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RESEARCH ARTICLE

eDNA sampling reveals no evidence of negative effects of beaver recolonisation on the catchment-scale distribution of migratory fish

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Abstract

1. Reintroduction of keystone species is considered part of the solution to the current biodiversity crisis. The Eurasian beaver (*Castor fiber*) is one such species, shaping its habitat by felling trees, building dams and creating wetlands. However, whilst the potential benefits to aquatic biodiversity and ecological functioning have been studied on a local scale, the impacts of beavers on catchment-scale processes such as fish migration remain understudied.
2. Sequencing of environmental DNA (eDNA metabarcoding) from water samples is a cost-effective method to study species distributions across large geographical scales. Here, eDNA samples ($n = 426$) were collected from 142 sites across Britain's oldest and largest established wild beaver population, located on Tayside, East Scotland and analysed using a vertebrate-specific metabarcoding assay. We combined detection/non-detection data from eDNA results with other environmental and anthropogenic variables to model the effects of beaver eDNA detections on the distribution of three migratory fish species.
3. Using generalised linear models, we found no effects of the current beaver eDNA detections on the distribution of Atlantic salmon or lamprey, but a positive co-occurrence with European eel at the catchment scale. Model outputs also reinforced previous findings on the impact of barriers to migration and other abiotic and biotic factors on fish species, demonstrating the effectiveness of eDNA sampling in rivers for understanding species distributions at a catchment scale.

4. *Synthesis and applications*. This study provides novel insights into the catchment-scale co-distribution of beavers and migratory fish, and there was no evidence of negative effects on the catchment-scale distribution of migratory fish species. More generally, this study highlights how catchment-wide eDNA monitoring can be applied by environmental managers to aid decision-making and impact assessment of multiple priority species at the catchment scale.

KEYWORDS
beavers, catchment-scale, environmental DNA, land-use, migration barriers, migratory fish, modelling, species distributions

1 | INTRODUCTION

Globally, the average size of monitored wildlife populations in freshwater systems has declined by 85% in the last 50 years (Deinet et al., 2024; Reid et al., 2019; Worldwide Fund for Nature, 2024). The reintroduction of beavers (*Castor* spp.) to their historic range has been proposed as a nature-based solution to address this freshwater biodiversity crisis (Law, Levanoni, et al., 2019; Stringer & Gaywood, 2016). Habitat modifications by beavers, primarily dam building, alter the hydraulic characteristics of rivers and slow the flow of water, thereby converting lotic systems to lotic–lentic mosaics (Naiman et al., 1988; Westbrook et al., 2011). The creation of these heterogeneous wetlands has been shown to benefit biodiversity (Brazier et al., 2021; Elmeros et al., 2003; Law et al., 2017). However, whilst the potential benefits to aquatic biodiversity and ecological functioning have been widely promoted at a local scale, the impacts of beavers on catchment-scale processes such as fish migration remain understudied (Brazier et al., 2021; Kemp et al., 2012).

Beaver-mediated habitat modifications such as dam building, channel excavation, woody debris accumulation and bank burrowing may significantly enhance fish communities by increasing habitat heterogeneity (Kemp et al., 2012). These activities create pools, backwaters and undercut banks, offering shelter, spawning grounds, temperature variations and improved foraging conditions which have been shown to support a more diverse community when compared to artificial structures and stream reaches (Pander et al., 2025). Both active and abandoned beaver modifications provided a higher contribution to local biodiversity when compared to flowing stretches and particularly benefit juvenile and small-bodied fish by reducing predation risk and flow stress (Fritz & Gangloff, 2022). Additionally, beaver-driven structural changes promote natural stream processes like sediment sorting and flow variability, which support diverse fish life histories and a greater variety of age classes (Bylak et al., 2014; Needham et al., 2021).

Negative effects might arise from dams which could restrict or delay the two-way passage of migrating fish, particularly during periods of low flow (Cutting et al., 2018; Needham et al., 2025) or reduce the availability of suitable spawning habitat (Collen & Gibson, 2000; Kemp et al., 2012). Lokteff et al. (2013), found interspecific variation in the passability of North American beaver (*Castor canadensis*) dams by Pacific salmonids in Utah where the movements of native Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) and non-native brook trout (*Salvelinus fontinalis*) were unaffected, although non-native brown trout (*Salmo trutta*) movements were restricted. Similar telemetry studies on bull trout (*Salvelinus confluentus*) in Montana were unable to determine whether dams restricted the upstream distribution of fish or if bull trout actively selected beaver-created wetlands (Marshall Wolf et al., 2024). Research in Norway demonstrated that Eurasian beaver (*Castor fiber*) dams were unlikely to be a barrier to Atlantic salmon (*Salmo salar*) and brown trout; however, salmonid movements were higher in control stretches than beaver dammed reaches (Malison & Halley, 2020). Finally, successful beaver dam passage for Arctic grayling (*Thymallus arcticus*) in Montana was strongly correlated with higher flows and the presence of bypass channels, warmer temperatures and dam breach status (Cutting et al., 2018). These studies highlight how dam passability varies depending upon stream geomorphology, underlying hydrology, environmental conditions, fish life history, individual fish attributes and the physical characteristics of dams.

The Eurasian beaver has been present in the wild within Tayside, East Scotland since at least 2001 (Campbell et al., 2012). Whilst the exact origin of these beavers is unknown, surveys by the lead Government Agency, NatureScot, estimate that the population has increased from approximately 146 individuals in 2012 to an estimated 954 individuals in 2021 (Campbell et al., 2012; Campbell-Palmer et al., 2021). In contrast to other European countries, there remains considerable unused habitat in Scottish catchments where beavers have naturally colonised such as the Forth (Halley et al., 2021); therefore, substantial population growth is expected. Meanwhile, the number of adult Atlantic salmon returning to Scottish rivers has continued to decline, which has prompted the IUCN to reclassify the British salmon population from Least Concern to Endangered (Darwall & Noble, 2023). In 2015, a mapping study estimated there would be a 72% habitat overlap between beavers and salmon across the Tay catchment (Beaver Salmonid Working Group, 2015), and there remains uncertainty surrounding the future of these two species of conservation concern and their interactions.

Whilst beaver and salmon interactions remain understudied in Scotland, Needham et al. (2021) found that beaver modifications to a Scottish stream benefited the local brown trout populations where the beaver-modified habitats supported higher abundances of larger trout and a wider variety of age classes. Subsequent telemetry studies highlighted that brown trout could successfully navigate the beaver dams, although successful passage was determined by environmental conditions and individual fish characteristics (Needham et al., 2025). These studies were, however, limited to a few streams and focused on potamodromous brown trout. Meanwhile the effects on conservation priority migratory species such as brook lamprey (*Lampetra planeri*), European river lamprey (*Lampetra fluviatilis*) and critically endangered European eel (*Anguilla anguilla*), which are particularly vulnerable to changes in water quality and habitat connectivity, remain unknown (Nunn et al., 2023). Globally, beaver distributions are expanding through conservation translocations (Halley et al., 2021), reduced exploitation, legal protection and natural colonisation (Campbell-Palmer et al., 2021). Therefore, the need to understand the impact of expanding beaver populations on migratory fish species is becoming increasingly important.

Environmental DNA (eDNA) has become an important monitoring tool to assess the status of freshwater biodiversity (Deiner et al., 2017; Hänfling et al., 2016; Pont et al., 2018). The development of high-throughput DNA sequencing of target regions ('metabarcoding') provides a cost-effective method to study species distributions across a large scale (Broadhurst et al., 2021; Griffiths et al., 2023). eDNA has also been shown to increase detection of rare fish species such as European eel when compared with conventional fish survey techniques (Griffiths et al., 2020). However, whilst eDNA has often been applied at a local scale within lakes (Hänfling et al., 2016), ponds (Harper et al., 2018) and rivers (Broadhurst et al., 2021; Pont et al., 2018), its potential for upscaling across entire catchments is only just starting to be realised (Blackman et al., 2024).

In the current study, we applied a catchment-scale eDNA survey across Tayside to characterise the co-distribution of beavers and migratory fish species. Specifically, we modelled the occurrence of beaver eDNA, alongside key anthropogenic (artificial migration barriers), environmental (habitat characteristics) and biotic (predator detections; Collen & Gibson, 2000) covariates on the occurrence of salmonids, lamprey and eel, across Tayside, to investigate if the detection of beavers affects the distribution of migratory fish at the catchment scale.

2 | METHODS

2.1 | Study region

The study area consisted of four large catchments (Tay, Earn, Forth and Lomond) which have an average catchment size of 2135.3 (±2008.5) km^2 alongside three small tributaries (Dighty, Huntly and Pitroddie) which flow directly into the Tay estuary. Total atmospheric rainfall across sites ranged from 875.1 to 2833 mm with an average of 1412 (±385.8) mm in 2023. Sites within catchments ranged in elevation from 8 to 416 m and were on average 123.3 (±88.03) m above sea level. Sites were up to 142.8 km inland with an average distance of 63.01 (±32.6) km. The dominant land-use across sites was agricultural land and broadleaved woodland accounting for 46.3% and 28% of upstream land-use, respectively.

2.2 | Site selection

The study region was gridded to ensure balanced spatial coverage, before 142 sites near beaver activity or suitable beaver habitat were selected (Figure 1) based upon a catchment-wide field signs survey carried out in 2021 (Campbell-Palmer et al., 2021). To identify river systems where beavers had not been recorded but were likely to have newly occupied since the 2021 survey, we integrated the data layer of 'Potential Core Beaver Woodland' produced by NatureScot to prioritise sites which had suitable beaver habitat (Stringer et al., 2018). In most river systems, three sites were selected upstream of presumed beaver activity at approximately 5 km intervals to ensure consistent and comprehensive coverage.

The 'Salmon Rivers in Scotland' layer (Marine Directorate, 2008) which has collated known information on the presence of salmon since the 1980s and is an update of Gardiner and Egglishaw (1986) using the UKCEH digital river network (Moore et al., 1994), was used to select sites that overlapped with beavers. Electrofishing data from the National Electrofishing Programme for Scotland (NEPS) surveys were used to provide quantitative information on juvenile salmonid densities that could be used to prioritise sampling productive salmon habitats (Malcolm et al., 2023). Finally, the distribution of other priority migratory fish species was taken from the 2018 NEPS electrofishing fish counts (Malcolm, Millidine, Jackson, et al., 2019). Of the 53 electrofishing sites which overlapped the current study, eels and lamprey were detected in 12 and 4 sites, respectively (Figure S1).

2.3 | Sample collection and filtration

Between 06 July 2023 and 18 August 2023, four hundred and twenty six 2-L surface water samples were collected at 142 sites (three replicates per site), following the methodology described in Griffiths et al. (2023). Field blanks ($n = 19$) of purified water were used daily to monitor contamination. Water samples were vacuum-filtered within 24 h of collection through sterile 0.45 µm mixed cellulose nitrate membrane filters with pads (47 mm diameter; Whatman, GE Healthcare) using Pall filtration units and then stored at −20°C. See Supporting Information—Methods for full details. Ethical approval was obtained under the application

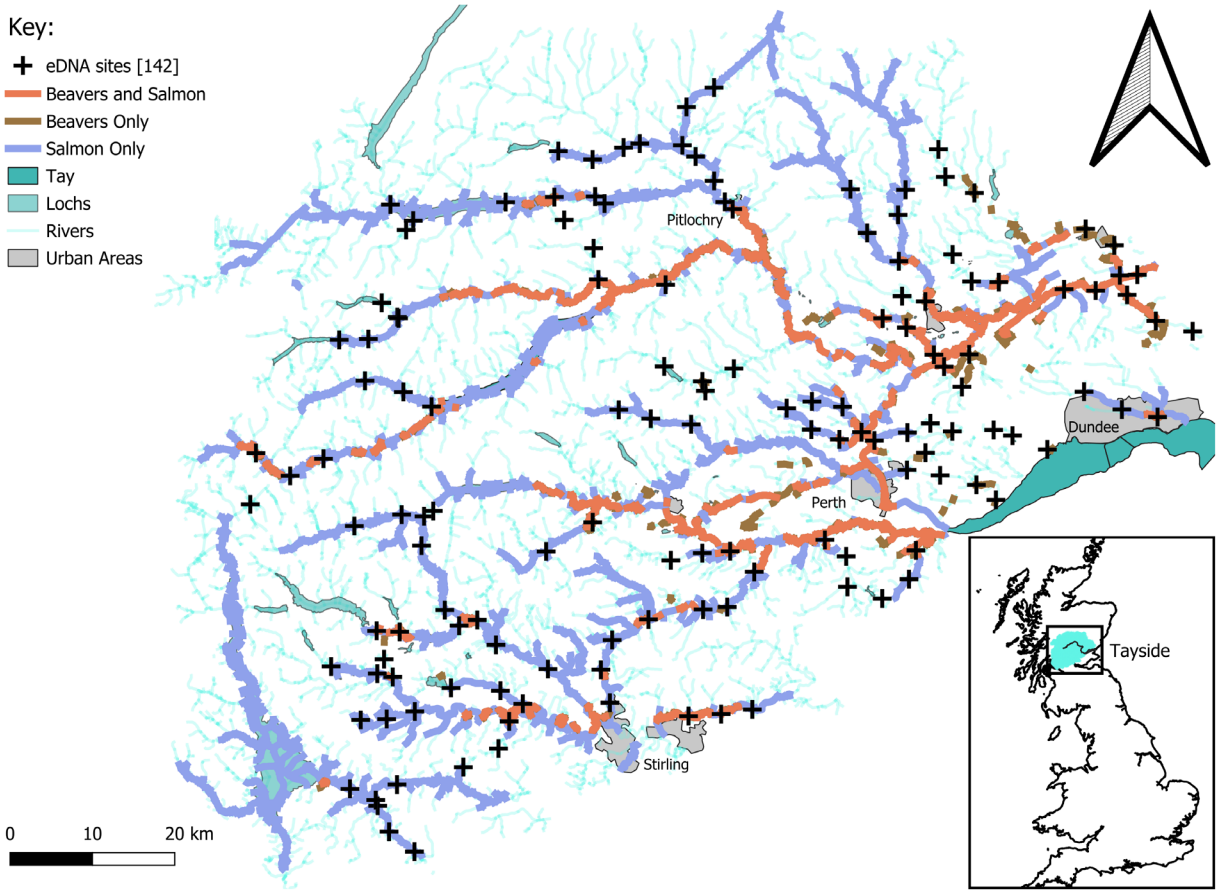

FIGURE 1 eDNA sites sampled across Tayside ($n = 142$; black cross). The beaver distribution is taken from the 2021 NatureScot survey (Campbell-Palmer et al., 2021). The salmon distribution is informed by the 'Salmon rivers in Scotland' (Marine Directorate, 2008), which is based on digital spatial data licensed from the UK Centre for Ecology & Hydrology, © NERC (UKCEH) and contains Ordnance Survey data © Crown copyright and database rights 2024.

'ETH2223-0838' to the UHI Animal Welfare and Environment ethics committee. No permit or licences were required for water sampling in the current study, but landowner permission was sought.

2.4 | DNA extractions

DNA was extracted using the mu-DNA lysis water protocol (Sellers et al., 2018) with modifications: during the lysis stage, instead of using garnet beads, 34 µL of 20 mg/mL proteinase K (VWR, Leicestershire, UK) was added to 750 µL of lysis solution and 250 µL of water lysis additive and incubated at 55°C overnight. Extraction blanks ($n = 20$) were used to monitor contamination.

2.5 | Metabarcoding

Library preparation followed a modified Griffiths et al. (2023) protocol. Nested metabarcoding followed a two-step PCR approach in which both PCRs used multiplex identification tags to enable sample identification (Kitson et al., 2019). A positive control (quantified at 0.05 ng/µL) from the cichlid (*Astatotilapia calliptera*) that is not found in the United Kingdom and a negative control of molecular grade water were used for each sub-library. The first PCR was carried out in triplicate (3× PCR replicates) to amplify a 106 bp fragment using published 12S ribosomal RNA primers (Kelly et al., 2014; Riaz et al., 2011). These primers have been validated in vitro, in silico and in situ for UK vertebrates (Hänfling et al., 2016), confirming that for the purpose of the current study, all UK migratory fish species can be detected. However, they cannot distinguish between river or brook lamprey, which are therefore assigned to the genus *Lampetra*.

Sub-libraries were cleaned using the ProNex® Size-Selective purification beads at a ratio of 1.5× to 50 µL. A second PCR was carried out in duplicate to bind pre adapters, indexes and Illumina adapters to each sub-library before a double size selection clean-up (Quail et al., 2009) was carried out at the ratios of 1.2× and 0.4× magnetic beads to 50 µL of PCR product.

Cleaned sub-libraries were quantified and diluted to 5 ng/µL before they were pooled proportionally based on the number of samples. The pooled libraries were then diluted to 4 nM and quantified via qPCR using the Collibri™ Library Quantification Kit for Illumina (Roche, Hertfordshire, UK). Final libraries were denatured and

sequenced at 13 pM with 10% PhiX Control on an Illumina MiSeq using a MiSeq Reagent Kit v3 (600 cycle) (Illumina Inc., San Diego, CA, USA).

2.6 | Data filtering

Reads were demultiplexed using a custom script then processed with Tapirs (https://github.com/EvoHull/Tapirs) for quality-trimming, merging and taxonomic assignment using a curated UK vertebrate reference database (Harper et al., 2018). Taxonomic assignment followed a lowest common ancestor approach based on basic local alignment search tool (BLAST) matches with minimum identity set at 98% (Griffiths et al., 2023).

All GIS and covariate extraction was done in QGIS (QGIS Development Team, 2025), analyses and graphical visualisation used R v.4.6.0 (R Core Team, 2026) with ggplot2 (Wickham, 2016) and sjPlot (Lüdecke, 2024). Following the bioinformatics, a minimum threshold of five reads was applied to remove low-frequency detections alongside a species-specific contaminant threshold. This was applied on a per flow cell basis to remove any reads in samples which were lower than detections in controls. Post-filtering, occupancy models using the R package 'unmarked' (Fiske & Chandler, 2011) demonstrated consistently high detection probabilities across the three replicates for beavers (>99.8%) and each migratory fish species (>99.9%) (Table S1). Therefore, field replicates were combined into site-level eDNA detections (1) or non-detections (0).

2.7 | Environmental metadata and covariates

Fifteen covariates that could explain the distribution of the three migratory species were selected from literature, based on available GIS data (Barnes & Turner, 2016; Ferreira et al., 2013; Griffiths et al., 2023; Malcolm, Millidine, Glover, et al., 2019). These included migration barriers (SEPA-WMS, 2018), geospatial variables related to the site's location (Davies et al., 2022; Eurogeographics, 2023), adjacent land use (Morton et al., 2024), physico-chemical parameters (Hollis et al., 2019; Johnson et al., 2005) and the detection of other key species such as predators (based on this study's eDNA data). See Table S2 for full details. Artificial and natural barriers downstream were combined before being reclassified into three types following SEPA's guidelines: 'passable barriers with fish passes', 'passable barriers without fish passes' and 'impassable barriers' (SEPA-WMS, 2018). Due to limited accurate information on the distribution of beaver dams at the time of surveying, their presence was not factored into the current study.

Land Cover Maps (Morton et al., 2024) were used to calculate upstream land-use within a 25 m buffer either side of all contiguous rivers located within a buffer extending 1 km upstream of each site. To simplify the land-use categories, composite groupings were created: Urban (Urban + Suburban), Wetland (Fen, Marsh and Swamp + Bog), Acid Moorland (Acid Grassland + Heather Grassland + Heather and Shrub) and Agricultural (Arable + Improved Grassland). Freshwater land-use was omitted from analyses as the rivers sampled were often too small to be recorded on the land cover map.

The detection of Northern pike (*Esox lucius*) was derived from the 2023 eDNA samples to assess the effect of the overlap of a potential predator species on migratory fish. Other predator species such as Eurasian otter (*Lutra lutra*) were not included in this analysis as they have a low detection probability based on eDNA sampling (Broadhurst et al., 2021). Lastly, the distribution of beavers was incorporated from the 2023 eDNA surveys as 1 (detections) and 0 (non-detections) to investigate the effects of beaver eDNA detections on the distribution of each migratory fish species.

2.8 | Model selection

Principal component analysis was used to reduce land-use, catchment and climate covariate complexity (Figure S2). Correlation matrices were used throughout to ensure highly correlated variables were omitted and a variance inflation factor threshold of <5 was used to avoid multicollinearity in the final models. Channel slope and mean atmospheric temperature, bankfull river width and acid moorland were all omitted from the final models as they were highly correlated with elevation, upstream catchment area and impassable barriers, respectively. All continuous variables except for pH and distance from coast were $\log_{10}$ transformed to improve their distribution. Variables were mean centred to 1 SD and scaled to improve comparability and reduce the impacts of outliers (Law, Baker, et al., 2019).

A series of binomial generalised linear models were used to investigate the effects of covariates on the eDNA detections of migratory fish species. A reverse stepwise approach was used to select the most parsimonious model for each species based on the lowest Akaike Information Criterion (AIC) (Table S3). Initially, catchment identity was added as a random effect in generalised linear mixed models using the R package 'lme4' (Bates et al., 2015); however, it did not improve the model AIC and was therefore removed. Between the full and most parsimonious models, the AIC improved by ≥10 for each migratory fish species whilst effect directions remained consistent (Table S3). We considered all variables which were retained following the model selection to be meaningful, but also report statistical significance at the 95% confidence level to highlight where relationships exhibit strong evidence versus weaker evidence (retention in the most parsimonious model but with $p > 0.05$). Finally, an interaction term between beavers and elevation was included as elevation was shown to have a significant negative correlation with beaver eDNA detections across Tayside (Figure S3).

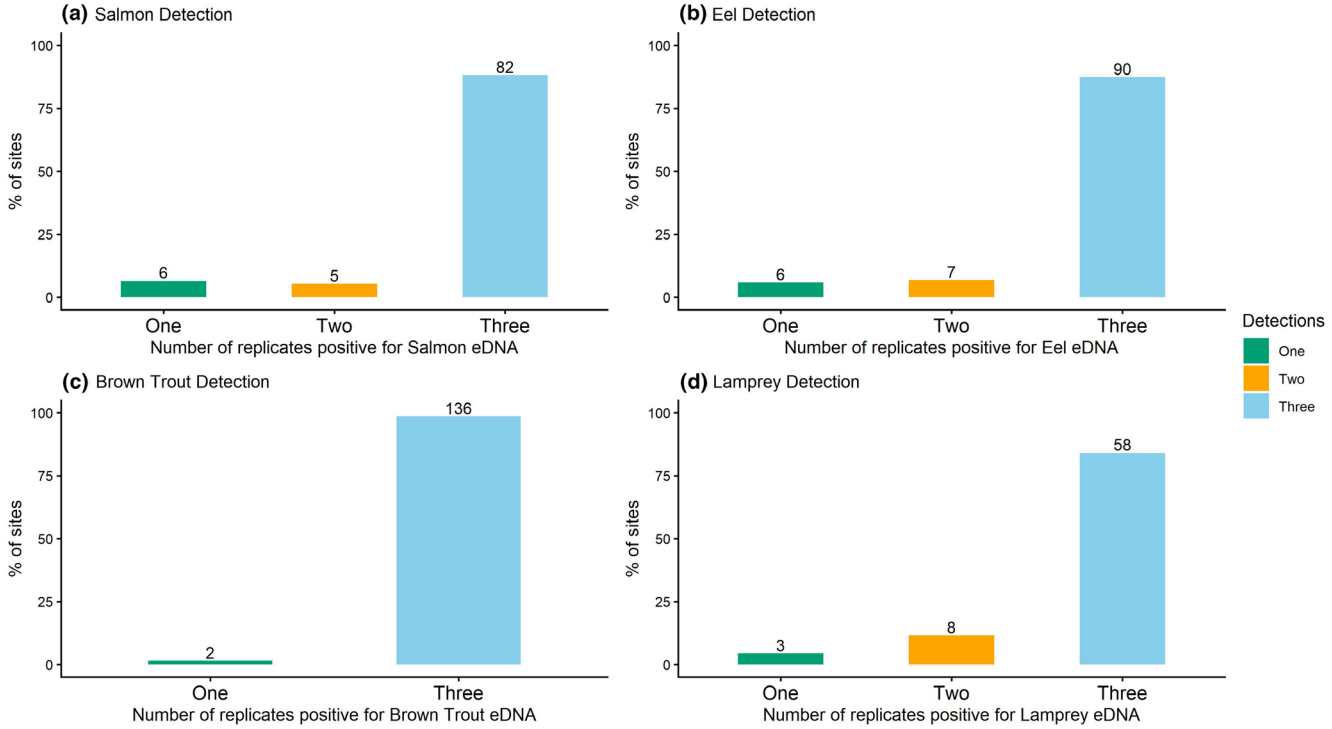

FIGURE 2 Species detections across the three biological replicates for the four migratory fish species (a, Atlantic salmon; b, European eel; c, brown trout; d, lamprey). Bars are coloured based on the number of replicates positive (one = green, two = yellow, three = blue) and the numbers above the bars represent the number of positive sites.

	Trout (%)	Salmon (%)	Eels (%)	Lamprey (%)
Beavers and migratory fish	48.6	35.9	44.4	30.3
Migratory fish only	48.6	29.6	28.2	18.3
Beavers only	2.1	14.8	6.3	20.4
Neither	0.7	19.7	21.1	31

TABLE 1 Percentage overlap between beavers and migratory fish across the 142 eDNA sites.

The full models were:

Migratory fish species ~ Impassable barriers + Passable barriers with fish passes + Passable barriers without fish passes + Upstream catchment area + Total rainfall + Elevation + pH + Distance from coast + Beavers + Pike + Agricultural + Broadleaved Woodland + Coniferous woodland + Urban + Wetland + Beavers × Elevation

3 | RESULTS

Beaver eDNA was detected in 72/142 (50.7%) sites, of which 79% were positive across all three replicates (Figure S4). Twenty-eight out of thirty-four (82.4%) sites with beaver field signs from 2021 within a 500 m circular buffer were positive for beaver eDNA in 2023. Beaver eDNA was detected at 44/108 (40.7%) sites which did not have field signs within a 500 m circular buffer from 2021, and 33/76 (43.4%) of these sites overlapped historic salmon distribution. Four migratory fish species: brown trout, salmon, eels and lamprey (*Lampetra* spp.) were detected across the 142 sites (Figure 2). Sea lamprey (*Petromyzon marinus*) were not detected in the current study. There was considerable overlap between beavers and migratory fish across Tayside (Table 1; Figures S9–S12). Brown trout were detected at 138 (97.2%) sites which meant there were insufficient absences to model drivers of their distribution. Salmon were detected in 93 (65.5%) sites, of which 88% were positive across three replicates (Figure 2). Lamprey were found at 69 (48.6%) sites (84% positive across three replicates) and eels at 103 (72.5%) sites (87% positive across three replicates). Occurrence of these three species was therefore modelled (Figure 3; Figures S5–S8; Tables S3–S5).

There was no evidence for an effect of beaver eDNA detections on the distribution of salmon or lamprey, with beavers not included in the final model for both species. However, a positive co-occurrence was demonstrated between beavers and eels ($p < 0.05$) (Figure S5). Contrastingly, the eDNA detections of pike had a moderately negative effect on the distribution of salmon ($p < 0.01$) but not on the other migratory fish species.

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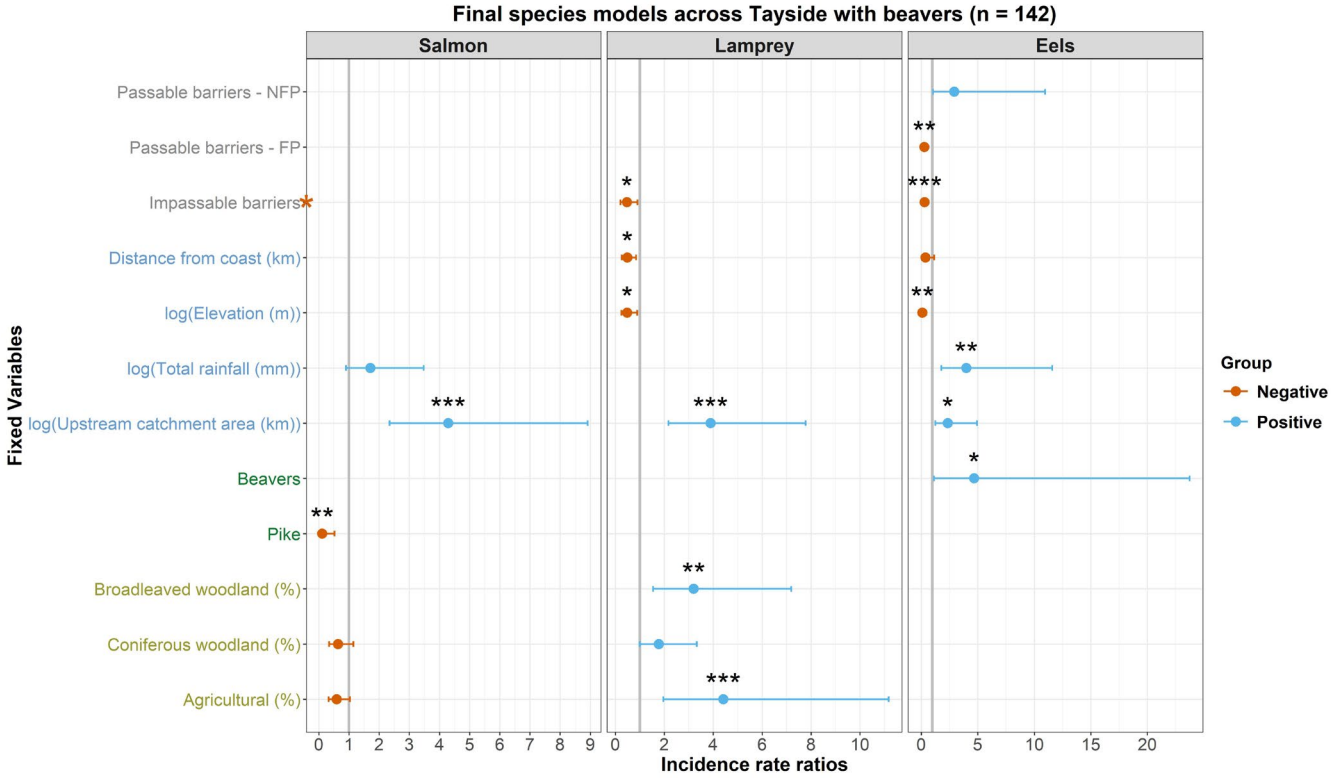

FIGURE 3 Final model outputs for the migratory fish species. Lines are coloured by effect (Negative = Orange, Positive = Blue) and asterisks denote the level of significance (* = 0.05, ** = 0.01, *** = 0.001). Covariate text is coloured by type (Barriers = Grey, Physical = Blue, Species = Green, Land-Use = Yellow) and the whiskers represent the 95% confidence interval. The orange * represents the effect of impassable barriers on salmon which could not be modelled as there were no detections upstream of these waterfalls. Fixed variables with log () refers to $\log_{10}$ transformation.

Impassable barriers had a consistent negative effect on all three migratory fish species (eels: $p < 0.001$; lamprey: $p < 0.05$). No salmon were detected upstream of impassable barriers; therefore the 22 sites upstream of impassable barriers were omitted from the salmon models. Barriers with fish passes also had a strong negative effect on the distribution of eels ($p < 0.01$). The distribution of all three migratory fish species was positively correlated with upstream catchment area (salmon: $p < 0.001$; lamprey: $p < 0.001$; eels: $p < 0.05$). Lamprey and eel eDNA detections were both negatively correlated with elevation (lamprey: $p < 0.05$; eels: $p < 0.01$). Distance from the coast had a negative effect on the distribution of lamprey ($p < 0.05$), and eels had a positive association with total rainfall (eels: $p < 0.01$).

The percentage cover of agricultural land had the largest positive effect of land-use on lamprey distribution ($p < 0.001$). Broadleaved woodland ($p < 0.01$) was also positively associated with the eDNA detections of lamprey. Land-use had no effects on eel eDNA detections and was dropped from the final model.

Finally, there was some evidence through their retention by AIC that the following variables influenced migratory fish species distributions; however, these effects were non-significant at the 95% level in the final models (Figure 3). Eels were positively associated with passable barriers without fish passes ($p = 0.073$) and negatively correlated with distance from the coast ($p = 0.111$). Salmon distribution was positively correlated with total rainfall ($p = 0.113$) and negatively associated with the percentage cover of coniferous woodland ($p = 0.137$) and agricultural land ($p = 0.071$). In contrast, lamprey distribution was positively correlated with coniferous woodland cover ($p = 0.057$).

4 | DISCUSSION

This study provides a novel, catchment-scale investigation into the possible effects of beaver detections on migratory fish distribution using eDNA metabarcoding. By integrating species eDNA detections with environmental and anthropogenic covariates, our results offer new insights into the renewed coexistence of beavers and fish species, particularly in the context of conservation translocation initiatives. Alongside this, these models revealed effects of both natural and anthropogenic barriers, distinct environmental and land-use correlates, and predator interactions consistent with existing literature and exemplifying the effectiveness of eDNA sampling as a basis for understanding species distributions and their drivers.

4.1 | Interactions between beavers and migratory fish

We found no evidence that beaver eDNA detection negatively affects the distribution of salmon, trout, eels or lamprey across Tayside, despite the ongoing expansion of beaver populations

(Campbell-Palmer et al., 2021). A number of prior studies corroborate these findings and have demonstrated that brown trout in Scotland (Needham et al., 2021, 2025) and juvenile salmonids in Norway (Malison & Halley, 2020) could navigate beaver dams. However, these studies were limited to a small number of streams or particular sets of dams, constraints that make it difficult to infer landscape-scale impacts. Beaver impacts are highly variable, being influenced by the surrounding environmental conditions, underlying hydrology, beaver densities and local habitat characteristics, all of which determine the type, size, stability and longevity of their habitat modifications (Cutting et al., 2018; Lokteff et al., 2013; Marshall Wolf et al., 2024; Naiman et al., 1986). In contrast, our study investigated the impact of eDNA-inferred beaver detections on catchment-scale migratory fish distributions where the current broad-scale coexistence of both beavers and migratory species is evident. It is important to note that few beaver dams were observed in the current study, as is typical of large, higher gradient or higher order riverine systems. Dams are also regularly removed as part of conflict mitigation largely in relation to agricultural activities (Campbell-Palmer et al., 2021); therefore, the full effects of beaver activity on migratory fish in Tayside are unlikely to currently be captured and might change as the beaver population expands.

Past studies on migratory fish species have primarily focused on salmonids (Cutting et al., 2018; Lokteff et al., 2013; Malison & Halley, 2020; Needham et al., 2021, 2025), whilst eDNA enabled us to additionally obtain robust detection estimates of non-salmonid fishes such as lamprey and eel. The finding that beavers are positively co-distributed with eels across Tayside is consistent with Elmeros et al. (2003) who suggested that due to their leaky nature, beaver dams were not barriers to eels. Indeed, it is likely that the modifications by beavers will provide increased habitat complexity through higher in-channel coarse wood and connectivity to the floodplain which would benefit eels (Harwood et al., 2022).

4.2 | Other drivers of fish distribution

The consistent negative effect of impassable barriers on migratory fish species demonstrates the utility of eDNA in confirming the passability of both natural and artificial barriers downstream. The degree to which impassable barriers affected each species varied; whilst salmon could not navigate any of the 17 known barriers, lamprey and eels were detected upstream of two and five barriers, respectively. This showcases the importance of classifying barrier passability relative to individual species (Silva et al., 2018). The complete absence of salmon eDNA above these waterfalls was unsurprising, as the barrier classification was largely informed by knowledge of existing salmon distribution (Gardiner & Egglishaw, 1986; SEPA-WMS, 2018), but it serves as a useful validation of the eDNA approach. The detections of lamprey eDNA upstream of two waterfalls likely reflect freshwater-resident populations of brook lamprey. However, these waterfalls are probably impassable to the anadromous river lamprey as recorded on the Endrick Water at the Pots of Gartness (Bull et al., 2016). Unfortunately, our current eDNA assay cannot distinguish these two closely related species.

Notably, our results indicated a negative effect of barriers with fish passes on the distribution of eels. This aligns with previous research showing that hydropower infrastructure can hinder the upstream migration of juvenile eels (elvers) (Feunteun, 2002). Whilst elver passes can improve access upstream (Solomon & Beach, 2004), the broader challenge is to ensure suitable downstream migration opportunities for adult silver eels (Piper et al., 2013). The current approach in Scotland is that since safe downstream passage through hydropower dams cannot be enabled, it is better to restrict access upstream entirely. However, with the continued decline of European eels throughout their range (Nunn et al., 2023) and the detection of eels upstream of these barriers in our present study, downstream passage solutions should be considered. This reinforces the need for species-specific passage solutions that account for the unique migratory behaviours and vulnerabilities of different life stages (Silva et al., 2018).

Our findings reveal distinct environmental and land-use correlates for species distributions, emphasising the need for species-specific conservation strategies. The positive association between upstream catchment area and the eDNA detections of all three fish species highlights the importance of larger, well-connected river systems in supporting migratory pathways and habitat availability. Distance from coast and elevation were both negatively associated with eel and lamprey eDNA detections. This is consistent with Griffiths et al. (2023) who found that eel eDNA detections in Cyprus declined with distance from coast, number of barriers and elevation. However, for lamprey, research from Portugal suggests that this relationship is a product of the shallow gradient microhabitats created in these conditions which provide a favourable silty substrate for ammocoete development (Ferreira et al., 2013). The distribution of lamprey across Tayside was positively correlated with agricultural, broadleaved and coniferous woodland cover which could all benefit ammocoetes through increased fine sediment (Bull et al., 2016). In contrast, there was some evidence that agricultural land had a weak negative effect on salmon eDNA detections, likely because fine sediment deposition could render spawning gravels unsuitable for salmonids (Soulsby et al., 2001). Meanwhile, eel distributions were not influenced by land-use, perhaps reflecting their high level of plasticity to environmental variation (Enbody et al., 2021).

Excluding sites upstream of impassable barriers, salmon were absent from 6 of the 19 sites across Tayside in which pike were detected. This finding could be a direct result of predation as pike are known to predate migrating salmonid smolts (Falkegård et al., 2023) or it could reflect differing habitat requirements of the two species as pike typically inhabit slower flowing systems (Beaver Salmonid Working Group, 2015) whilst salmon utilise faster flowing rivers (Soulsby et al., 2001). Beaver ponds on smaller water courses could support more predatory fish such as pike or piscivorous brown

trout; therefore, predation of juvenile Atlantic salmon might become more of an issue as the Tayside beaver population expands (Beaver Salmonid Working Group, 2015).

4.3 | Limitations of eDNA

The application of eDNA metabarcoding at the catchment scale represents a significant methodological advancement in ecological monitoring. However, several limitations must be acknowledged (Goldberg et al., 2016).

First, our study infers only the eDNA detection or non-detection of species, rather than providing semi-quantitative estimates of abundance. Whilst a clear correlation between DNA sequence abundance and relative fish abundance has been demonstrated (Di Muri et al., 2020; Griffiths et al., 2020), this relationship has not yet been established for other vertebrates. As such, our conclusions are limited to the spatial distribution of species across the catchment, and we are unable to assess the effects of beavers or other covariates on the abundance of migratory species. Additionally, eDNA does not allow for the identification of life stages; therefore, the detection of a species is treated as a composite signal encompassing all life stages. Consequently, we are unable to differentiate life-stage-specific habitat preferences (Harwood et al., 2022). We recommend that eDNA monitoring be complemented with targeted electrofishing surveys to assess changes in fish population dynamics and resilience following beaver-related habitat modifications.

Finally, the downstream transportation of eDNA may lead to false positives. In lotic systems, DNA can be carried from its source for distances ranging from hundreds of metres in small streams to over 100 km in very large rivers (Pont, 2024; Pont et al., 2018). Whilst transport distances vary with river size and flow conditions, the rivers in our study are small to medium-sized, disrupted by artificial barriers, and were sampled during low-flow summer conditions, which reduces the likelihood of extensive eDNA transport. Although we cannot entirely rule out occasional long-distance transport beyond our 5 km sampling intervals, we therefore consider this unlikely to be a major source of error. Regarding beaver–migratory fish interactions, the detection of migratory fish upstream of beaver activity suggests these species had successfully traversed beaver-occupied areas downstream to reach the sampling site.

4.4 | Wider applications

This study highlights the value of catchment-scale eDNA metabarcoding for assessing species distributions and interactions, offering a practical tool to evaluate the ecological impacts of beaver reintroductions and other environmental factors on migratory fish. Conventional methods for studying barrier effects on fish migration are often costly, spatially limited and potentially disruptive (Kemp & O'hanley, 2010). eDNA provides a non-invasive alternative, where discontinuity in species detections upstream versus downstream of a structure may signal an unrecognised migration barrier (Laramie et al., 2015). With its capacity for repeated, high-resolution sampling, eDNA also enables tracking of seasonal migration and evaluation of barrier mitigation efforts.

Our findings inform management strategies as beaver populations grow across Europe. The lack of evidence towards negative effects on the distribution of salmon, brown trout and lamprey suggests beaver reintroductions can align with their conservation, especially where habitat connectivity is maintained. The positive link with eels also points to potential habitat benefits for declining species. However, further research is needed to study the impacts of beaver-habitat modifications on migratory fish population structures and abundance. Enhancing fish passage infrastructure at anthropogenic barriers remains essential to maximise the ecological gains of beaver reintroductions whilst safeguarding migratory fish.

AUTHOR CONTRIBUTIONS

James A. Macarthur led on data collection, analysis, writing and conceptualisation. Alan Law and Nigel J. Willby advised on design and analysis. Dasha Svobodova provided laboratory support. Nathan P. Griffiths advised on laboratory work and conceptualisation. Roo D. Campbell provided data and assisted in contacting landowners. Martin J. Gaywood, Colin W. Bean, Lori Lawson Handley, Melanie Smith, Shaun Leonard, Chris Conroy and Victoria L. Pritchard advised on design and writing. Bernd Hänfling led on supervision and advised throughout conceptualisation. All authors contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

All scripts and corresponding data have been archived and made available at Zenodo: https://doi.org/10.5281/zenodo.20669069 (Macarthur, 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Existing data on migratory fish distributions, the distribution of non-salmonid migratory fish species were taken from the 2018 NEPS electrofishing fish counts.

Figure S2. PCA used throughout the model selection process to reduce land-use, climate and watershed covariate complexity.

Figure S3. Covariates significantly affecting beaver distribution across Tayside ($p < 0.05$) (Negative effect = orange) and the shading represents the 95% confidence interval.

Figure S4. Species detections across the three biological replicates for the Eurasian beaver. Bars are coloured based on the number of replicates positive (one = green, two = yellow, three = blue) and the numbers above the bars represent the number of positive sites.

Figure S5. The effects of beavers on the three migratory fish species before beavers are dropped from the salmon and lamprey models, the lines are coloured based on significance ($p < 0.05$) (non-significant interactions = grey, significant interactions = blue) and the shading represents the 95% confidence interval.

Figure S6. Covariates significantly affecting salmon distribution ($p < 0.05$) (Positive effect = blue, Negative effect = orange) and the shading represents the 95% confidence interval.

Figure S7. Covariates significantly affecting Lamprey distribution ($p < 0.05$) (Positive effect = blue, Negative effect = orange) and the shading represents the 95% confidence interval.

Figure S8. Covariates significantly affecting eel distribution ($p < 0.05$) (Positive effect = blue, Negative effect = orange) and the shading represents the 95% confidence interval.

Figure S9. Brown trout ($n = 138$) and beaver ($n = 72$) positive eDNA sites across the 142 sampling locations.

Figure S10. European eel ($n = 103$) and beaver ($n = 72$) positive eDNA sites across the 142 sampling locations.

Figure S11. Lamprey ($n = 69$) and beaver ($n = 72$) positive eDNA sites across the 142 sampling locations.

Figure S12. Atlantic salmon ($n = 93$) and beaver ($n = 72$) positive eDNA sites across the 142 sampling locations.

Methods S1. Detailed metabarcoding workflow.

Table S1. Detection probabilities in both a single replicate and across the three replicates for each migratory fish species and beavers calculated using occupancy models in the package 'unmarked' (Fiske & Chandler, 2011).

Table S2. Full list of model covariates alongside their appropriate spatial datasets.

Table S3. Model AIC values throughout the stepwise selection process.

Table S4. Final model covariates alongside descriptive statistics and which of the parsimonious final models each covariate was retained.

Table S5. Final model summaries.

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