storage capacity; however, the additional capacity provided by beaver dams mitigated this reduction, and there are recent signs of beavers restoring the functionality and extending the active life of these degraded human-built dams. Aquatic plant diversity increased, and vertebrate species richness was higher than a neighbouring stream; increases were observed from monitoring small mammals, amphibians, dragonflies and damselflies. Bat populations increased at locations and times that exactly corresponded with beaver activity. Our novel interdisciplinary monitoring approach clearly demonstrates the profound and interconnected impacts beavers have upon local hydrology, geomorphology and ecology.

1 | Introduction

Beavers are important ecosystem engineers, adjusting their surrounding environment to better meet their own needs (Brazier et al. 2021; Larsen et al. 2021; Fairfax and Westbrook 2024). In doing so, beavers can increase catchment resilience to climate change (Jordan and Fairfax 2022), especially via their adjustments to the local hydrology. Construction of dams and creation of large ponds can store substantial volumes of water (Gurnell 1998; Butler and Malanson 2005), attenuate high flows, slow water flow through river channels (Nyssen et al. 2011; Puttock et al. 2017, 2021) and help mitigate flooding downstream. Beyond flood reduction, so-called 'secondary impacts' of beaver activity can be identified. Improvement in water retention helps to maintain riparian plant growth and stream baseflows in times of drought (Fairfax and Small 2018). Structural changes to beaver-impacted sites adjust more than just the hydrology and generally increase the structural heterogeneity of the surrounding landscape (Rolauffs et al. 2001). Beavers' construction activities of both blocking and diverting water flows have large impacts on the site geomorphology and sediment fluxes (Puttock et al. 2018). Their tree felling often improves light penetration of forest canopies and improves the diversity of species and tree ages within a site (Levine and Meyer 2019; Zwolicki 2025). Consequently, this brings biodiversity benefits (Washko et al. 2022), modifies nutrient and chemical cycling (Murray et al. 2023) and impacts on water quality.

In the UK, the impact of beavers on aquatic and riparian ecosystems was reduced when once common Eurasian beavers (*Castor fiber*) were hunted to extinction in the 16th Century (Conroy and Kitchener 1996; Coles 2006). Following reintroduction schemes across Europe (Halley et al. 2021), recent years have seen licensed and monitored wild beaver reintroduction trials in south west England (Graham et al. 2022) and Scotland (Law et al. 2017; Willby et al. 2018) along with several schemes nationwide that have introduced Eurasian beavers into monitored enclosures. Such enclosure releases offer a relatively controlled opportunity for close observation of beaver populations and thereby provide evidence of whether reintroductions of Eurasian beavers can restore their wide-ranging impacts and benefits to a heavily-modified landscape such as the UK.

One such enclosure is located in Cropton Forest in Yorkshire, where two beavers were released in April 2019. This site was also the location of previously installed natural flood management (NFM) structures (e.g., instream timber bunds and large woody dams [LWD]) for flood reduction purposes (Thomas and Nisbet 2023) as part of the DEFRA (Department for Environment, Food & Rural Affairs) 'Slowing the Flow' pilot project in response to regular flooding in Pickering, North Yorkshire. Land-use changes and NFM techniques were applied in the upper catchments of both Pickering Beck and the adjacent River Seven catchment to reduce flood peaks by increasing the travel time of water through the catchments, including the planting of 23 ha of woodland and the construction of 50 instream wood dams and a further two larger timber bunds crossing the full width of the floodplain. Whilst a combination of such structures was effective in reducing flood peaks downstream, there remain key unknowns as to the degradation and ongoing effectiveness of these human-made structures without regular maintenance.

In response, a novel five-year trial was led by Forestry England and licensed by Natural England, releasing two Eurasian beavers (*C. fiber*) into a 10 ha woodland fenced enclosure, which included several in-stream dams and a large timber bund on a 824 m length of Sutherland Beck. Here, we present a novel interdisciplinary study, simultaneously using a wide range of monitoring methods to quantify beaver impacts and their interconnections. Methods range from eDNA metabarcoding to detect entire communities of species (Deiner et al. 2017) to three-dimensional terrestrial laser scanning surveys of dam structures and before–after/control–impact hydrological and water quality monitoring to provide a novel, cross-cutting, whole system analysis of beaver impacts in the enclosure over the 5-year trial period. Specifically, three objectives were addressed:

1. To examine how beavers interact with existing NFM structures and whether they will maintain such structures;
2. To evaluate the 'primary' hydrological impact of beaver release in changing water storage and mitigating hydrological extremes, including both reducing flood peaks and increasing baseflow during low-flow periods;
3. To quantify secondary effects of beaver release, including changing habitat availability, ecological diversity and water quality.

2 | Methods

Sutherland Beck is a shaded fourth-order tributary stream of the River Seven, with an upstream catchment area of 747 ha, which flows (with channel width of 3–6 m) through the beaver enclosure (Figure 1a) situated within Cropton Forest. The enclosure comprises a mixture of broadleaved trees and conifers, with a mixture of widely spaced beech and pine with a rhododendron understorey, plantations of Norway spruce planted in 1954, Scots pine planted in 1940 and Douglas fir planted in 1970. All the conifer crops had minimal understory and ground flora. Following conifer clearance, the west of the site is dominated by single-age silver birch stands, typically older to the north of Sutherland Beck (from the 1970s), with young regeneration (from 2012) to the south. At the eastern (upstream) end of the site, two ornamental human-made 'fish ponds' appear on maps from the early 1900s. At the start of the scientific trial, these had silted up and become overgrown with willow scrub with little open water remaining. The site experiences an annual mean maximum daily temperature of 11 °C and a mean annual rainfall of 978.9 mm (Met Office 2020). A pair of Eurasian beavers from Tayside in Scotland were released into the enclosure on 17th April 2019. They were already a pair, and in June, the female gave birth to two kits. The beavers felled many trees throughout the enclosure, restructuring the forest. The largest felled tree was over 400 mm in diameter; many stumps are regrowing, and a more complex coppiced forest structure emerged.

Terrestrial laser scanning and iPad LiDAR surveys were used to monitor the changing size, shape and function of beaver dams through the compound and any beaver interaction with existing NFM structures. Repeat photography provided a visual analysis of these interactions. Ponded areas behind dams were quantified with photogrammetric surveys from uncrewed aerial vehicles. Sonar depth measurements provided depths to convert areas into approximate stored volume estimates. Basic hydraulic modelling was used to quantify the additional water storage expected in flood events of different return periods. Hydrological monitoring before and after beaver release directly examined the hydrological impact of the beaver structures. Water quality sensors, eDNA sampling, vegetation surveys and multiple species monitoring surveys sought to quantify the secondary effects of beaver release.

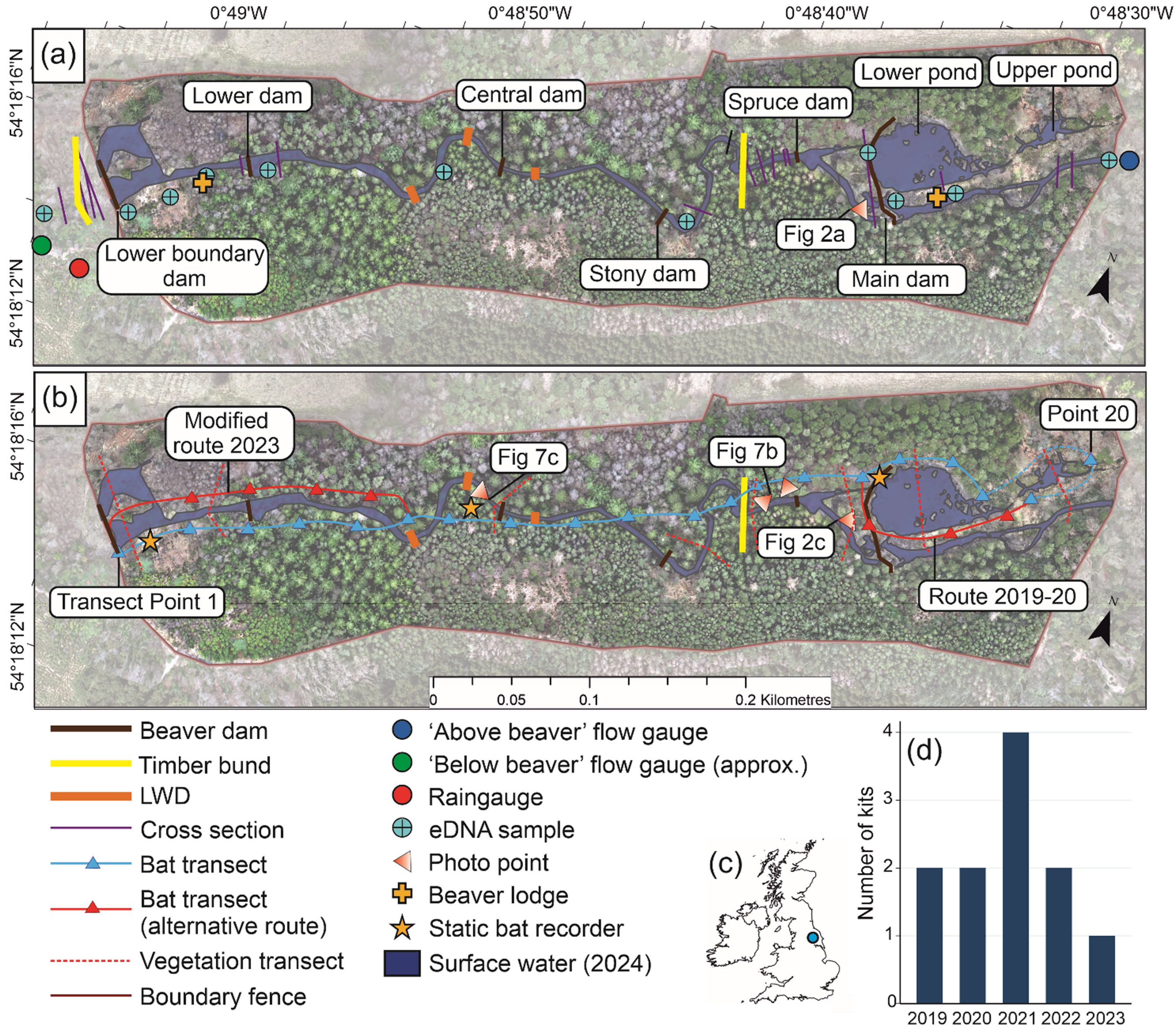

FIGURE 1 | (a) Map of beaver enclosure detailing the fence line, water surfaces (2024), gauge locations, dams, cross-section locations, beaver lodge locations, eDNA sample locations and some photo points relating to Figures. (b) Map detailing bat transects and sample points, static bat recorder locations, vegetation transects and photo points relating to Figures. (c) approximate location of the enclosure within the UK. (d) Number of beaver kits born during each year of the trial. TLS survey locations and locations of images in the Supplementary Information are shown in Figure S1.

2.1 | Uncrewed Aerial Vehicle (UAV) Photogrammetric Surveys

UAV surveys were undertaken primarily to quantify changes in surface water area over the course of the study. High-altitude (100 m) surveys were performed three times each year (spring, summer and winter), starting immediately following release in Spring 2019, with 30 mm ground-sampling resolution. A pre-release UAV survey was aborted due to unsafe weather. Additional lower-altitude (~50 m) surveys focused on the upper ponds were performed annually in early March (pixel size ~15 mm). Images with approximately 80% overlap and sidelap were collected, including oblique imagery to prevent doming effects in 3D reconstruction (James et al. 2017). Reflecting the multiple years over which surveys were undertaken and advancement in drone technology, surveys were undertaken with a range of UAVs, including DJI Mavic Pro (with 1/2.3 in. CMOS sensor), DJI Mavic Pro 2 (1 in. CMOS) or in later years DJI Mavic 3 Enterprise (4/3 CMOS) and DJI Phantom 4 (1 in. CMOS sensor) RTK UAVs connected with local base stations.

Imagery was processed in Agisoft Photoscan/Metashape Professional, using established Structure-from-Motion (SfM) methods to estimate 3D structure and viewing parameters jointly via a bundle adjustment algorithm (Smith et al. 2016; James et al. 2019) and subsequently processed to produce a dense 3D point cloud. In earlier surveys, reference data were provided via a network of targets distributed throughout the survey area. The 3D coordinate of each of these targets was measured by a Leica Viva reflectorless Total Station, measured to an accuracy of <5 mm. These targets were visible in the UAV imagery and used to georeference and provide a reconstruction error of the SfM-derived models (between 9 and 29 mm for the detailed pond surveys). From 2023 onwards, RTK UAVs were connected to a GPS base station to provide accurate GPS coordinates of the imagery. This 'direct georeferencing' method is slightly less accurate (~24 mm error in 2023); however, no major differences were reported when the two methods were tested in parallel in 2023. All surveys were georeferenced to the 2023 UAV survey, with georeferencing errors < 25 mm. Orthophotomosaics (10–20 mm resolution for the pond surveys) were created and used for manual delineation of water surface outlines. Whilst these were within centimetre-scale accuracy, for the more exposed upper enclosure ponds, there was a higher degree of uncertainty in forested areas, though fewer areas of open water were found at those locations. Water surface areas for the upper ponds were calculated within a consistent bounding box in each year. Acknowledging uncertainty in water areas under tree coverage, estimates of total surface water area and total volume over the site were made in three different years (i.e., not just that stored behind dams) during base flow conditions.

2.2 | Terrestrial Laser Scanning (TLS) Surveys

Three-dimensional surveys using a Riegl VZ-1000 Terrestrial Laser Scanner (TLS) provided fine details of beaver construction activities (dams, lodges, canals, pools), facilitating investigation of beaver construction structural diversity in response to local geomorphic, hydrological and resource availability controls. The VZ-1000 has a manufacturer-stated precision of 5 mm and accuracy of 8 mm. It acquired surface returns at 122,000 points per second with a point resolution of 3–4 mm at 10 m spacing. In practice, TLS surveys were limited by the multiple obstructions present in the beaver enclosure (i.e., trees, shrubs, branches), which created occlusions (i.e., shadows) in the point cloud behind the object. To mitigate this effect, multiple scans were conducted at each site and later merged together using a network of at least three coincident Leica 0.15 m diameter targets, which reduced this occlusion.

In 2019, prior to the beaver release, four TLS surveys were undertaken at separate locations in the enclosure, each comprising three scans. One of these was fortuitously located within the location of subsequent main beaver dam construction. This site became the focus of annual TLS surveys (2019–2025). All TLS surveys were undertaken in the first 2 weeks of March for consistency and minimal vegetation conditions. The mean registration error of scans was 3.87 mm (with a standard deviation of 1.91 mm), and errors were < 8 mm. Surveys were used to extract accurate estimates of water level changes in the main upstream pond and river adjacent to the main dam, each using an average of five-point samples. The height and topographic profile of this main dam were also extracted each year. Owing to the subaerial nature of the survey data and occlusions at the upstream side of the dam, dam height was measured from the dam crest to the point of submergence downstream. As detailed by Ronnquist (2021), this is a dynamic property that may underestimate the full dam height and does not capture variations in hydraulic head from upstream level fluctuations. The profile was taken along the centre line using a 100 mm width filter and summarising returned points within 10 mm elevation bins.

2.3 | Mobile LiDAR Surveys

As survey technology developed over the trial period, additional survey opportunities became available. In 2020, Apple released a LiDAR sensor built into an iPad Pro, equipped with a global navigation satellite system (GNSS) receiver and an inertial measurement unit (IMU) with a magnetometer to obtain orientation data. The main advantage of beaver enclosure surveys is that the device acts as a portable and mobile laser scanner, enabling full 3D point data of beaver dams to be extracted with minimal occlusion effects. Spreafico et al. (2021) suggest that it is suitable for centimetric precision projects (typically a 2 cm precision and 4 cm accuracy). Since the iPad LiDAR has not previously been deployed to survey beaver dams, we tested this functionality during surveys of 2024 and 2025. Using the SiteScape application, each dam was surveyed in detail, ensuring systematic coverage of each dam structure. Physically accessing parts of the dams was difficult as the stated maximum operational range of the iPad LiDAR sensor is < 5 m, albeit on high albedo surfaces. Previous field tests have found this to be < 3 m (Tavani et al. 2022), and the range obtained on lower portions of beaver dams was < 1 m when surveying dark, wet wood.

2.4 | Bathymetric Data

To supplement the above-water surveys and provide an approximate measurement of water depth, in March 2024, a Deeper CHIRP+ 2 sonar was used to survey depths of several beaver ponds in the enclosure. Whilst the GPS sensor is not sufficiently accurate to provide precise locations (Bandini et al. 2023), the depth sensors of such 'off-the-shelf' fish finders can provide approximate water body depths, often to within 5% of the true depth (Bradbury et al. 2023). The sonar was suspended from a telescopic pole and systematically moved across three water bodies. The point density of the main pond was 0.4 points m^{-2}; other depth surveys had a higher point density. However, owing to willow scrub in the main pond, points were not evenly distributed and should be interpreted with caution. The ponds were unsafe to traverse for more reliable depth measurement (e.g., Westbrook et al. 2020) or to create a DEM (e.g., Karran et al. 2017). These depth measurements should be treated with caution, especially when coupled with observations of water surface area, as they only provide an approximate indicator of storage volumes.

2.5 | Repeat Photography

A large number of images of the enclosure were taken prior to beaver activity. These were subsequently used for image comparison with annual repeats of images that were close to beaver activity sites, taken manually. Repeat images provide more qualitative but nevertheless rich visual indications of beaver structural changes to the enclosure.

2.6 | Hydrological Monitoring (Water Quantity and Quality)

Flows through Sutherland Beck were monitored at two locations, immediately upstream and downstream of the beaver enclosure (Figure 1a). At these locations, discharge was measured using an area-velocity flow meter (Nivus NivuFlow Mobile 750), checked against level data from in situ pressure transducers (MX2001 or U20L, HOBO ONSET or InSitu Rugged Troll 100) located within a stilling well. These were replaced with new level sensors (InSitu Rugged Troll 100) in December 2022. Barometric sensors were installed on site to correct level sensors for air pressure variations. Turbidity at each gauge location was continuously monitored using In Situ Aqua Troll 600 multi-parameter sondes, which were also configured to measure conductivity, temperature, dissolved oxygen and pH. All sensors collected data on a 15 min time step.

Baseline monitoring began in December 2018 and continued after beaver release (April 2019) until February 2024. Initially, this enabled a 'before–after' experimental design to quantify beaver baseline hydrological impact (Phase One); however, after 2022, the growing discrepancy between 5 months of pre-beaver monitoring and multiple years post-beaver required a shift in analysis owing to the much larger number and wider range of magnitude of events recorded in the longer post-release monitoring. Thus, from 2022 onwards, we also present a control–impact experimental design, with the upstream and downstream gauges respectively presented as 'control' and 'impact' sites (Phase Two). This analysis updates the previous multi-site analysis of Puttock et al. (2021) to encompass the entire trial period. Discharge percentiles are calculated from these records, particularly Q95 (low flows, exceeded 95% of the time), Q66, Q33 and Q5 (high flows, exceeded just 5% of the time). Q2 was also used to visualise the impact on the very largest events in the record. In addition to the widely used Q5 and Q95 high and low flow metrics (Puttock et al. 2021; Graham et al. 2022), the Q33 and Q66 were used for R2FDC, which analyses the slope of the flow duration curve, with a less steep slope indicating a less flashy flow regime (Addor et al. 2018; Ochoa-Tocachi et al. 2016).

A tipping-bucket rain gauge (RG3M, HOBO ONSET) was placed at the downstream enclosure boundary; however, given that a single-point rain gauge is typically non-representative in forested catchments (Younger et al. 2009; Zeng et al. 2018) to complement these point data, we downloaded NIMROD gridded rainfall radar data (Met Office 2003) at a 5-min temporal resolution and 1 km spatial resolution, extracted over the contributing catchment area. Total rainfall was then converted to mean rainfall rate, pre-processed for quality control (i.e., cleaned of noise and anomalous observations) and aggregated to 15-min time-steps to align with flow data (using the R exactextractr package; Bastion 2020). The extraction of rainfall–runoff events and corresponding metrics was undertaken using a semi-automated rules-based approach for the identification and pairing of rainfall and flow/stage geometries from the 15-min flow and rainfall timeseries (Ladson et al. 2013; Puttock et al. 2017). Stormflow was estimated by implementing flow separation on the time series to create event windows of elevated flow and rainfall (Ladson et al. 2013) with analysis performed in R v3.6.3. (R Core Team 2020). These are used to extract hydrological and rainfall information for a given storm event (Deasy et al. 2009; Glendell et al. 2014; Ladson et al. 2013). Full code for this analysis can be accessed at https://github.com/exeter-creww/Combined_Beaver_Hydro.

Statistical analysis was undertaken to test the following hypotheses: (1) beaver dams attenuate flow, reducing peak flows and increasing base flows; and (2) beaver dams slow and filter water, leading to reduced turbidity and improvements in other water quality metrics. Before–after analysis was undertaken on data pre- and post-beaver introduction and impact at the site. Control–impact analysis was undertaken using the inflow to the site as a non-beaver impacted dataset and the outflow to the site as a beaver impacted dataset. Hydrological data from storm events is non-normally distributed and, as such, all statistical analyses were undertaken using appropriate tests, either non-parametric or generalised linear models (GLM). Statistical significance for differences between pre- and post-intervention datasets was determined using the non-parametric Wilcoxon test. Given the large number of data points in the water quality data ($n > 50{,}000$ in all cases), differences in water quality variables upstream and downstream of the dam were also assessed using effect size, calculated as Cohen's d (using the "effsize" R package), which is the difference in group means divided by the average of their pooled standard deviation (Cohen 1988). Cohen's d is defined as the difference in group means divided by the pooled standard deviation (Cohen 1988) and was used here to quantify the magnitude of differences between locations, with values > 0.5 interpreted as indicating medium or greater effect sizes.

Direct comparison of hydrological metrics pre- and post-beaver provides an indication of beaver impact. However, this does not consider the amount of rainfall. As in Puttock et al. (2021), we therefore used GLMs, with a Gamma error distribution and identity link functions, where event rainfall is the control variable, event peak discharge is the response variable and beaver presence is considered as an additive explanatory variable. GLMs were chosen as they can handle non-normally distributed response variables (Dunn and Smyth 2018). This approach can also handle unbalanced sample sizes as GLMs do not require equal group sizes (Venables and Ripley 2002; Warton et al. 2016; Dunn and Smyth 2018). Two further considerations when dealing with unequal group sizes are relevant here: (i) the power of the model is limited by the size of the smallest group (Shaw and Mitchell-Olds 1993) and (ii) care should be taken when selecting a model and interpreting its results from an unbalanced design to ensure the hypothesis may be addressed (Hector et al. 2010; Warton et al. 2016). For (i), we acknowledge that before–after analysis used different sample sizes and also present our control–impact analysis, which used the same sample present to give a greater strength to findings. For (ii), imbalance is a greater problem with sample sizes smaller than those presented here (Warton et al. 2016), and any issues can be identified during model evaluation with visual diagnostic plots. This was undertaken using the 'performance' package in R (Lüdecke et al. 2021).

As in Puttock et al. (2021), estimated marginal means (i.e., adjusted or least-squares means), along with associated standard errors, were calculated for GLM results to compare differences in mean peak flows before and after beaver, over different hydrological seasons, and, where the above-beaver control site is used, between control and impacted (below beaver site outflow) sites. Estimated marginal means are useful for interpreting the outputs of regression analysis where the difference between, and or the effect of, factor levels is of interest and are designed to handle factor levels of different sizes by adding equal weight to each group (Castorani et al. 2018; Piepho and Edmondson 2018).

2.7 | Hydraulic Modelling

The existence of pre-release (2014) channel cross-sections offered the opportunity for comparative 1D hydraulic modelling to estimate the static water storage capacity of the site. Whilst more realistic 2D approaches are sometimes applied (e.g., Neumayer et al. 2020), these remain relatively rare. We restrict our modelling aims to estimating static water storage being held behind dams in steady state flows. The chosen approach matches both data availability and the study aim. However, 1D models introduce some uncertainty, as the full range of dam flow types cannot be represented (see Woo and Waddington 1990; Ronnquist and Westbrook 2021; Aguirre et al. 2024, and the discussion below). Results should thus be treated with caution.

To directly evaluate the impact of different dam structures on local water storage, a HEC-RAS (1-D) hydraulic model was established over the study reach to examine the impact of human-made structures installed along the beck as part of the 'Slowing the Flow' project (https://www.forestresearch.gov.uk/research/slowing-the-flow-at-pickering/). Modelling was repeated in both 2014 and 2024 to examine water storage changes in the installed structures (both installed large timber bunds and three smaller LWD within the enclosure; Figure 1a) and also the impact of subsequent beaver dams on total storage (of which four existed at the time of the 2024 survey). Both engineered bund structures were constructed by horizontally stacking logs against existing trees or driven timber posts, forming a robust timber wall with a maximum height of 1.5 m and extending into half the channel's frontal area to leave normal or low flows unimpeded. The upstream timber bund was 57.5 m wide, whilst the downstream bund was slightly below the beaver compound and was 16.5 m wide (Figure 1). Topographic data were obtained via 25 surveyed channel cross-sections supplemented with 1 m resolution LiDAR (Figure 1a). Manning's n values of 0.05 and 0.04 were adopted for the floodplain and channel, respectively, following Chow (1959). The location, size and characteristics of all dams were surveyed as part of the river geometry (height, length, width, hydraulic characteristics). The measured freeboard of beaver dams ranged between 0.2 and 0.4 m to accommodate increased water levels during high-flow events.

The hydrological effects of large wood in hydraulic models are commonly represented via roughness adjustment (Addy and Wilkinson 2019). However, owing to their channel-spanning nature at the site, dams were instead treated hydraulically as bridges, allowing determination of the exact proportion of the channel cross-section to be blocked to simulate their effect on flows. HEC-RAS bridge routines handle flow through and over structures that constrict waterways and induce energy losses, effectively mimicking how bunds obstruct flow and lead to overtopping during high water events. Minor gaps in the bunds could not be explicitly represented in the hydraulic model; however, only a negligible volume of water was lost through these small openings compared with the substantial volume impounded behind the structures. This approach allows for the effective assessment of dam flood storage and attenuation capabilities by accurately capturing backwater effects, overtopping and energy losses. With the majority of all dam structures at the site being crest-regulated at high flows, we present uncertainties in static water storage of 10% around the modelled value, reflecting the uncertainty in pond depth reported by Hart et al. (2025) when modelling such flows in a flume. Steady-state flow simulations were conducted on a range of flow conditions, from baseflow conditions and observed flood events, to design flows using the Flood Estimation Handbook (FEH) with a range of return periods up to 100 years.

2.8 | Environmental DNA (eDNA) Sampling

eDNA detected within a waterbody reflects the aquatic and semi-aquatic species living within it. Additionally, any terrestrial species that interact directly with the water body (e.g., through drinking, urinating; Harper et al. 2019) can be detected as well as animals living in the surrounding environment whose eDNA is transported via surface run-off and ephemeral flows after rainfall. eDNA metabarcoding of samples from a waterbody is therefore a convenient and effective way to describe the wider biodiversity in a given area (Sales et al. 2020; Broadhurst et al. 2021; Lyet et al. 2021; Mena et al. 2021). In May 2022, 10 water samples were collected within the beaver enclosure, moving in an upstream direction to avoid contamination (Figure 1a). For comparison, a further ten samples were collected from the adjacent Pickering Beck (to act as pseudo-control), also within the wider DEFRA project, but with no beaver release (Table S1). Samples were geographically distributed and included a range of flow rates (e.g., fast-flowing riffles and static ponds) with a focus on beaver dams and ponds. One sample was collected from the enclosure inflow immediately upstream of the fence, to sample the fauna present in the upstream catchment. For each sample, 2 L of water was collected in a sealable bag. Samples were then filtered on site using 0.45 μm PVDF Sterivex filters (Millipore, UK). Filtering was stopped when filters clogged, and the volume filtered was recorded, which ranged from 90 to 330 mL. A field blank of purified water was also filtered on-site.

DNA extraction was performed using the Mu-DNA method of Sellers et al. (2018) for water samples, with an inhibitor removal step, and lysis was performed inside the Sterivex capsule. DNA extracts were sequenced on an Illumina MiSeq, using primers that are specific to vertebrates, and amplified a 90–114 bp fragment of the mitochondrial 12S rRNA gene (12S-V5-F and 12S-V5-R; Riaz et al. 2011; Kelly et al. 2014) as described in Griffiths et al. (2023). Raw sequence reads were processed using a custom-built reproducible workflow, Tapirs (https://github.com/EvoHull/Tapirs) and a curated vertebrate reference database (https://github.com/HullUni-bioinformatics/Curated_reference_databases) as detailed in Griffiths et al. (2023). Sequence reads from domestic species and humans, and species with very low read counts were also removed from the final dataset (sea lamprey, *Petromyzon marinus*, 4 reads; red-legged partridge, *Alectoris rufa*, 19 reads; and dunnock, and *Prunella modularis*, 25 reads). Data were analysed in R version v4.2.1 (R Core Team 2022) using RStudio (Posit Team 2023). Species richness and Shannon diversity were estimated for each sample using the R package vegan (Oksanen et al. 2025). Non-metric multidimensional scaling (NMDS) with Jaccard dissimilarity (based on presence–absence), combined with pairwise PERMANOVA ("pairwiseAdonis" in vegan) was used to assess differences in community composition at Sutherland and Pickering Beck.

2.9 | Plant Abundance and Species Monitoring

Aquatic plant abundance and diversity were recorded using the DAFOR scale (Hill et al. 2005) in 2019, 2021 and 2023, with a comprehensive botanical survey conducted of any pond present at the time.

A grapnel was used whenever necessary to access submerged vegetation. Of specific interest was the abundance of *Lemna minor* (common duckweed), which was dominant prior to beaver introduction and shaded the water column, preventing submerged vegetation from developing. In addition, vegetation and terrestrial–aquatic transitions were captured using eight fixed transects cutting across the valley, and representative of the whole site (Figure 1b). Fixed 1 × 1 m quadrats were surveyed every 5 m along the transects, resulting in 102 fixed quadrats where the cover of vascular plant, bryophyte and tree canopy was estimated and assigned to either terrestrial, flowing water, standing water or swamp habitat types.

Directed monitoring of a number of species within the enclosure took place from 2019 to 2023. Acoustic bat surveys were undertaken using two methods: (i) a transect encompassing 20 recording points running the length of the enclosure sampled in June, July and August each year; and (ii) three static detectors located at fixed-points upstream and downstream ends and centre of the enclosure for seven nights of each month during the best weather window (Figure 1b). On the transects, five-minute recordings were made at each point using a Wildlife Acoustics EM3 full spectrum recorder with an external microphone mounted on a 50 cm aerial and commenced 10 min after sunset, providing a standardised protocol to capture peak bat emergence (Skalak et al. 2012). The upstream and downstream fixed points were fitted with Anabat Express machines, and recording was by Zero Crossing, whilst the central point was fitted with a Wildlife Acoustics SM4 full-spectrum machine with an external microphone on a 2 m pole. Results were analysed manually to species, a sample of which was sent to the British Trust for Ornithology (BTO) Pipeline for identification (https://www.bto.org/data/tools-products/acoustic-pipeline). For analysis purposes, all Myotis (mouse-eared bats) were grouped together. Multiple passes within a single audio file were only counted as a single bat. Both the transects and static points had to be relocated slightly throughout the trial due to beaver activity.

Dragonfly and damselfly surveys also took place in 2018, 2021, 2022 and 2023, yielding species counts each year. Monthly volunteer surveys were made in June, July and August each year in suitable weather. Species, sex and behaviour were recorded on each visit. For small mammals, 100 Longworth live traps (Chitty and Kempson 1949) were placed in five locations covering a variety of habitats across the enclosure, baited with wheat, peanuts, sunflower seeds, carrots and blowfly pupae, with a ball of hay for bedding. Traps were set for two nights each September, though they had to be relocated slightly over the trial duration to avoid flooded areas. Twelve camera traps were installed and moved regularly through the enclosure to monitor beaver behaviour during the trial. These were also used to analyse otter populations in the enclosure, with the frequency of manually confirmed positive otter sightings in footage calculated (2019–2024). A breeding bird survey following BTO standard methods (BTO 2025) was undertaken between March and June in 2020 and 2023; six visits and a further night visit were undertaken each time, with transects walked through the site and bird activity recorded. Opportunistic surveys of amphibians took place over the course of the trial.

3 | Results

3.1 | Beaver Population and Site Structural Changes

Following the introduction of a pair of Eurasian beavers from Tayside, Scotland, in April 2019, 11 kits were born in the enclosure (Figure 1d). To manage the population, four older juveniles were relocated to other projects across England (two in both 2022 and 2023). Camera trap footage shows that the beavers lived in an extended family group with just one dominant breeding pair. The beavers built four large lodges: the initial lodge at the upstream end, a second at the downstream end in 2022 and more recently two further lodges in the centre. All beavers were observed using the whole site.

For the first 3 years, dam building and activity were focused around the ornamental ponds at the upstream section of the enclosure (see Figures S1–S4). Figure 2a displays repeat annual images of this dam alongside the changing dam height and profile each year (Figures 2c–e), derived from TLS data. A dam of ~1 m in height was constructed in the river channel in 2019 to raise water levels for an underwater entrance to a burrow in the true-right bank. The dam steepened and almost doubled in height by 2021 and was extended across the floodplain at the downstream edge of the ponds, raising the water level to connect Sutherland Beck with the ornamental ponds (Figure 3a) and a second dam built slightly downstream in the main channel in 2022. This connection was eventually completed as measured the water bodies merged, and the pond level was raised by 0.74 m (Figure 3d). To this extent, the dam had developed into the largest beaver dam in England at over 70 m long and 2.52 m tall at the maximum height in the channel. The beavers split a large clump of irises from the middle of the ornamental pond into smaller clumps and 'planted' these along the dam by using them as dam-building material.

As Figure 2b shows, a partial dam breach event on 10th February 2024 resulted in a decrease in surface water levels from the peak (Figure 3d). Pond levels dropped gradually back to pre-release surface elevation and became disconnected from the river (Figure 3c). From UAV surveys, the surface area of this pond was monitored

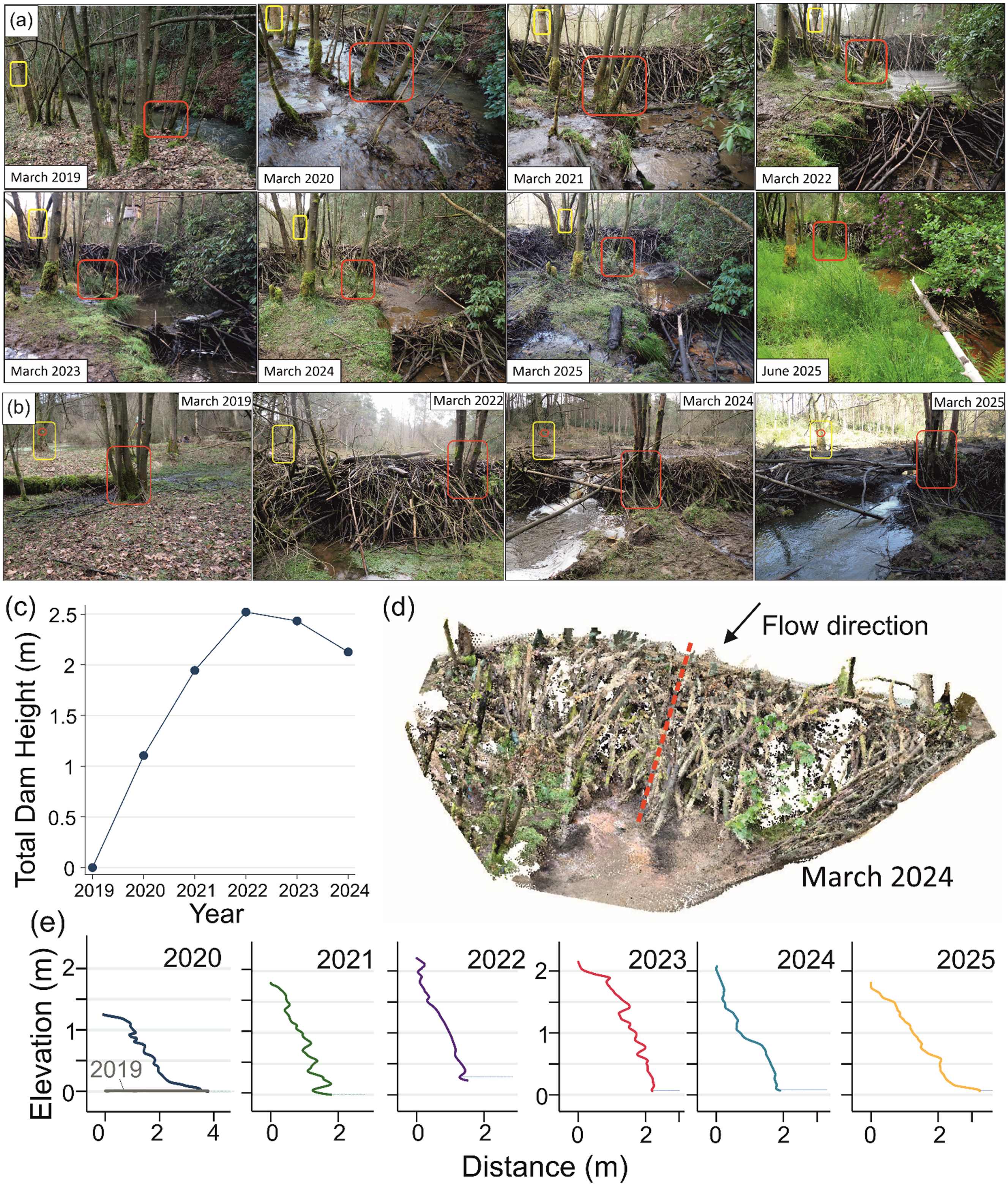

FIGURE 2 | Development of the first and largest beaver dam constructed in the enclosure. (a) Repeat fixed-point photography showing pre-beaver conditions (March 2019) and the subsequent growth of the dam in March each year. Summer conditions are displayed for June 2025; (b) repeat photography showing pre-release (March 2019), dam building (March 2022) and post-partial dam breach conditions (March 2024 and 2025). Features present in multiple images are indicated (c) changing total dam height, (d) 3D point cloud of main dam from March 2024 (from iPad LiDAR) with detailed profile located in red and (e) detailed profile of the dam in each year from TLS repeat surveys (downstream water height is indicated with a dashed line). See also Figures S2–S4.

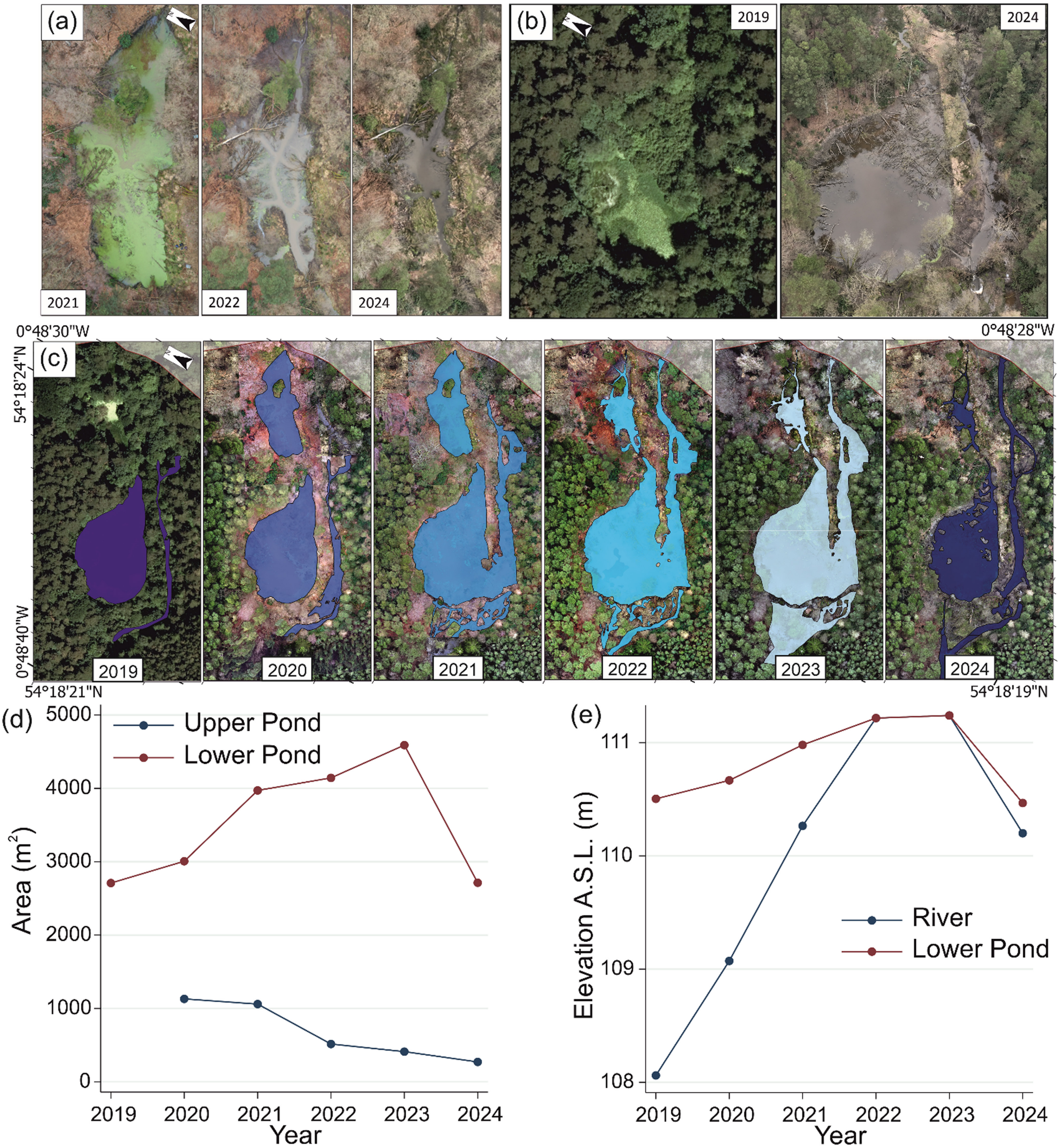

FIGURE 3 | Development of surface water bodies surrounding the ornamental ponds at the upstream end of the enclosure. (a) Changes in the upper pond noted between 2021 and 2024. (b) Comparison of pre-release (2019) and post-release (2024) imagery of the lower pond adjacent to the initial dam (pre-beaver 2019 aerial imagery accessed via Getmapping Aerial Imagery as part of a University of Exeter Research Project via Edina Digimap 2024). (c) annual time series of changing surface water area (from detailed UAV surveys in March each year). (d) annual time series of surface water areas in both ponds. (e) changing water surface elevations of the lower pond and river.

annually (Figure 3e) which increased from 2709 m^2 in 2019 to 4589 m^2 at the peak in 2023 (a 70% increase in area), returning to approximately pre-beaver extents in 2024. Beavers removed the willow scrub that was taking over this pond, leaving a much more open pond (Figure 3b). The sonar survey in 2024 yielded a median water depth of 0.76 m (ranging up to 1.11 m). The 2024 water level was 0.77 m below the 2023 peak, suggesting a mean depth of 1.53 m pre-dam breach (assuming minimal sedimentation of the pond since the breach) and a loss of approximately half the pond water depth in the breach event. The dam was not rebuilt or maintained by March 2025, and the dam profile became less steep compared with previous years (Figure 2e).

The upstream ornamental pond shows a contrasting trend (Figure 3a,d). Initially, the beavers blocked a leak with silt and horsetails, raising the water level by ~0.60 m and coppicing trees on the bank. In autumn 2022, the beavers dug a channel to drain water from the top pond, which decreased from a maximum of 1130 m^2 in 2020 to just 271 m^2 in 2024 (just 24% of the 2020 area). As seen in Figure 3a, this left a mosaic of water and marsh habitat with deeper channels and pools evident, along with a range of aquatic plants on the banks.

As the beaver population increased, signs of activity moved downstream, initially (in 2023) to a second dam built 50 m downstream near the dense spruce plantation (Table 1, Figure S5). Owing to the stony riverbed at this location, the dam had a foundation of stones, topped with sticks and earth and stood at a maximum height of 1.27 m. Water was stored behind and forced onto the floodplain on the true left bank at high flows, where beavers ring-barked a number of spruces. By March 2025, this 'Spruce dam' had also been partially breached as beaver activity moved further downstream (Figure 4), though signs of rebuilding were observed in June 2025 (Figure S5).

Beaver activity began at the bottom of the site in summer 2023 (Figure S6). This initially involved a dam incorporating pre-existing vertical posts put in to collect debris and protect the outflow grill ('lower boundary dam'). Here, the beavers diverted the course of the river, connecting it with the floodplain and refilling an old oxbow lake. The dam here is 24 m wide with a maximum height of 1.12 m in the channel and only ~0.20 m outside of the channel. The median water depth measured in the 2024 sonar survey was 1.01 m, though a second peak in the recorded depth distribution was observed at 0.75 m, indicating the floodplain and a deeper submerged channel. In 2024, a fourth dam ('Lower dam') was added, ~80 m upstream of the lower boundary, comprising a large structure at 1.86 m tall in the channel and 11.3 m in width. Here, the median water depth from sonar was 1.33 m, 0.6 m above that measured in the river immediately downstream of the dam. Shortly after the trial period, a further two dams were added in the centre of the enclosure (Table 1) suggesting further beaver expansion of water storage capacity (Figure 4). Flow types were observed for each dam, following the classification of Ronnquist and Westbrook (2021), building on the earlier work of Woo and Waddington (1990) (see Table 1). As identified by Aguirre et al. (2024), flow types are temporally variable; at baseflows, many dams were initially of the throughflow type.

From UAV surveys and depth estimates from sonar surveys, a mean depth of 0.70 m was used to convert areas to water volumes. This represents a conservative estimate given depths recorded on the site using sonar and agrees with typical values used and observed in previous research (Brazier et al. 2021; Bradbury et al. 2023). There is a high degree of spatial and temporal variability in pond depth and, therefore, low confidence in the accuracy of these figures. In 2020, 2022 and 2024, the measured surface water area was 5402, 5981 and 5850 m^2, respectively, corresponding to estimated volumes of 3781, 4187 and 4095 m^3. The real increase in water storage within the site is likely to be much greater due to raised local water tables due to damming.

3.2 | Hydrology

The Phase One (104 events) post-beaver period saw more rainfall and more intense rainstorm events than pre-release; the

TABLE 1 | Summary of beaver dams within the enclosure.

Beaver dam	Year built	Maximum height (m)	Maximum width (m)	Notes, including flow state (Ronnquist and Westbrook 2021; Woo and Waddington 1990)
Main dam	2019/20/21	2.52	70	Covered in vegetation. Extends to include the boundary of the ornamental pond. Sideflow onto floodplain until 2024 when breached. Gapflow since 2024. Breach widened to 3.5 m by 2025 with repairs in progress.
Spruce dam	2023	1.27	14.7	Stone foundation. Sideflow but also onto floodplain. Gapflow after breach in 2025 (1.3 m). Partially rebuilt by June.
Stony dam	2025	0.62	2.5	Stone core shallow gradient dam. Underflow.
Central dam	2024/25	0.60	4.0	Gapflow at true right edge of dam, water pushed onto floodplain in higher flows.
Lower dam	2023/24	1.86	11.3	Throughflow in baseflows but pushes water onto the true left floodplain in high flows, where a small secondary dam holds back the water. Throughflow is preferentially on the true left.
Lower boundary dam	2022/23	1.12	24	Utilises pre-existing wooden piles in channel. Expands onto floodplain where it is only < 0.20 m high. Gapflow with limited throughflow (mixed type).

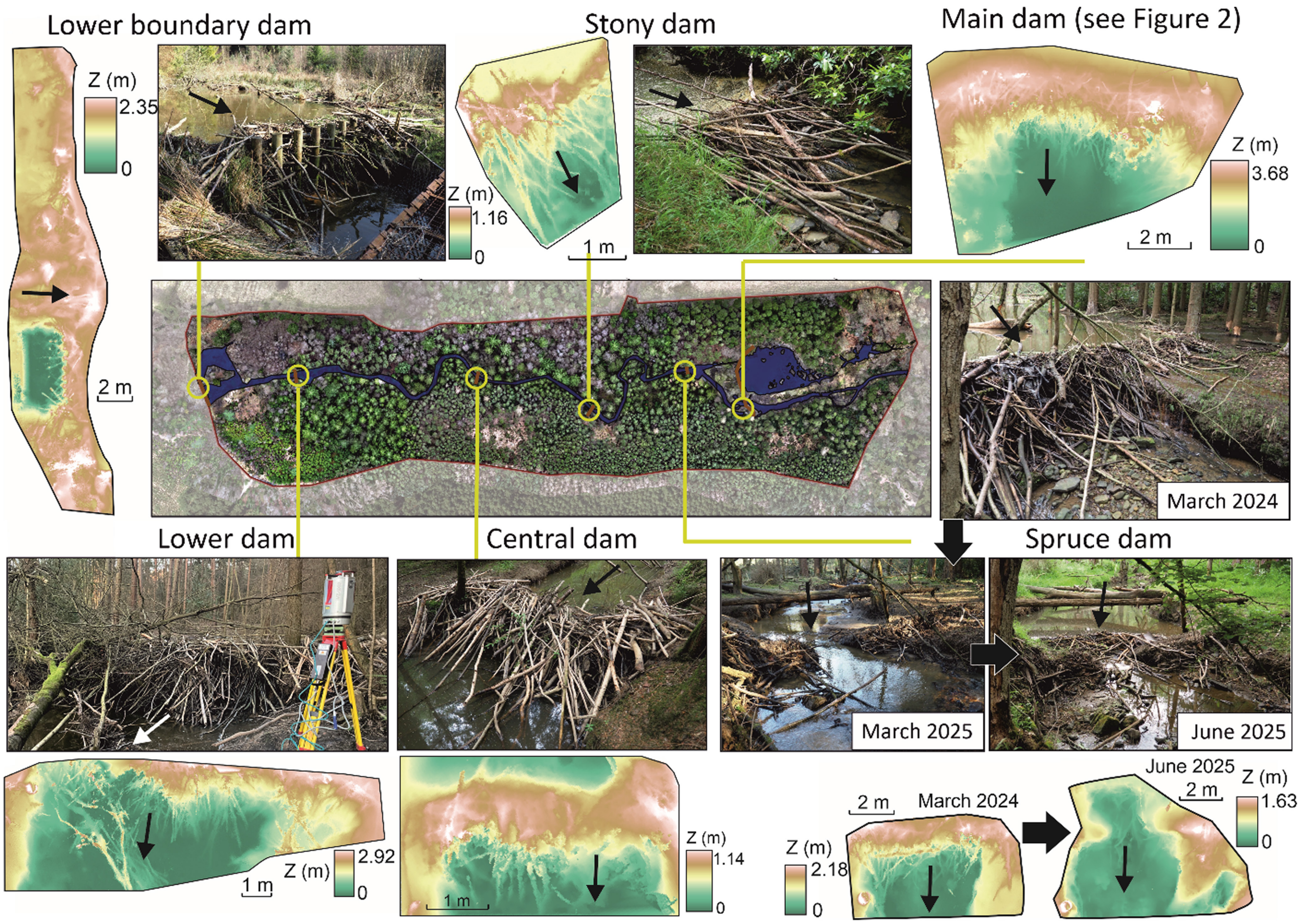

FIGURE 4 | Summary of beaver dams in the enclosure, including DEMs derived from LiDAR data (from 2025, in local coordinates with trees virtually chopped to stumps within the survey area). For the Spruce dam, repeat images from March 2024 and March/June 2025 are displayed (alongside DEMs from the first and last of these) detailing the partial breaching and rebuilding of the dam. Arrows on images and DEMs indicate the flow direction.

pre-beaver period had a mean event rainfall of 7.5 ± 7.1 mm (24.9 mm maximum) in contrast to 14.1 ± 9.04 mm (46.7 mm maximum) in the post-release period (Figure 5a). Despite increased rainfall, Q5 during the post-release period decreased from the pre-beaver value of 0.643 m^3s^{-1} to 0.395 m^3s^{-1} (Figure 5a). Whilst the post-release dataset saw larger storm events, there was an attenuated streamflow response to these rainstorms (i.e., a lower peak discharge for a given storm size).

To normalise for the impact of rainfall, GLM analysis (Figure 5b) was undertaken for all event data across the sites with beaver and rainfall as an additive variable (see Supplementary Information, Table S2). GLM analysis reinforces that beavers are reducing peak flows. As shown by marginal means, peak flow showed an overall slightly reduced response to rainfall across all sites and reduced peak flows by 5% (from 0.685 m^3s^{-1} prior to beaver release to 0.651 m^3s^{-1} following release). Across the events, rainfall had a positive effect on increasing peak flow (overall an increase of 0.023 m^3s^{-1} per mm of rainfall) whilst beaver presence had the opposite effect, reducing peak flow by 0.034 m^3s^{-1}. Flow attenuation persisted for large events, as GLM analysis on a > Q5 subset of events demonstrated a reducing impact of beaver upon peak flows (0.025 m^3s^{-1}). Marginal means and estimates showed that, even for this subset of the largest events monitored, there was still a reduction in peak flow downstream by 2% (estimated marginal mean peak flows of 1.015 m^3s^{-1} prior to beaver release and 0.993 m^3s^{-1} following release). This modest flow attenuation was nevertheless achieved in a much wetter post-release monitoring period and despite the multiple NFM dams at the site, which already contributed to reductions in peak flow (Nisbet et al. 2015).

The control–impact analysis (above versus below beaver) of Phase Two considers the continuous 15-min discharge data from the 6th of December 2022 until 28th February 2024 (89 events). There was a 46.6% reduction of median peak flows, from 1.16 m^3s^{-1} above the enclosure to 0.62 m^3s^{-1} below the beaver enclosure, which was a statistically significant reduction ($p < 0.01$) (Figure 6a). A reduction was observed for the subset of Q5 exceedance events (i.e., larger events), although this was not statistically significant ($p > 0.05$).

Comparison of the above and below enclosure hydrographs directly demonstrates both this attenuation of peak flows through the enclosure, but also the increased baseflows (Figure 6c) with a five-fold increase (417%) in mean Q95 (flow occurring 95% of the time) from 0.035 m^3s^{-1} at the inflow to 0.181 m^3s^{-1} at the outflow. Both effects are summarised in the flow duration

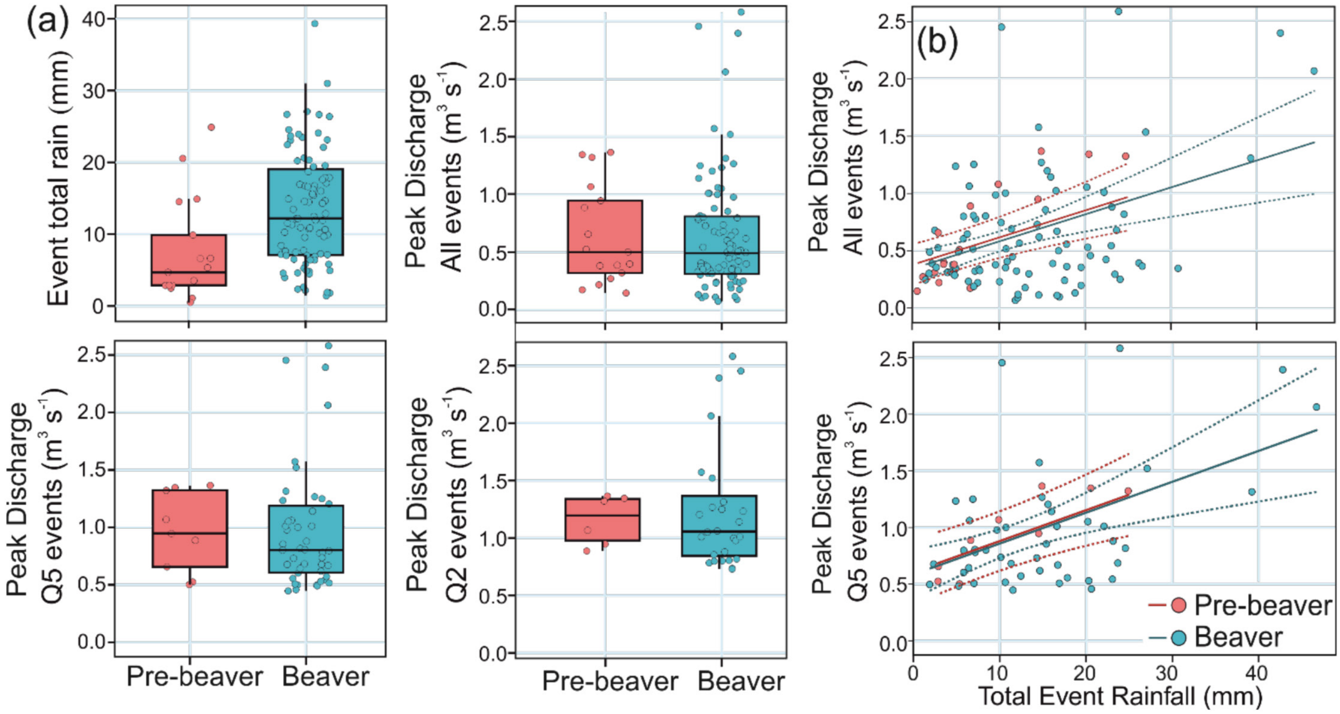

FIGURE 5 | 'Before–after' hydrological analysis of discharge at the downstream gauge below the beaver enclosure (Phase 1, 2019–2022). (a) Comparisons of event rainfall, event discharge and the event discharge of the largest flows (Q5 and Q2). (b) GLM analysis plotting peak flow against total event rainfall for all events and Q5 only. Full details of GLM models are presented in Table S2.

curves (Figure 6b), which display the percentage of time a given discharge was equalled or exceeded. The 'below beaver' gauge shows reduced high flow values (e.g., Q5) and increased low flow values (e.g., Q95) relative to the control site, indicating an overall attenuated hydrological flow regime. The slope of the 'below beaver' flow duration curve (between Q33 and Q66, using the R2FDC approach (Addor et al. 2018; Ochoa-Tocachi et al. 2016) is 0.28 versus 1.05 above the enclosure, indicating a much less flashy hydrological response.

3.3 | Hydraulic Modelling of Water Storage

Water storage volumes estimated from the steady-state hydraulic model are presented for a range of flows in Figure 7a. Results are separated by structure type (i.e., large timber bunds, smaller LWD and beaver dams) and do not include the final two beaver dams built after 2024 (Table 1). The survey of the timber bunds in 2024 shows a marked reduction in their flood storage capacity owing to degradation and channel erosion at the throttle point of the bunds. By 2024, timber bunds and LWD combined provided less water storage than beaver dams alone, for all but the largest 1 in 100-year return period flow. Figure 7c shows clear aggradation upstream of LWD in the enclosure, with the freeboard reducing from 0.93 m in 2019 (as measured with TLS) to a maximum of 0.52 m in 2025 (measured with iPad LiDAR), with considerable debris accumulation above that. Owing to their design and more limited freeboard, the beaver ponds' storage volumes are relatively static at ~2500 m^3 regardless of the flow event size (i.e., static water storage changes with return period are within uncertainty bounds), whereas the larger timber bunds are designed to let lower flows pass underneath. Whilst the beaver dams offer lower storage than the timber bunds did when originally installed, they have nevertheless approximately doubled the water storage volume of the site and more than mitigated the reduced storage potential of the degrading timber bunds. Indeed, the total volume of flood storage provided by the two timber bunds in their current condition, the three LWD and the four beaver dams exceeds that of the original timber bunds, across the range of modelled flood magnitudes (1 in 5 to 1 in 100-year floods).

3.4 | Water Quality

Wilcoxon tests revealed significant differences between upstream and downstream sites for all water quality variables. Turbidity was significantly higher at the enclosure inflow than below the enclosure ($p < 0.001$; Table 2, Figure 8a) and showed greater variability (interquartile range of 51.8 vs. 13.9 NTU). Median values of 13 NTUs 'above beaver' and 9 NTUs 'below beaver' reveal a 30.77% reduction. This downstream reduction was more pronounced (48%) in winter (October–March; 25 versus 13 NTU), suggesting higher sediment deposition in winter owing to in-stream structures. Conversely, in summer (April–September), turbidity was significantly (20%) higher at the outflow compared with the inflow (upstream and downstream median values of 5 and 6 NTU, respectively). In contrast, effect size, which is a more robust and meaningful measure for large samples (see Table 2), found only a small effect for turbidity (0.357), approaching a medium effect in winter (0.420).

Dissolved oxygen was significantly higher below the beaver enclosure, considering both the Wilcoxon tests and effect size, a high effect was especially pronounced in winter (0.906). pH was within the normal range for natural waters (slightly alkaline)

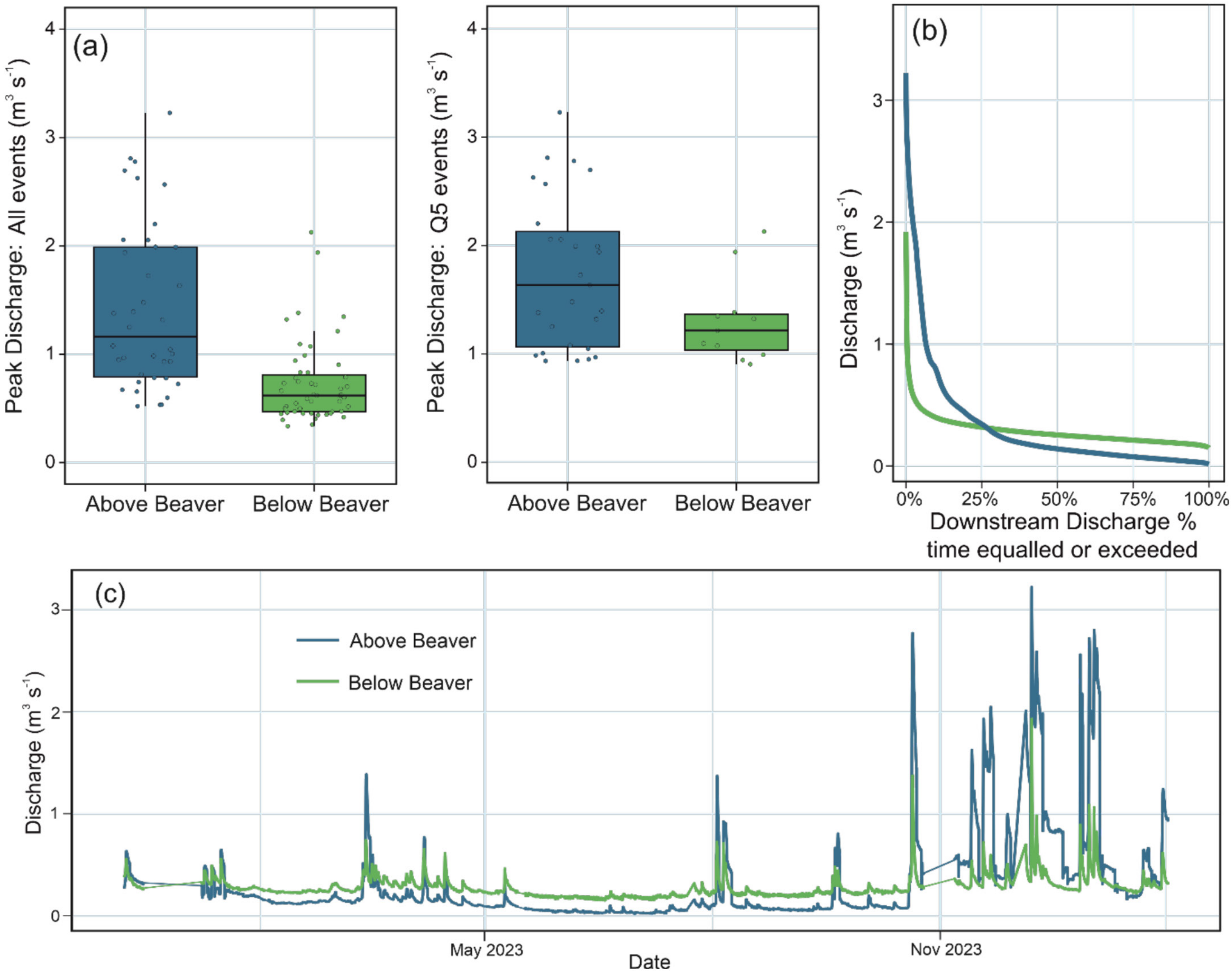

FIGURE 6 | 'Control–impact' hydrological analysis, comparing responses upstream and downstream of the beaver enclosure (Phase 2, 2022–2024). (a) Comparison of upstream/downstream peak discharges of all events and Q5 only. (b) Flow duration curves. (c) Extract from the discharge time series of both gauges.

and alongside specific conductivity showed small differences (effect size 0.336 and 0.126, respectively) between locations, with the latter showing a much greater range at the inflow, compared with the outflow below the enclosure (Figure 8e). In winter, pH was significantly higher and conductivity significantly lower below the beaver enclosure (using both statistics), with the conductivity difference being significantly reversed in summer. Water temperature was slightly lower at the outflow than the enclosure inflow, which was again pronounced in winter but reversed in summer, when downstream temperatures were higher. Temperature differences were significant using a Wilcoxon test, but not when using the effect size metric.

3.5 | Vegetation and Plant Diversity

On the vegetation transects, little change was recorded between 2019 and 2021, only reflecting the transition from terrestrial to standing water at the shore of the lower pond due to increased water levels. Going into 2023, transitions accelerated, resulting in 29 out of 102 fixed points being classified as wetland vegetation, including open waters and swamps, whilst there were only 12 in 2019. Most importantly, these transitions created increasing heterogeneity across the site (Figure 9a). Overall aquatic plant diversity increased over time in the ponds from 15 to 20 species (Figure 9b), despite the loss of two species. New colonisations included two species of *Potamogeton* (pondweeds), indicating a developing submerged vegetation and conditions suitable for recruitment. Duckweed diminished from being dominant to abundant using the DAFOR scale. Although duckweed also colonised newly created beaver ponds, it did not become dominant in these water bodies. The lower pond (Figure 3b) remained the most diverse over the period and hosted most species present at the site. However, the changes in water levels and beaver grazing resulted in the localised loss of emergent species such as *Sparganium erectum* (branched bur-reed) and *Potentilla palustris* (marsh cinquefoil), the latter not re-found anywhere at the site in 2023 or 2024.

3.6 | eDNA Analysis and Ecological Monitoring

Following quality control, one of the pseudo-control eDNA samples at Pickering Beck was removed due to very low read

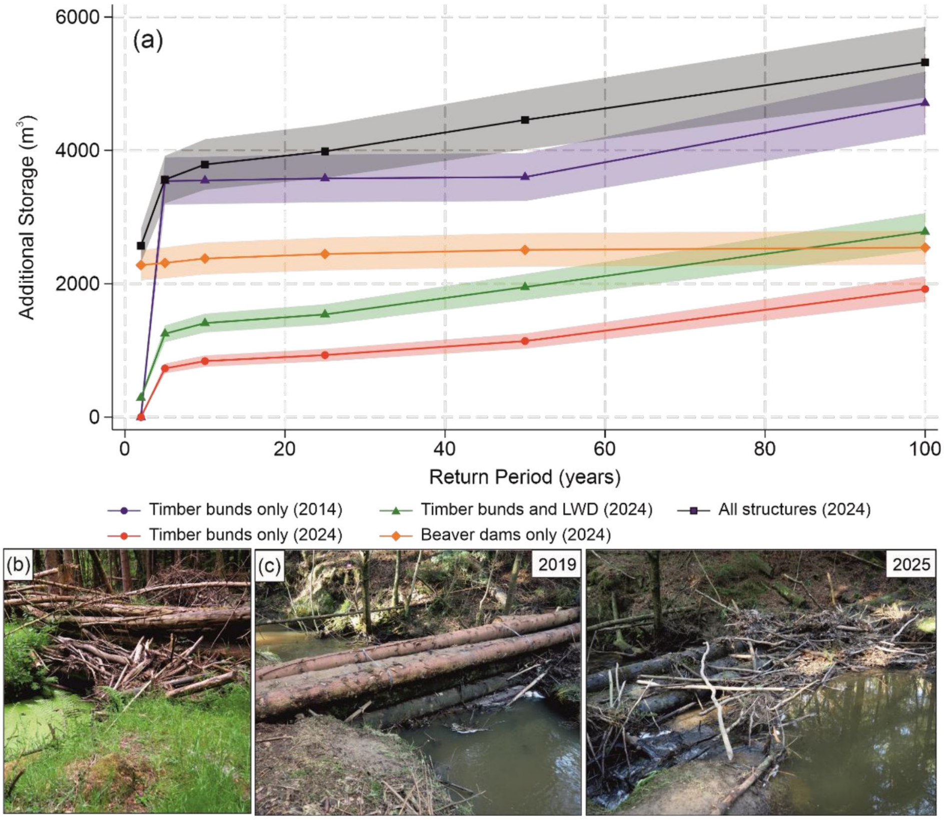

FIGURE 7 | (a) Modelled storm water storage in the beaver enclosure over a range of flow magnitudes up to a return period of 1 in 100 years. Results are separated by dam time with combinations included. Uncertainties of ±10% are shown with shaded areas. (b) An image indicating the deterioration in the large timber bund by June 2025. (c) Near complete aggradation upstream of LWD, with erosion around the true left of the dam and bypassing flow seen in the foreground.

count (2574 reads), and a final total of 707,349 sequence reads was obtained over 19 samples (average 37,229 reads per sample). Overall, 46 vertebrate taxa were detected in the combined Cropton (beaver-enclosure) and Pickering Beck (pseudo-control) samples (Table S3), of which 38 were assigned to species level, five taxa were assigned to genus level (*Columba*, *Fringilla*, *Regulus*, *Turdus* and *Apodemus)*, two to family level (*Anatidae* and *Corvidae)*, and one taxon to order level (*Passeriformes*). Thirty-nine taxa were detected in the Cropton samples, and 33 species were detected at Pickering. Four amphibians, 19 birds, nine fish and 14 mammals were detected.

Mean species richness per sample was 18.2 for Cropton and 16.5 for Pickering Beck, which was not a significant difference (Mann-Whitney *U* Test $W=57$, $p=0.140$) (Figure 10a). There was a clear difference in community composition between Cropton and Pickering Beck, based on NMDS (Figure 10b), and this structure is supported by PERMANOVA results (F 8.089, R^2 0.338, df 1, $p<0.001$; Figure 10b).

Nine fish species were detected in total, with six species detected at Cropton and seven detected at Pickering Beck. Brown trout (*Salmo trutta*), bullhead (*Cottus gobio*), river lamprey (*Lampetra fluviatilis*) and three-spined stickleback (*Gasterosteus aculeatus*) were detected at both sites. Tench (*Tinca tinca*) and common carp (*Cyprinus carpio*) were only detected at Cropton, whilst European eel (*Anguilla anguilla*), minnow (*Phoxinus phoxinus*) and stone loach (*Barbatula barbatula*) were only detected at Pickering.

Fourteen mammal species were detected in total, with 12 species detected at Cropton (including beaver), and 11 detected at Pickering Beck. Beaver eDNA was detected at all Cropton sites, apart from the sample just upstream of the enclosure. Wood mouse (*Apodemus sylvaticus*), bank vole (*Myodes glareolus*), brown rat (*Rattus norvegicus*), common shrew (*Sorex araneus*), field vole (*Microtus agrestis*), grey squirrel (*Sciurus carolinensis*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and water shrew (*Neomys fodiens*) were detected at both sites. Beaver, badger (*Meles meles*) and otter (*Lutra lutra*) were only detected at Cropton, whilst mole (*Talpa europaea*) and water vole (*Arvicola amphibius*) were only detected at Pickering. Camera traps showed a marked increase in otter footage, which more than trebled over the trial period to 2023 and almost trebled again in 2024 with a marked increase in activity (Figure 10c). This should be interpreted with some caution, as camera traps moved through the enclosure during the study, since their primary purpose was to monitor the beavers' health and well-being.

Wood mice were the most common small mammal captured in the Longworth surveys, with lesser numbers of bank voles, field voles and common shrews. However, the final mammal survey in 2024 trapped six species, with pygmy shrew (*Sorex*

TABLE 2 | Summary water quality statistics from the multi-parameter sondes for the period December 2019–February 2024. All parameter differences between the above and below beaver monitoring points were highly significant (Wilcoxon $p < 0.001$). Differences between locations using effect size are highlighted in bold where they are deemed to have a significant (medium) effect (> 0.5). SD = standard deviation.

WQ parameter	Above beaver			Below beaver			Effect size
	n	Median	SD	*n*	Median	SD	
All dates							
Turbidity (NTU)	139,118	13	887	139,086	9	46	0.357
Specific conductivity (μS/cm)	139,118	175	65	139,086	173	36	0.126
pH	139,045	7.33	0.40	139,086	7.45	0.27	0.336
Dissolved oxygen (mg/L)	139,118	9.5	3.5	139,086	10.2	1.5	**0.546**
Temperature (°C)	139,118	8.32	3.89	139,086	8.12	4.08	0.168
Winter (October–March)							
Turbidity (NTU)	80,195	25	1060	80,181	13	53	0.420
Specific conductivity (μS/cm)	80,196	173	38	80,181	158	25	**0.592**
pH	80,141	7.14	0.36	80,181	7.37	0.24	**0.771**
Dissolved oxygen (mg/L)	80,195	10.1	4.3	80,181	11.0	0.9	**0.906**
Temperature (°C)	80,195	5.95	2.45	80,181	5.63	2.51	0.138
Summer (April–September)							
Turbidity (NTU)	58,923	5	544	58,905	6	26	0.259
Specific conductivity (μS/cm)	58,923	184	89	58,905	203	34	**0.619**
pH	58,904	7.51	0.36	58,905	7.54	0.29	0.153
Dissolved oxygen (mg/L)	58,923	9.2	1.4	58,905	8.7	1.3	0.390
Temperature (°C)	58,923	12.51	3.11	58,905	12.95	2.89	0.092

minutus) and water shrew (*Neomys fodiens*) being added to the list, showing the highest species diversity of any of the annual mammal surveys. Notably observed small mammal activity included wood mice captured in 2022 along the downstream edge of the larger ornamental pond returning to the dam on release, rather than into the surrounding woodland, suggesting that mice are living in the dam structure. Also, in 2023, a released wood mouse ran across a dam into the woodland on the other side of the beck, indicating that they use the dams to expand their foraging area.

Nineteen bird taxa were detected in total in the eDNA sampling, with 17 detected at Cropton and 12 detected at Pickering Beck. In comparison, over the entire trial period, 49 species of birds were detected on the BTO surveys at Cropton. All of the bird taxa eDNA detected in the enclosure were also observed in the 2020 BTO bird survey at Cropton, with the exception of snow bunting. The BTO surveys and trail camera footage suggest a slow increase in birds associated with wetland habitats. In addition, BTO surveys observed Mandarin duck (*Aix galericulata*) in 2022 and 2023, and Water rail (*Rallus aquaticus*) became more regular in footage from 2022 onwards. Grey wagtail increased from one territory to two as beavers started building at the downstream end of the enclosure. There were just single records of moorhen and a pair of Greylag geese (*Anser anser*), whilst kingfisher (*Alcedo atthis*) are increasing late summer/autumn visitors. Meanwhile, there has been a decrease in great tit (*Parus major*) and chaffinch (*Fringilla coelebs*) territories, especially in the centre of the enclosure; however, this cannot be attributed to beaver activity, which was minimal in this location.

Four amphibian species were detected in eDNA samples, with common frog (*Rana temporaria*) and common toad (*Bufo bufo*) detected in every sample from both Cropton and Pickering. Palmate newt (*Lissotriton heleeticus*) was detected in all Cropton samples, and in all but three Pickering samples. By contrast, smooth newt (*Lissotriton vulgaris*) was only detected in Cropton (at just two sites, and with low read count). Pre-release amphibian surveys observed six clumps of spawn in the lower ornamental pond; the year after beaver release, the amount of spawn was countless, with frog and toad activity all around both ponds. Following this peak in 2019, levels stabilised at a much higher level than pre-release and across more locations. The first records of amphibian activity were recorded at the downstream end of the enclosure in 2023 (and later in the spring 2024 survey), coinciding with this location becoming the focus of beaver activity.

The pre-release survey of dragonflies and damselflies in 2018 yielded four species. By 2021, this had doubled to eight species and reached 12 by 2022. By the end of 2023, a total of 13 species had been recorded, of which at least 8 were considered breeding

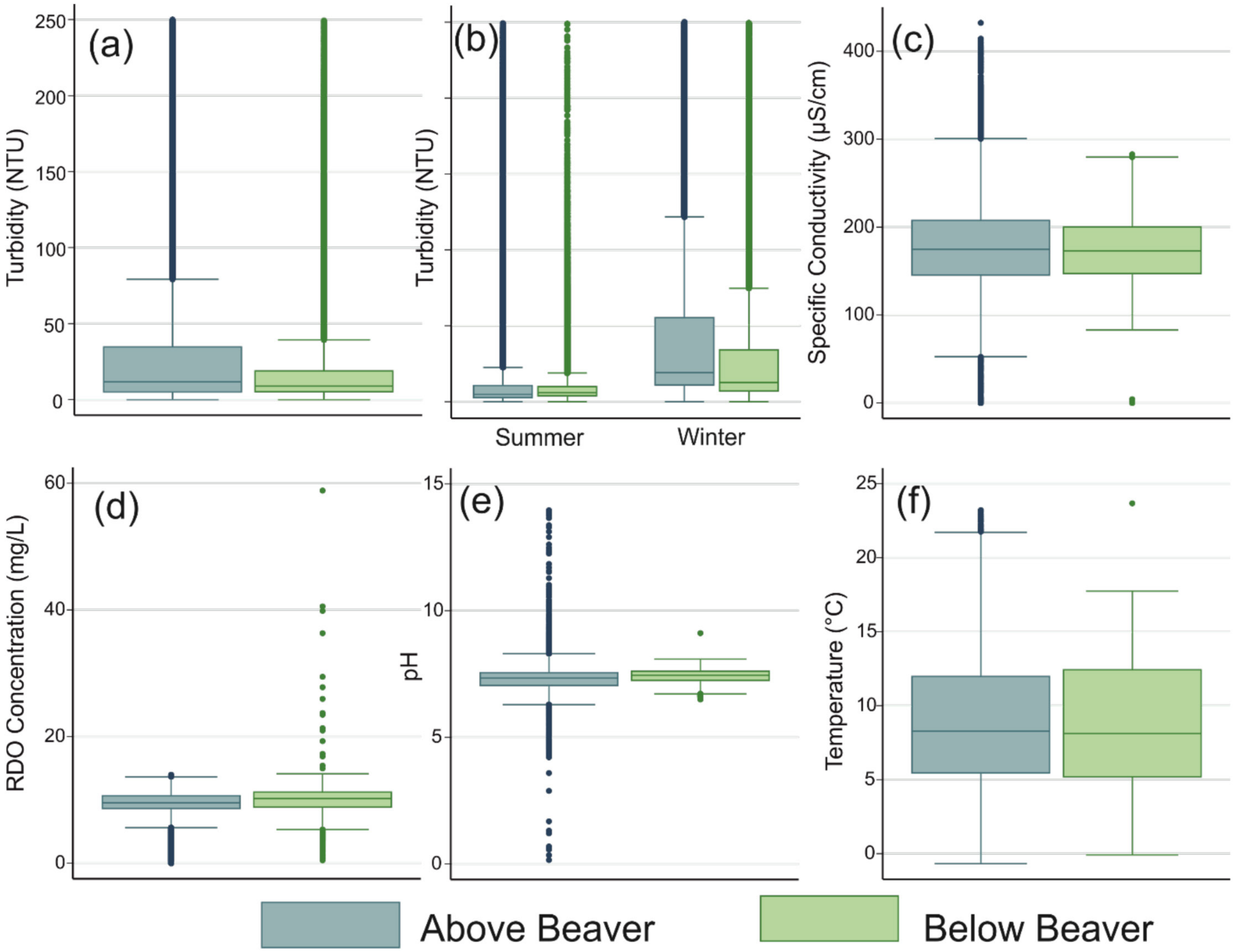

FIGURE 8 | Changes in water quality metrics recorded in the beaver enclosure, comparing upstream ('above beaver') and downstream 'below beaver' gauge records. (a) Turbidity. (b) Turbidity split into summer and winter periods. (c) Specific conductivity. (d) Dissolved oxygen. (e) pH. (e) Temperature. See Table 2 for details of sample sizes and significance tests.

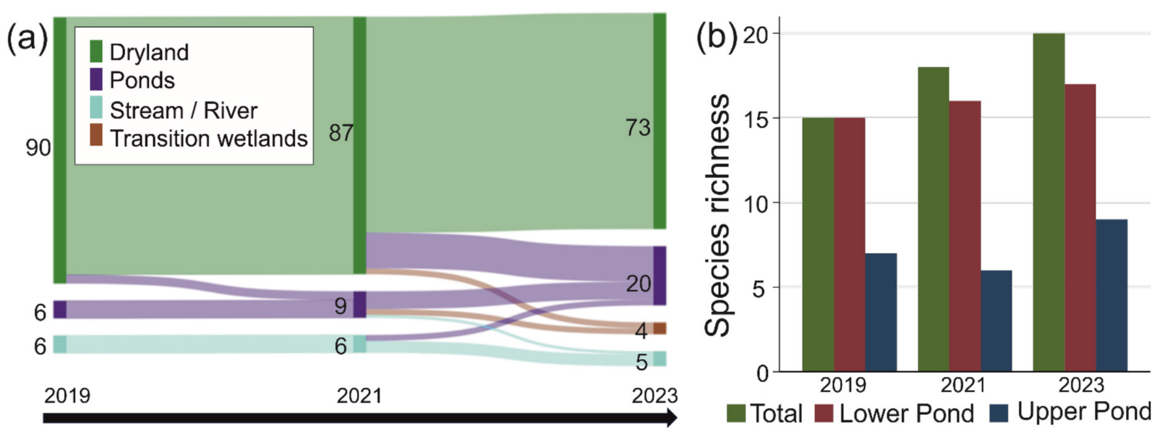

FIGURE 9 | (a) Habitat type changes across the 102 fixed points. (b) Number of aquatic plant species recorded in beaver ponds. Total includes additional beaver ponds that emerged in 2023.

(mating behaviour or ovipositing recorded). The most notable of these, the Golden-ringed dragonfly (*Cordulegaster boltonii*), normally associated with moorland streams and bogs, appears content to breed in beaver ponds. Three species recorded in 2018, Southern Hawker (*Aeshna cyanea*), broad-bodied Chaser (*Libellula depressa*) and large red Damselfly (*Pyrrhosoma nymphula*) continue to breed but are now joined by azure damselfly (*Coenagrion puella*), four-spotted chaser (*Libellula*

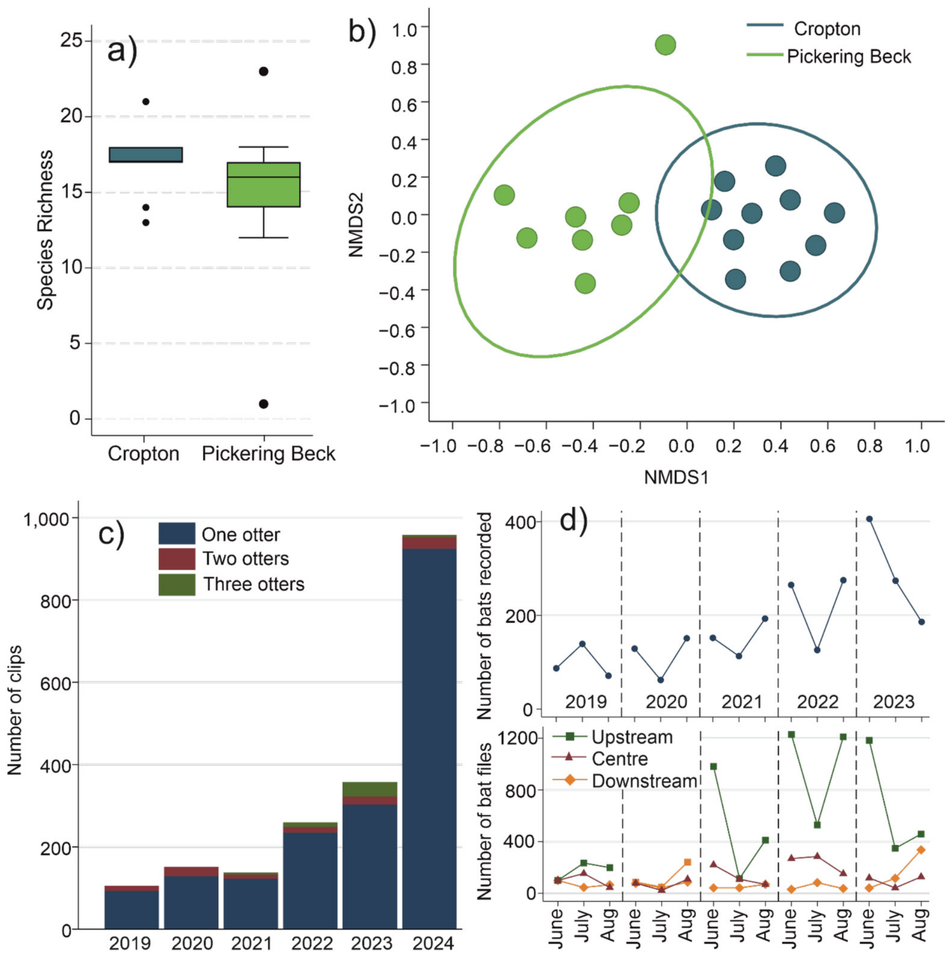

FIGURE 10 | Vertebrate richness and bat survey results. (a) Comparison of Shannon Index reported at Cropton and Pickering Beck; (b) NMDS of community composition between Cropton and Pickering Beck; (c) otter footage recorded on trail cameras (2019–2024); (d) bat recordings on transects and at fixed-points in the enclosure (upstream, centre and downstream, 2029–2023). Month 1 is used as a baseline.

quadrimaculata) and common darter (*Sympetrum striolatum*). These species are also found more widely across the site due to the increase in ponds/wetlands.

3.7 | Bat Surveys

Natterer's (*Myotis natteri*), Daubenton's (*Myotis daubentonii*) and whiskered/Brandt's (*Myotis mystacinus/Brantii*) have all been detected along with common (*Pipistrellus pipistrellus*) and soprano pipistrelle (*Pipistrellus pygmaeus*), brown long-eared (*Plecotus auritus*) and noctule (*Nyctalus noctula*). Figure 10d shows the steady increase in bat activity recorded on the 20-point transect throughout the trial. Fixed-point recorders also showed marked increases in activity that exactly matched locations and timings of beaver activity. The upstream recorder placed at the lower ornamental pond was initially a focus of beaver activity and showed an almost 10-fold increase, such that bat activity is essentially continuous throughout the night. This is mainly down to the increase in pipistrelle activity, with Myotis numbers being very variable (see Supporting Information for species relative abundance). The location of the central recorder had very limited beaver activity, and the bat activity there has shown only a moderate increase. The downstream recorder showed no change until July and August 2023, following beaver activity at this location beginning the previous winter. There was subsequently a dramatic increase in bat activity with the two highest figures for this recording point, reflected in the dramatic change to the number of pipistrelle and Myotis bats using the location.

4 | Discussion

In combination, the lines of evidence of beaver impacts combined in this novel, long-term and interdisciplinary monitoring project reveal a diverse range of influences on the site.

4.1 | Water Storage and Interaction With Existing NFM Structures

The human-made NFM structures already in place upon beaver release were not initially adopted by the beavers during the study period and have degraded over the project duration, with a modelled 50% decrease in storage capacity for high flow events. Such degradation shows that a 'build and forget' strategy is not appropriate for such structures, and that beaver releases cannot be relied upon to provide this maintenance. However, the beavers incorporated existing wooden supports into their dam at the lower end of the enclosure (Figure 4), and only once the functionality of human-built structures was severely compromised at the end of the trial period in late 2024 did the beavers first incorporate a degraded NFM dam into one of their own dams.

Conversely, the ornamental ponds at the upstream end of the enclosure were heavily modified by the beavers from the outset. The larger pond was incorporated into the initial dam, first constructed in 2019, thereby becoming hydrologically connected with Sutherland Beck and raising the water surface by 0.74 m, alongside a 70% increase in surface area. Behind this 'primary dam', the beavers constructed their first lodge and expanded the wetland habitat. When the raised water surface level intercepted the upper pond, the beavers drained much of the water from the upper pond (despite previously blocking leaks from this pond). A network of beaver canals remained here, with underwater access from the lodge retained.

Whilst 1D models have a limited ability to represent intricate beaver dam flow states or flow types, they are highly effective for calculating longitudinal storage and water surface profiles across the scales investigated here. In the absence of a formal sensitivity analysis, we recognise that uncertainties are inherent to these modelling results. Nonetheless, a clear result emerged. The increased water storage by beaver dams across the enclosure has more than mitigated the reduced storage potential of the degrading timber bunds. However, two of the dams were gradually partially breached at the end of (and slightly after) the 5-year trial, including the main dam. The dam breach in February 2024 coincided with a heavy rainfall event, suggesting that flooding or changes in the water level were the main trigger (as per Westbrook et al. 2020 and Ronnquist 2021), with no evidence of wildlife-triggered flow state change (Aguirre et al. 2024). Dam breaches are typically seen during site abandonment, potentially owing to excessive sedimentation or reduced local food resources (Ives 1942), though rebuilding has since been observed at this location. Whilst there is concern that partial dam breaches could potentially make large flood events worse (Butler and Malanson 2005; Westbrook et al. 2020), we found no evidence of this. The relocation of the beaver activity and dam construction to the downstream end of the enclosure likely mitigated these effects, as would the large timber bunds and the partial nature of the breach, as the remnant dam continues to have a hydrological and geomorphological legacy impact. After the end of the trial, six beaver dams were recorded across the site, with signs of active construction continuing and the partial breach being repaired as the site continues to evolve. With an average dam density of 7.3 dams per kilometre, much of Sutherland Beck throughout the enclosure is now under the influence of dam impoundment, resulting in a step-pool morphology. Offline water storage is also observed in an old ox-bow lake at the downstream extent of the enclosure. Overall, the water storage induced by beaver activities was highly dynamic, in terms of both the total volume and specific locations.

Consideration of both interactions between human and beaver dams and also how beavers engineer and maintain their wetlands is particularly relevant as policymakers consider how beavers can contribute to the delivery of nature-based solutions (NbS). The continuous evolution of the site due to beaver engineering, whilst the existing human-built leaky dams degraded, is a valuable example of the role 'nature-led NbS' may play in creating resilient landscapes delivering multiple NbS (Puttock et al. 2025).

4.2 | Impacts of Beaver Release on Water Flows

In combination, these beaver structures led to a reduction in flow peaks travelling through the enclosure, likely owing to the beaver engineering increasing storage, enhancing lateral connectivity by forcing flows onto the floodplain where roughness is higher, and the reconnection of offline storage at the downstream end of the enclosure (Puttock et al. 2017; Graham et al. 2022). Beaver structures have resulted in some limited adjustments to high-flow hydrological signatures, which can have both flood risk and ecological impacts (McMillan 2020). From the before–after analysis, the 5% reduction in peak flows was lower than seen at other monitored enclosures in England (Puttock et al. 2021), likely due to the pre-existing NFM dams already providing some attenuation benefit and the significantly wetter period following beaver release. A more substantial impact of beavers on hydrology at the site was supported by comparison of flows entering and those leaving the enclosure, which revealed a 46.6% reduction of median peak flows, though this will include the impacts of the human-made LWDs. These findings reflect the general uncertainty in the literature regarding the magnitude of beaver impacts on flood magnitude and timing, which includes both 'before–after' and 'upstream–downstream' modes of analysis (e.g., Westbrook et al. 2006; Nyssen et al. 2011; Puttock et al. 2021).

For low-flow signatures, baseflows leaving the enclosure during drier periods were five times higher than inflows. The continuous slow release of the additional water storage on the site will thus increase baseflows, leading to potentially increased drought resilience, similar to the reduced flow variability and buffering of extremes reported elsewhere (e.g., Smith et al. 2020). This increased baseflow can be seen clearly in the hydrograph covering summer 2023, a notably dry period (Figure 6d). Further quantification of beaver impacts on a more diverse range of hydrological signatures would yield valuable information on cascading effects for a range of downstream processes (McMillan 2020).

4.3 | Secondary Impacts on Water Quality and Ecological Diversity

Water quality parameters showed a consistent pattern: changes in turbidity, specific conductivity, temperature (all decreasing), pH and dissolved oxygen (both increasing) were recorded when comparing the downstream and upstream gauges. Each of these changes was more pronounced in winter and reversed in summer, with the below-enclosure gauge generally recording lower variability. Turbidity changes are likely due to reduced sedimentological connectivity through the impacted reach that decreases sediment transport. Evidence for this can be seen from widespread sediment deposition on the upstream side of beaver (Figures S3–S4) and NFM dams (Figure 7). Whilst this above-below comparison should be interpreted with caution without a full BACI study design for water quality data, increases recorded in summer are potentially due to beaver construction activities (excavation of burrows, canals and dam maintenance; Hood and Larson 2015), though when accounting for the large sample size, turbidity differences were slightly below the medium effect size significance threshold.

The reduction in variability in specific conductivity suggests the beaver modifications are creating more stable water solute concentrations through biochemical buffering or physical settling out in ponded areas; the significant rise in summer is potentially linked to the slightly higher turbidity. Anaerobic respiration may be greater in the beaver ponds than upstream due to microbes in deeper oxygen-deficient areas of the ponds using alternatives to oxygen, such as nitrate, in respiration. This has been shown to reduce nitrate concentrations in beaver ponds (Puttock et al. 2017) and may impact pH. Although beaver ponds tend to have abundant aquatic plant growth, which oxygenates water, they have high amounts of organic matter due to naturally high ecological productivity and turnover being supplemented by the addition of plant material, especially woody material by the beavers, which undergoes accelerated breakdown during warmer summer temperatures, consuming more oxygen from the water.

Both extent and heterogeneity of wetland habitat in the enclosure visibly increased during the trial period (e.g., Figures 3c and 10a), though less than recorded in other studies (e.g., Hood and Bayley 2008). This mosaic of habitats had clear and consistent impacts on the ecology of the site, alongside the increased sunlight reaching the ground from tree felling. The decreasing water temperature observed, especially in winter, was potentially due to stronger groundwater interactions with these water bodies and is consistent with previous studies (e.g., Westbrook et al. 2006; Janzen and Westbrook 2011; Majerova et al. 2020; Wade et al. 2020; Dittbrenner et al. 2022); however, in summer, the habitat responded quicker to radiant sunlight with slight solar heating (1 °C) observed. The difference in fish community composition reflects this greater heterogeneity in the hydrology of the enclosure, which is now a mosaic of lentic and lotic habitats and different flow rates. Cropton samples included species such as tench and common carp, which favour lentic environments, as well as species that are typically found associated with running water. The greater heterogeneity in beaver-engineered sites presents a wider mosaic of habitats for different species.

In general, beaver activity has created more diverse habitats within the enclosure, providing a wider variety of niches for small mammals and opportunities for specialists such as water shrews. Standing waters were transformed from a duckweed-dominated, poor-condition habitat (Scheffer et al. 2003), into an assembling aquatic vegetation displaying increasing taxonomic and growth form diversity. Diversity in aquatic plant growth forms in ponds and lakes is known to support more diverse invertebrate assemblages (Law et al. 2019; Cook et al. 2025). Repeat surveys of dragonflies and damselflies that showed a tripling in species count support this interpretation. The clearest impact on the wider ecology was observed in the systematic bat surveys undertaken, demonstrating that beavers have a positive impact on bat populations, likely due to the greater openness of the site, greater heterogeneity or the increase in the invertebrate prey and the development of a more complex food chain within the ecosystem. The impact was most clearly seen in the fixed-point surveys where increases in bat population were only seen when beaver activity began close to the monitoring point (i.e., immediately at the upstream location, in 2023 at the downstream location and no impact in the centre). This correspondence of population increases with both the timing and location of beaver impacts is strong evidence that the beaver-induced structural changes are bringing near-immediate ecological and biodiversity co-benefits. Whilst the review of Burgher et al. (2026) noted the increase of riparian specialist bird species following beaver engineering, BTO bird surveys here revealed no major differences in overall territory numbers or species observed, and suggest that, overall, there are winners and losers from the beaver activities. Repeat bird surveys showed no systematic changes, with very limited colonisation by wetland species. However, one may also expect a response time-lag from biodiversity, allowing time to colonisation and ecosystem assembly (Jackson and Sax 2010) reinforcing the need for long-term monitoring of both abiotic and biotic change, in order to fully appreciate the potential of beavers to contribute to nature recovery.

5 | Conclusion

Results demonstrate the profound impacts beavers have had upon local hydrology, geomorphology and ecology. Simultaneous monitoring of hydrology, geomorphology and ecology has enabled tracking of each of these impacts, and their interactions can be identified. Beaver activity within the site showed a high level of dynamism and spatial variability. Whilst human-made NFM structures degraded over the course of the project, beaver dams too were breached on multiple occasions, though not before downstream structures had already been built. This cycle of wetland evolution is a natural feature of beaver engineering. Nevertheless, consistent impacts of beaver structures on reducing downstream flood peaks and increasing water storage were seen from both monitoring and modelling. Improvements in water quality and increased ecological diversity were observed in aquatic plants, insects, fish and mammals.

The interdisciplinary approach enabled the identification of synergies between each of the monitored components. Most apparently, geomorphological changes and expansion of surface waters in one part of the enclosure were followed almost immediately by responses in bat populations in the same location. With the UK government committing to reintroducing beavers into the wild and the increased focus on multi-benefit NFM/NbS projects, new interdisciplinary scientific evidence of their expected impacts, such as that gathered from this closely monitored trial enclosure, is especially relevant to inform the reintroduction of beavers to intensively managed anthropogenically-altered landscapes such as England.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data underlying the study have been uploaded into an Excel spreadsheet provided with the manuscript.

References

Addor, N., G. Nearing, C. Prieto, A. J. Newman, N. Le Vine, and M. P. Clark. 2018. "A Ranking of Hydrological Signatures Based on Their Predictability in Space." *Water Resources Research* 54: 8792–8812. https://doi.org/10.1029/2018WR022606.

Addy, S., and M. E. Wilkinson. 2019. "Representing Natural and Artificial In-Channel Large Wood in Numerical Hydraulic and Hydrological Models." *Wiley Interdisciplinary Reviews: Water* 6: e1389. https://doi.org/10.1002/wat2.1389.

Aguirre, I., G. A. Hood, and C. J. Westbrook. 2024. "Short-Term Dynamics of Beaver Dam Flow States." *Science of the Total Environment* 919: 170825. https://doi.org/10.1016/j.scitotenv.2024.170825.

Bandini, F., L. Kooij, B. K. Mortensen, et al. 2023. "Mapping Inland Water Bathymetry With Ground Penetrating Radar (GPR) on Board Unmanned Aerial Systems (UASs)." *Journal of Hydrology* 616: 128789. https://doi.org/10.1016/j.jhydrol.2022.128789.

Bastion, D. 2020. "exactextractr: Fast Extraction From Raster Datasets Using Polygons (R package version 0.4.0)" https://cran.r-project.org/package=exactextractr.

Bradbury, G., A. Puttock, G. Coxon, S. Clarke, and R. E. Brazier. 2023. "Testing a Novel Sonar-Based Approach for Measuring Water Depth and Monitoring Sediment Storage in Beaver Ponds." *River Research and Applications* 39: 266–273. https://doi.org/10.1002/rra.4082.

Brazier, R. E., A. Puttock, H. A. Graham, R. E. Auster, K. H. Davies, and C. M. Brown. 2021. "Beaver: Nature's Ecosystem Engineers." *Wiley Interdisciplinary Reviews Water* 8: e1494. https://doi.org/10.1002/wat2.1494.

Broadhurst, H. A., L. M. Gregory, E. K. Bleakley, et al. 2021. "Mapping Differences in Mammalian Distributions and Diversity Using Environmental DNA From Rivers." *Science of the Total Environment* 801: 149724. https://doi.org/10.1016/j.scitotenv.2021.149724.

BTO. 2025. "Methodology and Survey Design". Accessed November 21, 2025. Available from: https://www.bto.org/get-involved/volunteer/projects/bbs/research-conservation/methodology-and-survey-design.

Burgher, J. A., J. Hallza, M. R. Lambert, and J. Piovia-Scott. 2026. "Beaver-Related Restoration and Freshwater Climate Resilience Across Western North America." *Restoration Ecology* 34: e70194. https://doi.org/10.1111/rec.70194.

Butler, D. R., and G. P. Malanson. 2005. "The Geomorphic Influences of Beaver Dams and Failures of Beaver Dams." *Geomorphology* 71: 48–60. https://doi.org/10.1016/j.geomorph.2004.08.016.

Castorani, M. C., D. C. Reed, and R. J. Miller. 2018. "Loss of Foundation Species: Disturbance Frequency Outweighs Severity in Structuring Kelp Forest Communities." *Ecology* 99: 2442–2454. https://doi.org/10.1002/ecy.2485.

Chitty, D., and D. A. Kempson. 1949. "Prebaiting Small Mammals and a New Design of Live Trap." *Ecology* 30: 536–542. https://www.jstor.org/stable/1932457.

Chow, V. T. 1959. *Open Channel Hydraulics*. McGraw Hill.

Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*. second ed. Lawrence Erlbaum Associates.

Coles, B. J.. 2006. *Beavers in Britain's Past*. WARP Occasional Paper 19. Oxbow.

Conroy, J., and A. Kitchener. 1996. "The Eurasian Beaver (Castor fiber) in Scotland: A Review of the Literature and Historical Evidence. Scottish Natural Heritage Review No. 49" https://www.nature.scot/sites/default/files/2025-06/naturescot-review-49.pdf.

Cook, P., A. Law, Z. Pattison, and N. J. Willby. 2025. "Beaver Wetlands Create a Buzz and a Flutter for Pollinators." *Journal of Applied Ecology* 62: 3288–3299. https://doi.org/10.1111/1365-2664.70193.

Deasy, C., R. E. Brazier, A. L. Heathwaite, and R. Hodgkinson. 2009. "Pathways of Runoff and Sediment Transfer in Small Agricultural Catchments." *Hydrological Processes* 23: 1349–1358. https://doi.org/10.1002/hyp.7257.

Deiner, K., H. M. Bik, E. Mächler, et al. 2017. "Environmental DNA Metabarcoding: Transforming How We Survey Animal and Plant Communities." *Molecular Ecology* 26: 5872–5895. https://doi.org/10.1111/mec.14350.

Dittbrenner, B. J., J. W. Schilling, C. E. Torgersen, and J. J. Lawler. 2022. "Relocated Beaver Can Increase Water Storage and Decrease Stream Temperature in Headwater Streams." *Ecosphere (Online)* 13: e4168. https://doi.org/10.1002/ecs2.4168.

Dunn, P. K., and G. K. Smyth. 2018. *Generalized Linear Models With Examples in R*. Springer. https://doi.org/10.1007/978-1-4419-0118-7.

Fairfax, E., and E. E. Small. 2018. "Using Remote Sensing to Assess the Impact of Beaver Damming on Riparian Evapotranspiration in an Arid Landscape." *Ecohydrology* 11: e1993. https://doi.org/10.1002/eco.1993.

Fairfax, E., and C. Westbrook. 2024. "The Ecology and Evolution of Beavers: Ecosystem Engineers That Ameliorate Climate Change." *Annual Review of Ecology, Evolution and Systematics* 55: 323–345. https://doi.org/10.1146/annurev-ecolsys-102722-122317.

Glendell, M., C. Extence, R. Chadd, and R. E. Brazier. 2014. "Testing the Pressure-Specific Invertebrate Index (PSI) as a Tool for Determining Ecologically Relevant Targets for Reducing Sedimentation in Streams." *Freshwater Biology* 59: 353–367. https://doi.org/10.1111/fwb.12269.

Graham, H. A., A. Puttock, J. Chant, et al. 2022. "Monitoring, Modelling and Managing Beaver (*Castor fiber*) Populations in the River Otter Catchment, Great Britain." *Ecological Solutions and Evidence* 3: e12168. https://doi.org/10.1002/2688-8319.12168.

Griffiths, N. P., R. M. Wright, B. Hänfling, et al. 2023. "Integrating Environmental DNA Monitoring to Inform Eel (*Anguilla anguilla*) Status in Freshwaters at Their Easternmost Range: A Case Study in Cyprus." *Ecology and Evolution* 13: e9800. https://doi.org/10.1002/ece3.9800.

Gurnell, A. M. 1998. "The Hydrogeomorphological Effects of Beaver Dam-Building Activity." *Progress in Physical Geography* 22: 167–189. https://doi.org/10.1177/030913339802200202.

Halley, D. J., A. P. Saveljev, and F. Rosell. 2021. "Population and Distribution of Beavers *Castor fiber* and *Castor canadensis* in Eurasia." *Mammal Review* 51: 1–24. https://doi.org/10.1111/mam.12216.

Harper, L. R., L. L. Handley, A. I. Carpenter, et al. 2019. "Environmental DNA (eDNA) Metabarcoding of Pond Water as a Tool to Survey Conservation and Management Priority Mammals." *Biological Conservation* 238: 108225. https://doi.org/10.1016/j.biocon.2019.108225.

Hart, J., A. Law, C. Westbrook, M. Rubinato, and N. Willby. 2025. "Flume Experiments Reveal How Beaver Dam Characteristics Influence Pond Depth Regulation." *Journal of Hydrology* 662: 133872. https://doi.org/10.1016/j.jhydrol.2025.133872.

Hector, A., S. von Felten, and B. Schmid. 2010. "Analysis of Variance With Unbalanced Data: An Update for Ecology and Evolution." *Journal of Animal Ecology* 79: 308–316. https://doi.org/10.1111/j.1365-2656.2009.01634.x.

Hill, D., M. Fasham, G. Tucker, M. Shewry, and P. Shaw, eds. 2005. *Handbook of Biodiversity Methods: Survey, Evaluation and Monitoring*. Cambridge University Press.

Hood, G. A., and S. E. Bayley. 2008. "Beaver (*Castor canadensis*) Mitigate the Effects of Climate on the Area of Open Water in Boreal Wetlands in Western Canada." *Biological Conservation* 141: 556–567. https://doi.org/10.1016/j.biocon.2007.12.003.

Hood, G. A., and D. G. Larson. 2015. "Ecological Engineering and Aquatic Connectivity: A New Perspective From Beaver-Modified Wetlands." *Freshwater Biology* 60: 198–208. https://doi.org/10.1111/fwb.12487.

Ives, R. L. 1942. "The Beaver-Meadow Complex." *Journal of Geomorphology* 5: 191–203.

Jackson, S. T., and D. F. Sax. 2010. "Balancing Biodiversity in a Changing Environment: Extinction Debt, Immigration Credit and Species Turnover." *Trends in Ecology & Evolution* 25: 153–160. https://doi.org/10.1016/j.tree.2009.10.001.

James, M. R., J. H. Chandler, A. Eltner, et al. 2019. "Guidelines on the Use of Structure-From-Motion Photogrammetry in Geomorphic Research." *Earth Surface Processes and Landforms* 44: 2081–2084. https://doi.org/10.1002/esp.4637.

James, M. R., S. Robson, and M. W. Smith. 2017. "3-D Uncertainty-Based Topographic Change Detection With Structure-From-Motion Photogrammetry: Precision Maps for Ground Control and Directly Georeferenced Surveys." *Earth Surface Processes and Landforms* 42: 1769–1788. https://doi.org/10.1002/esp.4125.

Janzen, K., and C. Westbrook. 2011. "Hyporheic Flows Along a Channelled Peatland: Influence of Beaver Dams." *Canadian Water Resources Journal* 36: 331–347. https://doi.org/10.4296/cwrj3604846.

Jordan, C. E., and E. Fairfax. 2022. "Beaver: The North American Freshwater Climate Action Plan." *WIREs Water* 9: e1592. https://doi.org/10.1002/wat2.1592.

Karran, D. J., C. J. Westbrook, J. M. Wheaton, C. A. Johnston, and A. Bedard-Haughn. 2017. "Rapid Surface-Water Volume Estimations in Beaver Ponds." *Hydrology and Earth System Sciences* 21: 1039–1050. https://doi.org/10.5194/hess-21-1039-2017.

Kelly, R. P., J. A. Port, K. M. Yamahara, and L. B. Crowder. 2014. "Using Environmental DNA to Census Marine Fishes in a Large Mesocosm." *PLoS ONE* 9: e86175. https://doi.org/10.1371/journal.pone.0086175.

Ladson, A., R. Brown, and R. Nathan. 2013. "A Standard Approach to Baseflow Separation Using the Lyne and Hollick Filter." *Australasian Journal of Water Resources* 17: 25–34. https://doi.org/10.7158/13241583.2013.11465417.

Larsen, A., J. R. Larsen, and S. N. Lane. 2021. "Dam Builders and Their Works: Beaver Influences on the Structure and Function of River Corridor Hydrology, Geomorphology, Biogeochemistry and Ecosystems." *Earth-Science Reviews* 218: 103623. https://doi.org/10.1016/j.earscirev.2021.103623.

Law, A., A. Baker, C. Sayer, et al. 2019. "The Effectiveness of Aquatic Plants as Surrogates for Wider Biodiversity in Standing Fresh Waters." *Freshwater Biology* 64: 1664–1675. https://doi.org/10.1111/fwb.13369.

Law, A., M. J. Gaywood, K. C. Jones, P. Ramsay, and N. J. Willby. 2017. "Using Ecosystem Engineers as Tools in Habitat Restoration and Rewilding: Beaver and Wetlands." *Science of the Total Environment* 605-606: 1021–1030. https://doi.org/10.1016/j.scitotenv.2017.06.173.

Levine, R., and G. A. Meyer. 2019. "Beaver-Generated Disturbance Extends Beyond Activedam Sites to Enhance Stream Morphodynamics and Riparian Plant Recruitment." *Scientific Reports* 9: 8124. https://doi.org/10.1038/s41598-019-44381-2.

Lüdecke, D., D. Makowski, M. S. Ben-Shachar, and I. Patil. 2021. "Performance: An R Package for Assessment, Comparison and Testing of Statistical Models." *Journal of Open Source Software* 6: 3139. https://doi.org/10.21105/joss.03139.

Lyet, A., L. Pellissier, A. Valentini, T. Dejean, A. Hehmeyer, and R. Naidoo. 2021. "eDNA Sampled From Stream Networks Correlates With Camera Trap Detection Rates of Terrestrial Mammals." *Scientific Reports* 11: 11362. https://doi.org/10.1038/s41598-021-90598-5.

Majerova, M., B. T. Neilson, and B. B. Roper. 2020. "Beaver Dam Influences on Streamflow Hydraulic Properties and Thermal Regimes." *Science of the Total Environment* 718: 134853. https://doi.org/10.1016/j.scitotenv.2019.134853.

McMillan, H. 2020. "Linking Hydrologic Signatures to Hydrologic Processes: A Review." *Hydrological Processes* 34: 1393–1409. https://doi.org/10.1002/hyp.13632.

Mena, J. L., H. Yagui, V. Tejeda, et al. 2021. "Environmental DNA Metabarcoding as a Useful Tool for Evaluating Terrestrial Mammal Diversity in Tropical Forests." *Ecological Applications* 31: e02335. https://doi.org/10.1002/eap.2335.

Met Office. 2003. "Met Office Rain Radar Data From the NIMROD System" http://catalogue.ceda.ac.uk/uuid/82adec1f896af6169112d09cc1174499.

Met Office. 2020. "UK-Climate-Averages Climate Information - Met Office" https://www.metoffice.gov.uk/research/climate/mapsand-data/uk-climate-averages.

Murray, D., B. T. Neilson, and J. Brahney. 2023. "Beaver Pond Geomorphology Influences Pond Nitrogen Retention and Denitrification." *Journal of Geophysical Research: Biogeosciences* 128: e2022JG007199. https://doi.org/10.1029/2022JG007199.

Neumayer, M., S. Teschemacher, S. Schloemer, V. Zahner, and W. Rieger. 2020. "Hydraulic Modeling of Beaver Dams and Evaluation of Their Impacts on Flood Events." *Water* 12: 300. https://doi.org/10.3390/w12010300.

Nisbet, T., P. Roe, S. Marrington, H. Thomas, S. Broadmeadow, and G. Valatin. 2015. "Project RMP5455: Slowing the Flow at Pickering Final Report: Phase II." Department for Environment, Food and Rural Affairs. https://cdn.forestresearch.gov.uk/2022/02/stfap_final_report_apr2011.pdf.

Nyssen, J., J. Pontzeele, and P. Billi. 2011. "Effect of Beaver Dams on the Hydrology of Small Mountain Streams: Example From the Chevral in the Ourthe Orientale Basin, Ardennes, Belgium." *Journal of Hydrology* 402: 92–102. https://doi.org/10.1016/j.jhydrol.2011.03.008.

Ochoa-Tocachi, B. F., W. Buytaert, B. De Bièvre, et al. 2016. "Impacts of Land Use on the Hydrological Response of Tropical Andean Catchments." *Hydrological Processes* 30: 4074–4089. https://doi.org/10.1002/hyp.10980.

Oksanen, J., G. Simpson, F. Blanchet, et al. 2025. "*Vegan: Community Ecology Package*." R package version 2.8–0, https://vegandevs.github.io/vegan/.

Piepho, H. P., and R. N. Edmondson. 2018. "A Tutorial on the Statistical Analysis of Factorial Experiments With Qualitative and Quantitative Treatment Factor Levels." *Journal of Agronomy and Crop Science* 204: 429–455. https://doi.org/10.1111/jac.12267.

Posit Team. 2023. "RStudio: Integrated Development Environment for R." Posit Software, PBC. http://www.posit.co/.

Puttock, A., R. E. Auster, N. Gatis, and R. E. Brazier. 2025. "Human, or Nature-Led? A Spectrum of Nature-Based Solutions." *Nature-Based Solutions* 8: 100249. https://doi.org/10.1016/j.nbsj.2025.100249.

Puttock, A., H. A. Graham, J. Ashe, D. J. Luscombe, and R. E. Brazier. 2021. "Beaver Dams Attenuate Flow: A Multi-Site Study." *Hydrological Processes* 35: e14017. https://doi.org/10.1002/hyp.14017.

Puttock, A., H. A. Graham, D. Carless, and R. E. Brazier. 2018. "Sediment and Nutrient Storage in a Beaver Engineered Wetland." *Earth Surface Processes and Landforms* 43: 2358–2370. https://doi.org/10.1002/esp.4398.

Puttock, A., H. A. Graham, A. M. Cunliffe, M. Elliott, and R. E. Brazier. 2017. "Eurasian Beaver Activity Increases Water Storage, Attenuates Flow and Mitigates Diffuse Pollution From Intensively-Managed Grasslands." *Science of the Total Environment* 576: 430–443. https://doi.org/10.1016/j.scitotenv.2016.10.122.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing (3.6.3), Vienna, Austria. URL https://www.R-project.org/.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing (4.2.1), Vienna, Austria. URL https://www.R-project.org/.

Riaz, T., W. Shehzad, A. Viari, F. Pompanon, P. Taberlet, and E. Coissac. 2011. "ecoPrimers: Inference of New DNA Barcode Markers From Whole Genome Sequence Analysis." *Nucleic Acids Research* 39: e145. https://pmc.ncbi.nlm.nih.gov/articles/PMC3241669/.

Rolauffs, P., D. Hering, and S. Lohse. 2001. "Composition, Invertebrate Community and Productivity of a Beaver Dam in Comparison to Other Stream Habitat Types." *Hydrobiologia* 459: 201–212. https://doi.org/10.1023/A:1012507613952.

Ronnquist, A. 2021. *Dam Different! How the Physical Properties of Beaver Dams Influence Water Storage Dynamics*. MSc thesis. University of Saskatchewan. https://harvest.usask.ca/server/api/core/bitstreams/2c6413c1-a01b-4d8e-9298-e0244db15c4d/content.

Ronnquist, A., and C. Westbrook. 2021. "Beaver Dams: How Structure, Flow State, and Landscape Setting Regulate Water Storage and Release." *Science of the Total Environment* 785: 147333. https://doi.org/10.1016/j.scitotenv.2021.147333.

Sales, N. G., M. B. McKenzie, J. Drake, et al. 2020. "Fishing for Mammals: Landscape-Level Monitoring of Terrestrial and Semi-Aquatic Communities Using eDNA From Riverine Systems." *Journal of Applied Ecology* 57: 707–716. https://doi.org/10.1111/1365-2664.13592.

Scheffer, M., S. Szabo, A. Gragnani, et al. 2003. "Floating Plant Dominance as a Stable State." *Proceedings of the National Academy of Sciences* 100: 4040–4045. https://doi.org/10.1073/pnas.0737918100.

Sellers, G. S., C. Di Muri, A. Gómez, and B. Hänfling. 2018. "Mu-DNA: A Modular Universal DNA Extraction Method Adaptable for a Wide Range of Sample Types." *Metabarcoding and Metagenomics* 2: e24556. https://doi.org/10.3897/mbmg.2.24556.

Shaw, R. G., and T. Mitchell-Olds. 1993. "ANOVA for Unbalanced Data: An Overview." *Ecology* 74: 1638–1645. https://doi.org/10.2307/1939922.

Skalak, S. L., R. E. Sherwin, and R. M. Brigham. 2012. "Sampling Period, Size and Duration Influence Measures of Bat Species Richness From Acoustic Surveys." *Methods in Ecology and Evolution* 3: 490–502.

Smith, A., D. Tetzlaff, J. Gelbrecht, L. Kleine, and C. Soulsby. 2020. "Riparian Wetland Rehabilitation and Beaver Re-Colonization Impacts on Hydrological Processes and Water Quality in a Lowland Agricultural Catchment." *Science of the Total Environment* 699: 134302. https://doi.org/10.1016/j.scitotenv.2019.134302 Get rights and content.

Smith, M. W., J. L. Carrivick, and D. J. Quincey. 2016. "Structure From Motion Photogrammetry in Physical Geography." *Progress in Physical Geography* 40: 247–275. https://doi.org/10.1177/0309133315615805.

Spreafico, A., F. Chiabrando, L. Teppati Losè, and F. Giulio Tonolo. 2021. "The iPad Pro Built-In lidar Sensor: 3d Rapid Mapping Tests and Quality Assessment." *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences* 43: 63–69. https://doi.org/10.5194/isprs-archives-XLIII-B1-2021-63-2021.

Tavani, S., A. Billi, A. Corradetti, et al. 2022. "Smartphone Assisted Fieldwork: Towards the Digital Transition of Geoscience Fieldwork Using LiDAR-Equipped iPhones." *Earth-Science Reviews* 227: 103969. https://doi.org/10.1016/j.earscirev.2022.103969.

Thomas, H., and T. R. Nisbet. 2023. "Assessing the Decay and Integrity of Timber Structures Used for Natural Flood Management (NFM) on Sutherland Beck, Pickering, North Yorkshire. Report to Forestry England." Accessed November 21, 2025. Available: https://www.forestresearch.gov.uk/research/forestry-and-natural-flood-management/assessing-the-decay-and-integrity-of-timber-structures-used-for-natural-flood-management/.

Venables, W. N., and B. D. Ripley. 2002. *Modern Applied Statistics with S*. Springer.

Wade, J., L. Lautz, C. Kelleher, et al. 2020. "Beaver Dam Analogues Drive Heterogeneous Groundwater-Surface Water Interactions." *Hydrological Processes* 34: 5340–5353. https://doi.org/10.1002/HYP.13947.

Warton, D. I., M. Lyons, J. Stoklosa, and A. R. Ives. 2016. "Three Points to Consider When Choosing a LM or GLM Test for Count Data." *Methods in Ecology and Evolution* 7: 882–890. https://doi.org/10.1111/2041-210X.12552.

Washko, S., N. Willby, and A. Law. 2022. "How Beavers Affect Riverine Aquatic Macroinvertebrates: A Review." *PeerJ* 10: e13180. https://doi.org/10.7717/peerj.13180.

Westbrook, C., D. Cooper, and B. Baker. 2006. "Beaver Dams and Overbank Floods Influence Groundwater-Surface Water Interactions of a Rocky Mountain Riparian Area." *Water Resources Research* 42: 1–13. https://doi.org/10.1029/2005WR004560.

Westbrook, C. J., A. Ronnquist, and A. Bedard-Haughn. 2020. "Hydrological Functioning of a Beaver Dam Sequence and Regional Dam Persistence During an Extreme Rainstorm." *Hydrological Processes* 34: 3726–3737. https://doi.org/10.1002/hyp.13828.

Willby, N. J., A. Law, O. Levanoni, G. Foster, and F. Ecke. 2018. "Rewilding Wetlands: Beaver as Agents of Within-Habitat Heterogeneity and the Responses of Contrasting Biota." *Philosophical Transactions of the Royal Society B: Biological Sciences* 373: 20170444. https://doi.org/10.1098/rstb.2017.0444.

Woo, M. K., and J. M. Waddington. 1990. "Effects of Beaver Dams on Subarctic Wetland Hydrology." *Arctic* 43: 223–230. https://www.jstor.org/stable/40511261.

Younger, P. M., J. E. Freer, and K. J. Beven. 2009. "Detecting the Effects of Spatial Variability of Rainfall on Hydrological Modelling Within an Uncertainty Analysis Framework." *Hydrological Processes* 23: 1988–2003. https://doi.org/10.1002/hyp.7341.

Zeng, Q., H. Chen, C. Y. Xu, et al. 2018. "The Effect of Rain Gauge Density and Distribution on Runoff Simulation Using a Lumped Hydrological Modelling Approach." *Journal of Hydrology* 563: 106–122. https://doi.org/10.1016/j.jhydrol.2018.05.058.

Zwolicki, A. 2025. "Can Beavers Canopy Alterations Affect Managed Forests More Than Natural Forests?" *Forest Ecology and Management* 577: 122407. https://doi.org/10.1016/j.foreco.2024.122407.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Coordinates of pseudo-control eDNA samples from Pickering Beck. **Table S2:** GLM model results displayed in Figure 5b. **Table S3:** Species detected in eDNA samples (May 2022). **Figure S1:** Map of beaver enclosure detailing the fence line, dams, water surfaces (2024), photo points relating to Supplementary Figures and TLS survey locations (encompassing a wider area than shown). **Figure S2:** Repeat imagery showing the development of the main dam, taken from the true left bank of the channel slightly downstream. **Figure S3:** Repeat UAV imagery showing the development of the main dam, taken from the true right side of the channel facing downstream. **Figure S4:** Repeat imagery comparing pre- and post-release conditions at the main dam. Image is taken from the true right bank of the channel. **Figure S5:** Repeat imagery showing the development, breach (March 2025) and initial rebuilding (June 2025) of the Spruce dam, taken from the true right bank of the channel facing upstream. **Figure S6:** Repeat UAV imagery showing the development of the lower boundary dam, taken facing upstream. The enclosure fenceline can be seen at the bottom of each picture.