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A national scale floodplain model revealing channel gradient as a key determinant of beaver dam occurrence and inundation potential can anticipate land-use based opportunities and conflicts for river restoration

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ABSTRACT

The Eurasian beaver (*Castor fiber*) has expanded its range considerably due to reintroduction and conservation efforts and the species is now found in more than 30 countries across Europe. This expansion brings with it opportunities for nature restoration, the provision of river ecosystem services and the return of naturally functioning floodplains. It also has the potential for conflict with existing human land-use through dam induced floodplain inundation and wetland development. To maximise restoration benefits and minimise conflict, modelling approaches are needed that can predict the likelihood of dam building and include scenarios for subsequent floodplain inundation. This study describes the first national-scale comprehensive study on the drivers of beaver dam occurrence and beaver floodplain inundation potential. This revealed that channel gradient was the overriding driver of both dam occurrence and potential land-use impact. Although widely considered to be a key constraint, channel width exhibited considerably lower explanatory power. The delineation of areas reflecting overall opportunities and conflict reveals that the reintroduction of *Castor fiber* into Switzerland implies a net benefit from a landscape restoration perspective, though outcomes scaled closely with catchment position. Given the rapidly expanding population range and popularity of continuing beaver reintroductions, this approach could help maximise landscape restoration goals whilst minimising undesirable land-use conflicts that may harm conservation efforts.

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1. Introduction

Natural habitats are in global decline (Dornelas et al., 2023) and measures to aid their recovery require practical tools for the identification and implementation of restoration opportunities whilst avoiding threats to livelihoods and societal needs. One such measure involves the reintroduction of keystone species into their former ranges to restore lost processes important for nature recovery. The Eurasian Beaver (*Castor fiber*) has expanded its range considerably since reintroduction efforts first began in the 1950s and the species is now found in more than 30 countries across Europe with more than 1.5 million individuals (Halley et al., 2020). This expansion is likely to continue according to recent modelling work that shows as yet unoccupied areas of suitable habitat in Europe (Serva et al., 2023). Beavers are a highly influential mammalian ecosystem engineer, heavily modifying rivers and floodplains and influencing hydrology, geomorphology, nutrient cycling, and ecology (Larsen et al., 2021, Wohl, 2019). They do this by constructing dams, digging canals and burrows, felling trees and introducing wood into streams. This in turn impounds water, raises shallow water tables, and alters the water balance, sediment transport and channel patterns, biogeochemical cycling, and aquatic and terrestrial habitats (Larsen et al., 2021). Damming behaviour by beavers can provide important ecosystem services including: increased surface and subsurface water storage, site specific flood attenuation, increased water and nutrient residence times, increased carbon and nutrient storage, decreased export of nitrate and increased aquatic primary production on a reach scale. Profound changes to biodiversity within beaver-impacted ecosystems have also been demonstrated (Rosell et al., 2005).

The expansion of this species in Europe and its ecological effects have been keenly monitored (Orazi et al., 2022; Law et al., 2019; Mori et al., 2024; Serva et al., 2024). In this regard, there is much interest in their damming behaviour, being the principal mechanism through which the species is thought to disproportionately impact biodiversity (Minnig et al., 2024; Muller-Schwarze 2011; Nummi et al., 2019; Wright et al., 2002). However, their ability to modify and restructure riparian habitats presents both opportunities from an ecological restoration point of view as well as challenges from a conflict management perspective. A current challenge, that this paper seeks address, is to understand the environmental and societal constraints, as indicated by current land-use, that will influence whether the impacts of damming are likely to have positive or negative outcomes throughout the river network. In particular, the avoidance of potential conflicts, such as when flood damage to local infrastructure (e.g. buildings, roads; Wróbel and Krysztofiak-Kaniewska, 2020) or to agricultural and forestry land (TBSG, 2015) occurs, is critical to ensuring successful conservation outcomes (Auster et al., 2021). Conversely, it is important to identify sites where beavers are likely to contribute to nature restoration and re-naturalisation efforts, particularly in heavily managed landscapes. For example, wetlands are named as priority habitats within current EU nature restoration laws (European Commission, 2022) and beaver populations may provide a cost-effective route to achieving aligned goals.

In the North American context, the beaver (*Castor canadensis*) has been viewed as a driver of desirable hydro-ecological outcomes such that the American beaver is considered a landscape restoration option with associated toolkits for planning and verification (Macfarlane et al., 2017; Majerova et al., 2015; Majerova et al., 2020; Weber et al., 2017, Wohl, 2019). However, the capacity of beavers to build dams, and its subsequent environmental effects, is highly context dependant (Larsen et al., 2021). This context needs to be at the core of planning or projecting potential environmental impacts and feedbacks. Hence, models developed for the North American context, are likely not directly transferable to Europe due to climatic, geomorphic, and cultural differences, and human population density. More specifically, Europe has a long, spatially variable history of river-floodplain modification including river channel engineering and floodplain agricultural land-use, which today manifests itself as a heterogeneous mix of cultural landscapes with variable population densities (Tieskens et al., 2017) with limited natural processes and feedbacks. This context dependency of beaver dam effects, in combination with the absence of beavers for hundreds, sometimes thousands, of years from many parts of Europe, means that the potential for conflict with existing land-use in highly managed landscapes in the European context is very high. Therefore, for beaver dam models to be useful, they must consider not only the ecological context, but also human activity in areas susceptible to beaver damming. It is therefore important that such models are spatially explicit, emphasising potential areas susceptible to beaver dam-related flooding.

Restoration tools such as the Beaver Restoration Assessment Tool (BRAT, McFarlane et al., 2017) have been used to model restoration opportunities primarily for *Castor canadensis*, and consider dam capacity along rivers. This method has been adapted in Great Britain (Graham et al., 2020). More recently, Mori et al. (2024) have mapped the return and initial expansion of beaver to Italy and Serva et al. (2023); (2024) have estimated likely habitat suitability at the European scale and expansion of beaver throughout Italy and in the Iberian Peninsula. Although these studies have produced important knowledge on likely range expansion, they do not provide information on the likelihood that beavers will build dams, which is necessary in order to predict where beavers will have greatest social and environmental impact. Indeed, habitat suitability and damming "suitability" are not commensurate. This is because of the possibility that high habitat suitability may in fact coincide with low damming probability (e.g. in locations with ample food resources and where existing within-channel water depth is already sufficient for beavers to have underwater access to their lodge). Therefore, existing approaches to modelling beaver distribution do not provide any information on the potential floodplain area affected, which is an essential component of the river corridor impacted by beavers. There is thus a need to estimate the potential floodplain area impacted by damming, e.g. through flooding of adjacent land-use and the creation of wetlands, so that the relative extent of positive (e.g. increased water retention, biodiversity gains) and negative (e.g. damage to infrastructure, loss of crops) outcomes can be estimated. Previous studies have demonstrated that local context is critical to perceived and realized impacts in terms of both ecological and societal outcomes (Auster et al., 2020). However, understanding the impacts of beaver colonisation of river catchments at scale is also of vital importance in order for administrative powers and environmental agencies to develop both restoration and mitigation strategies for this highly adaptive and successful species. The aim of this paper is to address that need.

1.1. High context-dependency of beaver impacts requires spatially-explicit riparian restoration tools

Understanding the controls on the spatial distribution of beaver dams and their inundation potential is a key pre-requisite for effective management of this species and the targeting of specific goals. However, understanding the large-scale potential impacts of beaver ecosystem engineering is limited by a lack of spatially explicit information. For example, Thompson et al. (2021) estimated the total benefit of beaver modifications to riparian landscapes at scale via an assessment of related ecosystem services. However, the study employed coarse-grain beaver range maps (e.g. as produced by Halley et al., (2012)) and made predictions of dam building likelihood based on broad assumptions that may easily be violated at local scales. Graham et al., (2020) predicted beaver dam capacity for river catchments in Great Britain at a fine scale, but did not develop this into estimations of inundation (i.e. impact) potential. In order to ensure effective implementation of restoration strategies through the presence of beaver, it is essential to better understand the environmental conditions under which such interventions are likely to be successful. This requires fine-grained information on both the likelihood of beaver dam building, the resulting inundation potential and the impact on surrounding land-use. This requires the integration of key indicators to a) identifying constraints in river networks that determine where dam building is likely to occur and why, b) the development of potential floodplain inundation scenarios to extrapolate at scale and c) the integration of land-use data and criteria to estimate, and avoid, potential conflicts with other land-uses in productive landscapes. Such approaches can then be operationalised to maximise benefits to ecosystem recovery whilst avoiding undesirable land-use conflicts. This study provides the first method for the comprehensive and large-scale assessment of the overall (i.e. integrating positive and negative) impacts of the (re) introduction of *Castor fiber*.

1.2. Context dependant, floodplain-wide models of beaver impacts are needed

Beaver dams reduce water velocity and increase the in-channel water level, creating a beaver pond, which corresponds to the extent of the created backwater effect. Within un- or semi-confined river valleys where the river channel can more easily hydrologically connect with its floodplain, these ponds can be spatially extensive and grade into wetlands or swamps (often termed beaver meadows) (Chaubey and Ward, 2006; Naiman et al., 1988). Through flow diversion of stream water from the channel onto the floodplain, associated with the rise of the water table within the shallow alluvial aquifer, floodplain inundation can also be far more extensive in space and time than would otherwise occur without beaver dams, especially during flood events (Westbrook et al., 2011). Typically, mature beaver meadows span the entire floodplain width (John et al., 2010, Wohl, 2013). The main positive (e.g. increased biodiversity, drought mitigation) and negative (e.g. infrastructure and crop damage) impacts associated with damming therefore critically depend on the extent of inundation possible, which varies considerably with the flow conditions, local topography and channel morphology.

1.3. Understanding physical constraints on beaver dam occurrence

Amongst all the physical properties of river networks, channel width is often used exclusively to estimate the limits of beaver damming ability, and in the few studies that have compiled stream geometry information where beaver dams occur, they generally find a decrease in dam occurrence frequency with increasing stream width. In Sweden, Hartman and Törnlöv (2006) found that at stream widths > 4 m, beaver dams were far less likely to occur compared to streambank burrows. In Germany, Zahner et al. (2015) also found a large decrease in dam frequency at channel widths > 4 m and Neumayer et al. (2020) after 5 m. It seems intuitive that beavers would have increasing difficulty damming larger rivers due to a combination of hydraulic and force balance considerations, but it is unclear whether a threshold (of e.g. 4 or 5 m) is representative of these physical limits and therefore useful to managers aiming to estimate the likelihood of beaver dams occurring. This is because the width thresholds are also subject to sampling bias from two important sources:

1) the far greater abundance of smaller channels relative to larger ones in river networks. This means there are many more smaller channels than larger channels for beavers to occupy, which may naturally generate a higher frequency of dams being counted in smaller channels, but does not confirm the selection of smaller streams versus large ones.

2) a decrease in the capacity for higher dam densities (e.g. number of dams per km) with decreasing channel slope. Low stream order channels (also usually smaller in width) are typically located in catchment headwaters which tend to have greater slope than higher stream order channels (which also have increasing channel width). Beavers are therefore less likely to be able to maintain high dam densities at low channel slopes regardless of channel width, thus also diminishing the dam frequency in these larger channels.

In combination, these effects may skew dam frequency distributions towards smaller channels. This may largely account for the approximate 4 m threshold currently found in the literature, rather than local hydraulic and force balance processes. In order to understand these effects and estimate the probability of dam occurrence throughout entire river networks, data on existing dam locations across a range of river geometry attributes are required to determine the key drivers. Here, we determine these drivers for beaver damming behaviour and the resulting expected impounding of water (hereafter referred to as "beaver floodplains") based on an extensive dataset of beaver dam locations and riparian environment characteristics for Switzerland (Angst et al., (2023); Info Fauna Switzerland (2023)). We focus on Switzerland here for two main reasons: 1) its large range of topographic and hydromorphic conditions in combination with a long history (between 1956 and 1977) of beaver re-introduction resulting in a comparatively large beaver population (estimated 4900 beavers in 2022 (Angst et al., 2023) and 2) the availability of an extensive and long-term dataset on beaver dam locations for the whole country. We used the size and location of modelled beaver floodplains to predict areas of potential conflict and opportunity, characterised as a function of land-use and land-cover.

Our general expectation was that the relative impacts (both opportunities and conflicts) of beaver floodplains would be highly constrained by physical processes. We supposed that both beaver damming behaviour and anthropogenic land-use (i.e. the presence of agriculture and settlements) would be constrained by topography (i.e. channel and floodplain dimensions and location). This is because beaver dam locations are closely related to river geometry and the distribution of high value land-use that is potentially vulnerable to flooding, as a result of the creation of beaver floodplains, is likewise constrained by topographic factors, where highly productive agricultural land generally occurs on flat floodplain areas. In natural systems, it would be expected that areas suitable for beavers to build dams (i.e. streams of low width with low to moderate slope) should generally occur within a specific range satisfying these conditions, likely at mid-to-low-altitudinal levels within the catchment (Fig. 1). At elevations higher than this, topographic characteristics, principally slope, and climatic conditions will often exceed the upper range at which beavers can colonise and effectively dam. Likewise, at elevations lower than this, the main river channel width is likely to exceed the damming capabilities of beavers. This suggests that regions with large rivers and associated floodplains with high agricultural productivity should generally be free from the impacts of beaver-derived flooding. However, most modern-day agricultural systems also contain a high density of artificial channels and watercourses, many of which may be of a suitable width and gradient for dam creation by beavers. This issue, in addition to the smaller natural streams that may otherwise join the main channel in larger floodplains, may lead to significant potential conflict between land-use and free-living beaver populations even in relatively low-lying watersheds with larger rivers (Fig. 1). Given these expected tensions, we hypothesized that the greatest potential for landscape restoration through the introduction of beaver should occur within mid-elevation zones where slope is within the range of tolerance from a beaver dam-building perspective and outside of typical high productivity land-use contexts. Above this zone (i.e. at high elevations) we assumed that increases in both potential benefits and conflicts would be negligible given both the low-intensity of land-use and the high constraints placed on dam construction and floodplain size by topographic conditions.

2. Methods

We compiled existing datasets on beaver dam locations, and hydro-geomorphic river-floodplain characteristics. We used an extensive dataset of beaver dam locations from 1993 to present for the entire area of Switzerland (Info Fauna Switzerland 2023), consisting of 2931 dam locations. We compiled characteristics of streams thought to influence damming behaviour from the global literature, and tested these against the same characteristics from available data for Switzerland. We assembled eco-morphological data on river networks in Switzerland from the Swiss Federal Office for the Environment (FOEN, 2013). Land-use data and the river network were obtained from the Swiss TLM3D (Topographic Landscape Model: SwissTopo 2021).

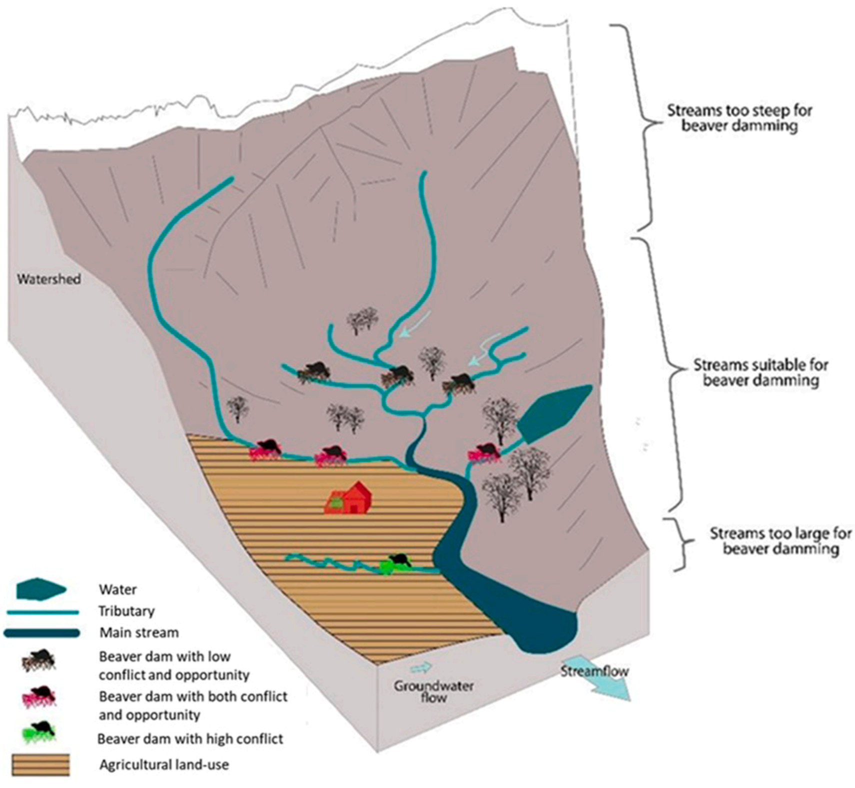

Fig. 1. Zonation of beaver impacts at the catchment scale.

2.1. Geo-statistical approach to model development

We calculated candidate eco-geomorphological predictor variables: channel gradient, channel width, terrain slope, discharge, stream power as well as the proportion of major land-covers (forest, arable, pasture, urban) for a range of buffer widths around stream channels: (100–5000 m). We created GIS layers for each predictor variable. Channel width was obtained from the Eco-morphology dataset produced by the FOEN (2013) and joined to the TLM3D river network using the "Join attributes by location" tool in QGIS 3.34.10 (QGIS.org, 2022). The Eco-morphology and TLM3D datasets are both provided as vector (polyline) data. All other variables computed to characterise river sections were derived from raster data sets and extracted to the TLM3D. Resolutions and sources of these rasters are summarised in Table 1. Channel gradient and terrain slope were computed using a 2 m digital terrain model (DEM) for the whole of Switzerland (SwissTopo 2022). Terrain slope reflects the mean change in elevation between a focal cell in the DEM and its eight neighbours and describes the slope of the terrain around the stream channel. Here, high values denote stream sections that are particularly incised or that lack a well-formed floodplain. Minimum channel gradient was calculated by first rasterizing the stream network using the 2 m DEM as a template (to ensure the same resolution and origin) with the Extract by Mask tool in ArcGIS Pro 2.8.2. Subsequently, minimum gradient was established by calculating, for each cell along the stream channel, the difference in elevation between the cells immediately upstream and downstream of the focal cell (corresponding to a distance of approximately 4 m). The minimum raster cell value for each section in the TLM river network was then recorded. Minimum terrain slope was computed by extracting all cell values from the terrain slope raster to the river network and, for each section, returning the minimum value.

Site measurements of river discharge were not available so instead we used model based estimates of total annual catchment runoff (FOEN, 2019). These estimates are derived from FOEN (2019) data and the PREVAH model developed by Viviroli et al. (2009). Briefly, PREVAH is a spatially distributed rainfall-runoff model that combines topographic information with sub-models for interception (Menzel, 1997), soil water storage and depletion by evapotranspiration (Zappa and Gurtz, 2003) to estimate runoff. In order to convert yearly runoff in units of LT^{-1} to discharge in units of L^3T^{-1} we followed the procedure set out by Pfaundler and Zappa (2006). This involves delineating watersheds for each reach in the stream network from automatically assigned pour points and a 25 m DEM (SwissTopo, 2004), executed in Whitebox (Lindsay, 2016) using the *Whitebox* package in R (Wu and Brown, 2022). Subsequently, we took the mean of all yearly run-off values in a 500 m raster that intersected the catchment polygon. This value is then multiplied by the area of the catchment and converted to $m^3 s^{-1}$ (by dividing by the number of seconds in a year).

Stream power (ω) was calculated as:

$$\omega = \rho\, g\, Q\, s \tag{1}$$

Where ρ is the specific weight of water, g is acceleration due to gravity, Q is discharge and s is channel gradient.

In addition we calculated unit stream power as a function of river width (w):

$$\omega / w \tag{2}$$

Where w is channel width.

A description of all data sources used is given in Table 1.

For each predictor variable we extracted values from the corresponding geo-spatial layer to each river section in the TLM and assigned them to known beaver dam locations in the Beaver Monitoring Census (BMC) based on their spatial intersection. All dams were snapped to the nearest point on the river network with a tolerance set to 20 m. Dams with coordinates outside of this tolerance distance or that intersected river sections with missing data on width were removed from the analysis. We assessed outliers using histograms of width and discharge (Figures S1 and S2). This revealed a small number (~ 2 %) of dams that were snapped to sections of large rivers (with > 0.7 $m^3 s^{-1}$ discharge or > 12 m width). These were inspected individually, suggesting high values were the result of

Table 1
Description of data sets used in this study.

Name	Description	Use in the model	Source
Topographic Landscape Model (swissTLM3D), ver. 1.9	Entire river network and major land-cover for Switzerland	Location of river network and basis of floodplain delineation; identification of forests, wetlands, buildings, roads, rail and built infrastructure for opportunity and conflict mapping	SwissTopo (2021)
River eco-morphology	Data on river characteristics	Extraction of width data for dam distribution model	FOEN (2013)
25 m Land-use raster	Information on land-use at 25 m resolution	Filling in urban land-uses not covered in the TLM	Giuliani et al. (2022)
CCHydro	Total yearly run-off values as 500 m resolution raster averaged for the period 1981–2009	Calculation of discharge for river sections.	FOEN (2019)
Beaver Monitoring Census	Monitoring census of beaver habitats	Location of beaver dams to train the dam distribution model	Angst et al. (2023); National Database Info Fauna (2022)
Swiss Alti 3D	Digital elevation model at 2 m resolution	Calculation of channel gradient and terrain slope, delineation of floodplain areas below simulated dam height.	SwissTopo (2022)
DHM25	Digital elevation model at 25 m resolution	Delineation of watersheds for all streams.	SwissTopo, (2004)

either inaccuracy in the dam coordinates or errors in the river morphology data, and subsequently removed. The final data set for model training consisted of 2481 dams. Although the BMC is comprehensive, and river reaches where dams were not observed can confidently be said to be free of dams, absence points were not formally recorded. We therefore generated pseudo-absence points for model development. Pseudo-absence points were chosen by generating at random a sampling point on each river section in the Eco-morphology dataset that did not intersect dam presence points. This resulted in approximately 115,000 pseudo-absences. From these, an appropriate final number for modelling was ascertained by running consecutive models and sequentially adding 1000 pseudo-absence points until the model performance statistic stabilised. As for dam (presence) locations, we extracted information on predictor variables to the pseudo-absence locations. We then used the presence-absence data to train a distribution model based on standard species distribution modelling algorithms: a general linear model (GLM) and Random Forest. The GLM was parameterized using the *glm* function in base R (R Core Team, 2022) and the Random Forest model was implemented though the *Ranger* package (Wright and Ziegler, 2017). To assess the performance of candidate variables for use in the prediction model we ran univariate GLMs and calculated the contribution of each predictor via the model AIC value. Variables exhibiting significance ($p < 0.05$) in univariate models were entered as candidate variables into the prediction model. All combinations of significant variables were tested with the final model established as that returning the highest area under the receiver-operator's curve (AUC), determined with the *auc* function in the *precrec* package (Saito and Rehmsmeier, 2017). To ensure maximum accuracy and interpretability by users (i.e. to ensure dam occurrence probabilities scaled 0–1 with values >0.5 indicating high damming probability) we employed a weighting scheme such that the weighted sum of presence points equalled that of pseudo-absences according to recommendations elsewhere (Barbet-Massin et al., 2012). We tested for collinearity between predictor variables by computing the variance inflation factor (VIF) of each using the *vif* function in the *CAR* package (Fox and Weisberg, 2019). To test the relative influence of terrain versus land-cover, we ran terrain-only (channel slope, terrain slope, channel width and stream power) and land-cover-only (percentage cover by woodland, urban, arable and pasture) GLM models comparing the performance of each.

Model accuracy was assessed via a spatially partitioned cross-validation approach. This was achieved through a blocking method with the study area divided into a grid (using the *st_make_grid* function in the *sf* package; Pebesma, 2018) so that presence and pseudo-absence points were separated into six folds (regions) using the *st_contains* function in the *sf* package. Five folds were used for model training and the remaining fold for testing, iterating over all folds until each one had been used for testing. We used the best performing model to build a final prediction model that split the entire river network into sections likely and not likely to promote damming behaviour. We adopted a 0.496 threshold for determining predicted presence/absence of beaver dams chosen as the threshold that maximised true positive and true negative rates in the model evaluation. For small (low-order) river sections where information on width was not available, a second model, trained without the addition of width as a covariate, was used to make predictions. Some major rivers had their width entered as zero in the eco-morphology data. These were identified manually and isolated according to their spatial intersection with a polygon layer delineating these major rivers, the latter selected using a search query based on their respective names in QGIS. Intersecting river sections were then set to zero probability in the prediction layer. The search query containing names of all these rivers is given in Section S2.

2.2. Development of Inundation Scenarios

Once the sections of the TLM were identified as "likely" (dam-supporting) or "unlikely" (do not support dams), we built subsequent inundation scenarios in order to assess local impacts. For this, we did not attempt to hydrologically model the flow of water but, rather, our aim was to build broad inundation scenarios to reflect potential floodplain development. We delineated potential beaver floodplains based on the height differential between channels with "likely" dam location status and the surrounding topography. First, we split the dam-supporting river reaches into 50 m sections and selected those with channel gradients of <=4 % as potential damming locations (this value was identified through visual inspection of a histogram of gradient values at known beaver dam locations: Figure S3). Based on the dam-supporting streams and high-resolution surface terrain data (2 m resolution), we then delineated floodplain areas well-suited for the creation of beaver ponds and meadows using an objective (and therefore easily transferable) statistical procedure specifically created to fit this purpose. Here, the potential inundation area is delineated based on the elevation of the local floodplain relative to the stream (water surface) elevation plus an assumed beaver dam height of 0.5 m (chosen according to median dam height in the BMC, Angst et al., 2023). To estimate potential inundation extent, we first masked the 2 m digital elevation model (DEM) within a 100 m buffer perpendicular to dam-supporting locations (the 50 m river sections). This is based on the experience that beaver meadows in Switzerland do not extend more than 100 m away from the main river, and beaver feeding trails are rarely longer than 30 m (Gable et al., 2023). We then identified the lowest point on the river section surface according to the DEM and raised this value by 0.5 m. The potential floodplain extent was then delineated by selecting all cells in the masked DEM below this height. A cost distance measure was employed such that all cells above the dam height and all cells within the channel of major rivers (those listed in Section S2) were set to NA (i.e. cannot be traversed) and cells below dam height set to 1. This ensured that cells separated from the stream channel (e.g. by larger rivers, bunds or areas of higher ground) were removed from the estimated floodplain area if the cost of reaching them exceeded the 100 m threshold. It should be noted that the purpose of the model was to generate a hypothetical inundation without the constraint of needing to identify a fixed dam location, but rather generalized to the stream section. We therefore assume the surface to be agnostic to site specific hydraulics, but conservative in scale by prioritising the lowest point of the discretised river reach. The efficacy of the model was validated against known well-developed beaver wetland complexes.

2.3. Identifying the location and extent of impacts related to beaver inundation potential

Estimated beaver floodplain areas, from the initial dam distribution modelling process, were assigned values reflecting opportunities and potential conflicts. Opportunities reflect potential increases in plant, invertebrate and vertebrate abundance and richness as a function of beaver reintroduction (Law et al., 2019; Orazi et al., 2022), and the potential to improve water quality and storage. Potential conflict arises with proximity to areas of productive land-use, especially settlement areas, transport networks, agriculture, and water management. Different land-uses were delimited using high resolution (2 m) raster data of high value agricultural land, and vector datasets from the Swiss Topographic Landscape Model (TLM: FOEN, 2013) for forest, other natural or semi-natural land-cover and built infrastructure (roads and buildings). Some parts of urban areas were not covered by the TLM dataset and were captured using a recent (25 m) land-cover map of Switzerland (Giuliani et al., 2022). For the road network, all road classes were included but smaller tracks and paths (<3 m width) were assigned the land-use (and subsequent impact value from Table 2) that they intersected.

Land-uses that coincided with beaver influenced floodplain areas were determined using the Intersect tool in ArcGIS Pro 2.8.2 and assigned positive ("opportunity") and negative ("conflict") outcomes according to the values in Table 2. Although some locations may imply both opportunities and conflicts (for example beaver floodplains on highly productive farmland but with the potential to mitigate water quality impacts of agricultural run-off), for simplicity, we assigned only one outcome to each location in the study area. To achieve a conservative estimate of beaver floodplain opportunities, we assumed all land-use polygons with potentially high negative impacts (e.g. high productivity farmland and grey infrastructure) to represent only conflict, even if potential benefits (e.g. biodiversity gains or flood mitigation) were plausible. We assigned low-productivity agricultural land (grasslands, pasture and poor quality arable land) as areas representing opportunity. This reflects the need for the additional allocation of open land for biodiversity. In Switzerland, current projections call for an extra 242,000 ha of land to support nature conservation (Rutishauser et al., 2023). Similar to policy mechanisms in other countries with extensive cultural landscapes (e.g. www.defrafarming.blog.gov.uk), the transition of low value agricultural land to natural habitat is a key mechanism in meeting such goals. Although this scheme provides a template for framing and mapping opportunity and conflict, we note that the emergence of conflict is closely related to the social, economic, ecological and cultural contexts of individual sites. Therefore, although our approach to defining opportunity and conflict facilitates a conservative estimate that allows for large-scale extrapolation, the method and resulting model outputs should, in practice, be interpreted in light of local land management options, stakeholder interests and planning policies.

Fig. 2 gives an overview of the workflow.

3. Results

The dam distribution modelling revealed that stream geometry attributes exhibited the greatest explanatory power for predicting dam occurrence. The area under the receiver operator's curve (AUC) statistic for terrain-only and land-cover-only GLM models was 0.96 and 0.83 respectively. Primary constraints on beaver dam probability were stream gradient, terrain slope and stream power. Although unit stream power exhibited better performance than stream power in univariate models, predictive distribution models performed best (according to AUC score) when stream power and width were entered as separate variables. Similarly, although arable land-use within 100 metres of the channel exhibited a low AIC score in univariate models the inclusion of this variable did not significantly improve the AUC of the final predictive model relative to topographic variables. This was likely a reflection of this land-use acting as a surrogate for landform characteristics (i.e. occurring primarily in areas with low channel gradient and terrain slope). For all land-cover variables, summarizing cover within 100 m produced best model performance.

Table 3 gives AIC scores from univariate models showing that channel gradient explained the greatest amount of variance in the data.

Optimal model performance was achieved through the inclusion of channel gradient, channel width, minimum channel gradient, minimum terrain slope, percentage woodland cover within 100 m of the channel, percentage cover by urban land-use within 100 m of the channel and percentage cover by pasture within 100 m. Models showed no issues associated with collinearity, with acceptable variance inflation factor values (<2). Although the Random Forest model (AUC= 0.99) performed better than the GLM (AUC=0.97)

Table 2
Land-use impacts ("+" indicates opportunities; "-" indicates conflicts and "0" indicates a negligible impact).

Land-use	Impact
Forest	+
Lakes	0
High productivity agricultural land	-
Low productivity agricultural land (grassland, pasture and unproductive arable land).	+
Urban (including urban green spaces and gardens)	-
Rivers	+
Riparian vegetation	+
Scrub	+
Wetlands	+
Rail	-
Transport infrastructure	-
Other productive land-use (industry, horticulture, allotments)	-

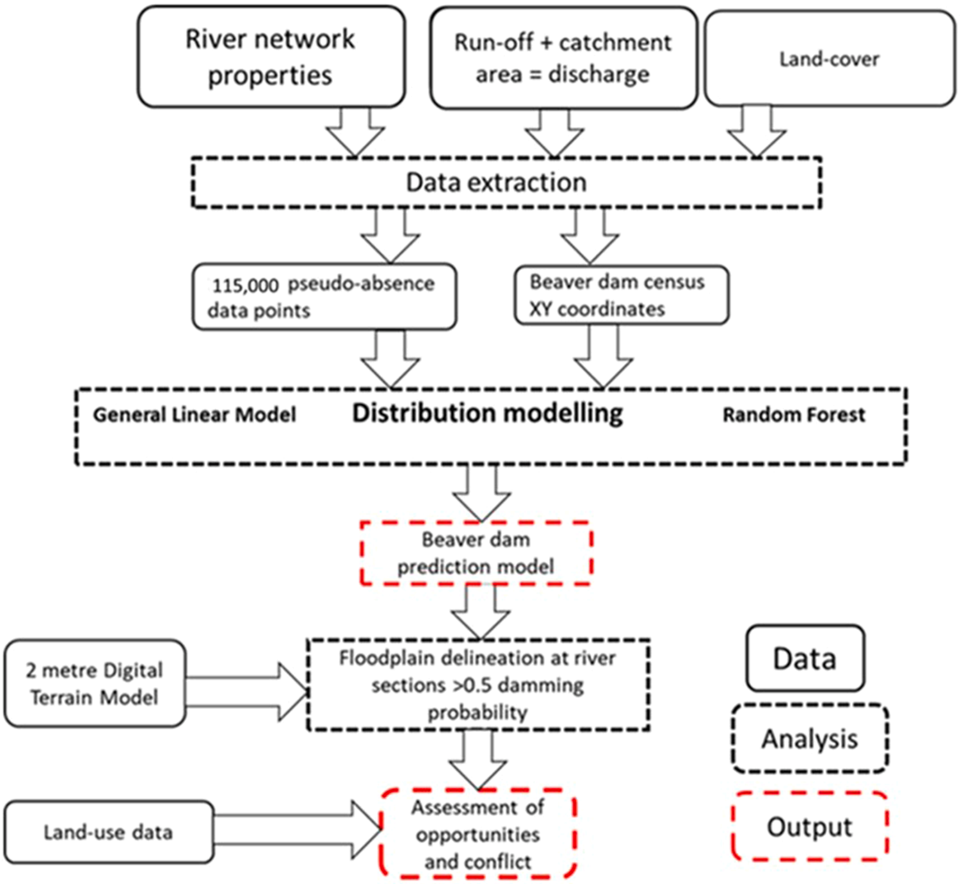

Fig. 2. Work-flow of the analysis.

Table 3
Univariate model results (lower AIC indicates better model performance).

Variable	AIC
Channel Gradient	1635
Terrain slope	2398
Unit Stream Power	2724
Stream Power	2929
Grassland 100 m	3461
Arable 100 m	2767
Discharge	3742
Wood 100 m	3708
Width	3832
Urban 100 m	3930

validated against the entire dataset, the latter exhibited better predictive power in the spatially partitioned cross-validation (AUC=0.97 versus 0.96). The Random Forest model also showed evidence of over-fitting, often predicting dams in rivers of very high width. For this reason, the GLM was used as the basis of the dam prediction layer which informed the subsequent beaver floodplain delineation step. The required number of pseudo-absence points to achieve relative model stability was c. 100,000 but we used the full 115,000 computed for completeness as this did not imply significant extra computational demand. The GLM trained without width also achieved a high level of accuracy (AUC = 0.96).

Channel gradient in particular exhibited a strong negative association with dam occurrence with high dam probability up to gradients of ~ 4 %. Dam probability exhibited a non-linear response to channel width with increases in channel width reducing probability of occurrence to zero beyond approximately 8 m (Fig. 3).

Fig. 4 gives the distribution of dam suitability for all river reaches in Switzerland. In total the length of channels estimated to be able to support at least one beaver dam (i.e. the length of all sections > 0.496 in Fig. 4) equalled 9848 km.

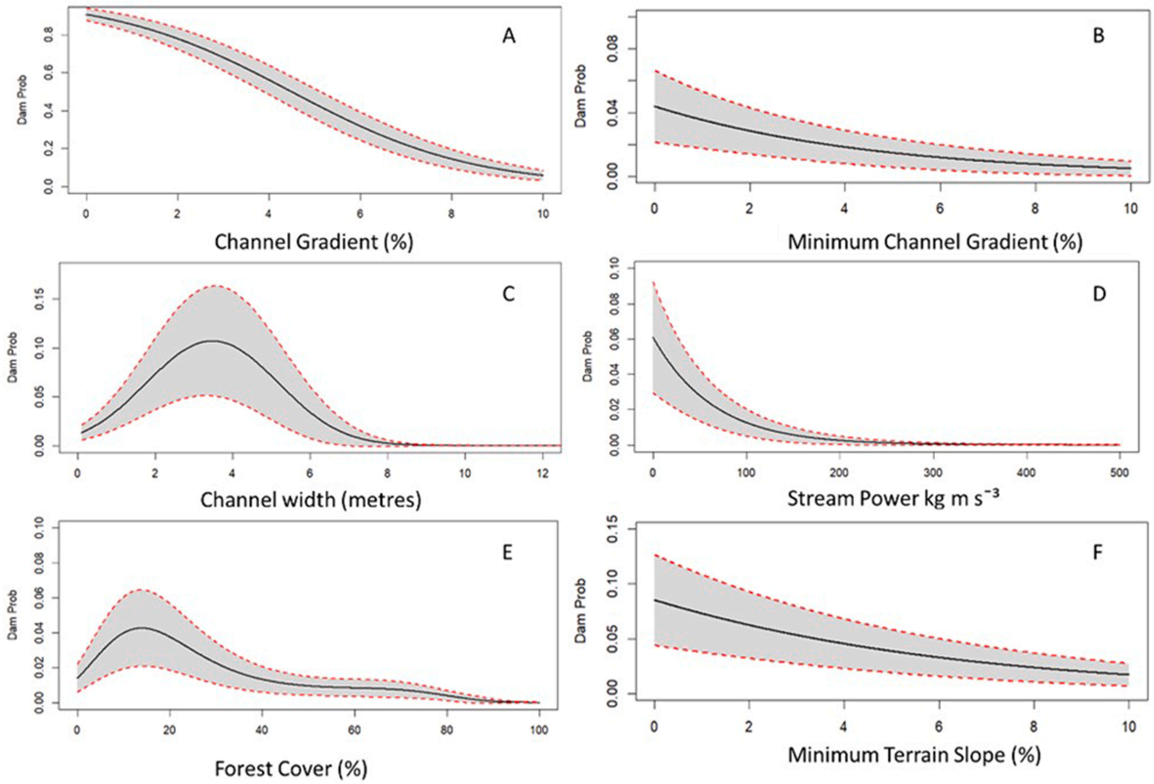

Fig. 3. Model response plots. A: Channel gradient, B: Minimum channel gradient, C: Channel width, D: Stream power, E: Forest Cover, F: Minimum terrain slope. Values on the x-axis relate to predictor variables with the contribution to dam probability on the y-axis. Grey zones represent 95 % confidence intervals.

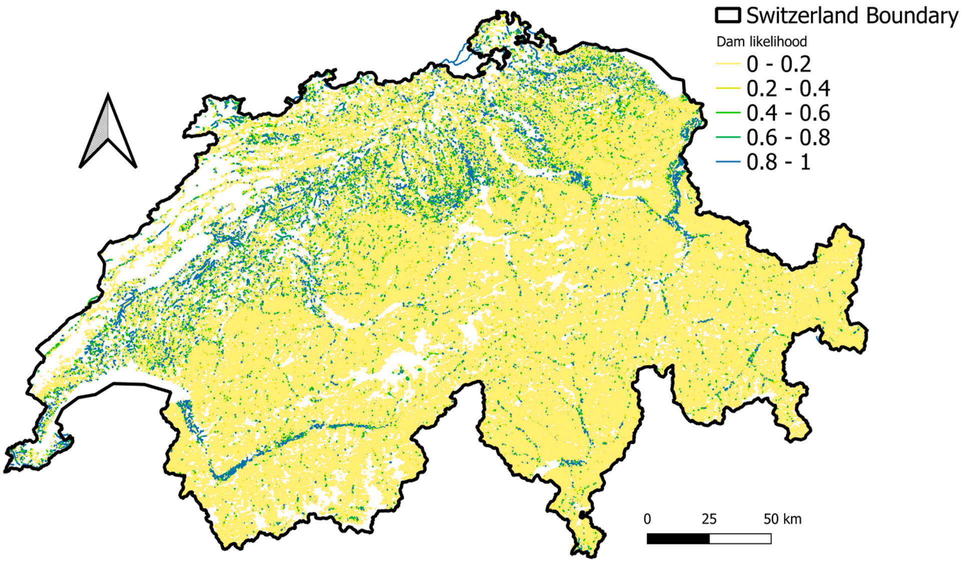

Fig. 4. Suitability values for all sections in the Swiss river network.

A comparison of delineated floodplain polygons from the model with known beaver wetland complexes is given in Fig. 5.

The total area of floodplain and potential for opportunities and conflicts for each Canton in Switzerland, according to the scheme in Table 2, is presented in Table 4.

Of the total area predicted to represent conflicts, 64.65 per cent was attributed to high productivity agriculture, 29.05 per cent to

Fig. 5. Examples of known beaver wetlands with the river section from the Swiss TLM (left) and the corresponding floodplain delineation from our model (right).

buildings and urban land-use, and 6.30 percent to roads and other infrastructure. Opportunities were in the majority associated with grasslands and low productivity agricultural land (37.88 per cent), followed by forests and other wooded areas (34.32 per cent), riparian vegetation (18.46 per cent), wetlands (7.47 per cent) and rocky areas (1.84 per cent). Beaver floodplains inside forests accounted for 19.42 per cent of the total predicted floodplain area. Including trees and wooded areas outside forests, this increased to 22.76 per cent of the total predicted area. Fig. 6 shows the distribution of opportunities and conflicts throughout Switzerland at a resolution of 1 km^2 and Fig. 7 provides the same information as a histogram where 1 km^2 cells are assigned as majority opportunity (i.e. where the area of opportunity > the area of conflict) or as majority conflict.

In terms of elevation, the distribution of predicted dams peaks at around 500 m which also sees the greatest prediction of opportunity over conflicts. This is consistent with our supposition that benefits from the presence of beaver should peak at intermediate levels of elevation within catchments. Fig. 8 gives a more fine-grained example of the relative frequency of opportunity and conflict along an individual river channel. Fig. 8B gives the cumulative frequency (in metres) of both opportunity and conflict adjacent to the main channel (highlighted in Fig. 8A) calculated every 10 m. The black line in Fig. 8B describes the profile of the main channel as distance from the source against elevation. Note that land-cover representing both opportunities and conflict can occur in the 100 m riparian zone adjacent to each river section (see Fig. 9). Therefore, 10 m sections are assigned "opportunity" if the land area representing opportunity in the riparian zone is greater than that representing conflict, and vice versa.

The example in Fig. 8 demonstrates the principle whereby stream sections higher in the catchment exhibit channel gradients that prevent dam construction followed by lower gradient sections that primarily reflect opportunity given adjacent natural land-cover (e.g. forest, scrub, grassland). At lower elevations, low gradients become associated with agricultural land-use and sharply increasing chances of conflict before entering the lower catchment at which the main channel becomes too wide for damming.

Combinations of low-high opportunity and conflict are summarised in Table 5. Here "low" is defined as areas (1 km^2 grid cells) where the model suggests no likely beaver activity (note that this accounts for the majority of the study area) and "high" is defined as

Table 4
Beaver floodplain by area and proportion of the modelled 100 m riparian zone for all Swiss Cantons (assumed 0.5 m dam height).

Canton	Total Area (km^2)	Total Opportunity (km^2)	Total Potential Conflict (km^2)	Percentage of riparian zone	Percentage of riparian zone representing opportunity	Percentage of riparian zone representing conflict
Aargau	29.14	16.16	12.98	7.72	4.28	3.44
Appenzell Ausserrhoden	1.35	1.26	0.09	0.92	0.86	0.06
Appenzell Innerrhoden	0.65	0.60	0.05	0.64	0.59	0.05
Basel-Landschaft	6.31	3.55	2.76	4.99	2.81	2.18
Basel-Stadt	0.03	0.01	0.02	0.40	0.15	0.25
Bern	80.12	47.88	32.25	3.48	2.08	1.40
Fribourg	25.56	19.87	5.69	4.37	3.39	0.98
Genève	8.35	6.10	2.26	14.70	10.73	3.97
Glarus	3.59	3.03	0.56	0.93	0.78	0.15
Graubünden	19.12	14.11	5.01	0.50	0.37	0.13
Jura	12.56	7.04	5.52	9.20	5.16	4.04
Luzern	39.16	21.92	17.24	5.65	3.17	2.48
Neuchâtel	5.34	3.23	2.11	5.86	3.54	2.32
Nidwalden	1.01	0.75	0.26	0.74	0.55	0.19
Obwalden	2.60	2.23	0.37	0.99	0.85	0.15
Schaffhausen	4.03	1.97	2.07	7.51	3.66	3.85
Schwyz	8.60	7.63	0.98	1.74	1.54	0.19
Solothurn	19.10	9.77	9.33	9.51	4.87	4.64
St. Gallen	23.76	19.09	4.67	2.24	1.80	0.44
Thurgau	25.69	18.16	7.53	8.70	6.15	2.55
Ticino	12.87	10.11	2.76	0.76	0.59	0.17
Uri	2.20	1.94	0.26	0.40	0.35	0.04
Valais	26.45	16.53	9.92	1.22	0.76	0.46
Vaud	42.71	31.13	11.58	5.01	3.65	1.35
Zürich	44.35	29.73	14.62	7.40	4.96	2.44
Zug	5.87	4.62	1.25	5.43	4.28	1.16
Total	450.53	298.40	152.13	2.60	1.72	0.87

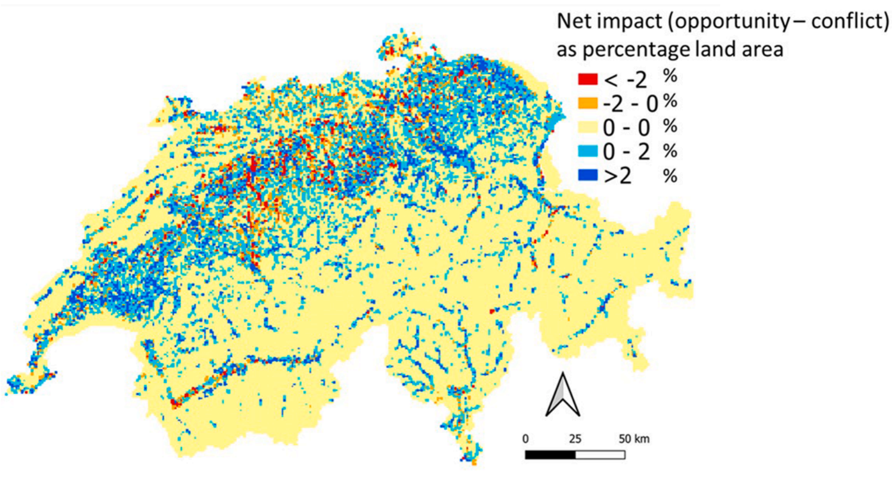

Fig. 6. Map showing combinations of low-high opportunity and conflict per 1 km^2 cell.

areas where the respective impact (i.e. opportunity or conflict) is predicted to be >= 2 % of that area (and therefore, "medium" reflects >0 and <2 % of the grid cell).

4. Discussion

Our study presents the first analysis of its kind to reveal key processes related to both the probability of beaver dam occurrence, floodplain inundation and subsequent impacts. A visual inspection of known beaver wetlands gives support to our approach as an effective method for anticipating inundation through beaver damming behaviour. Our general expectation that positive and negative impacts resulting from colonisation of river reaches by beaver should be directed by physical processes was upheld. Beaver dam

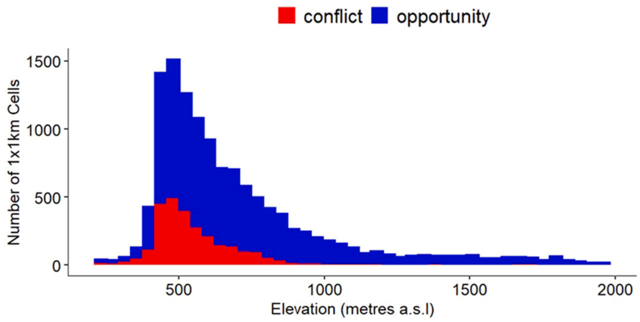

Fig. 7. Total number of 1 km^2 grid cells representing greater opportunities than conflict (blue bars) and greater conflict than opportunities (red bars) plotted against elevation (metres above sea level, points represent max elevation of 1 km^2 grid cells, grouped by 100 equal intervals; note only elevations <2000 m are relevant and higher altitudes not considered).

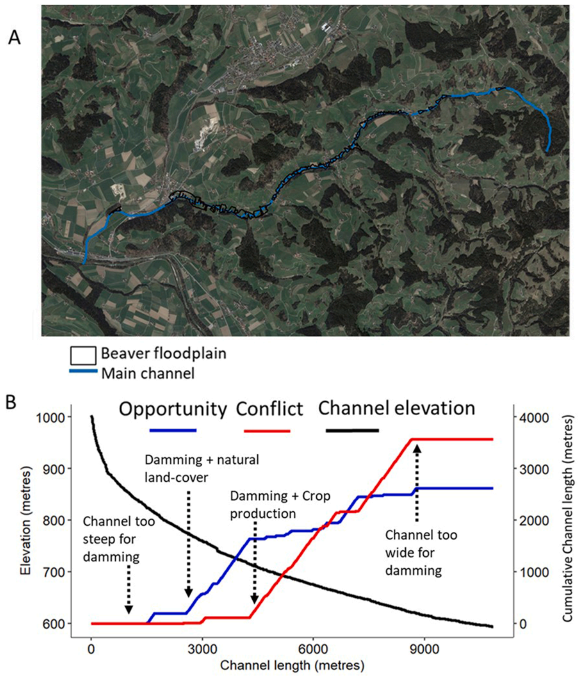

Fig. 8. Relative frequency of opportunity and conflict (B) along an individual river (shown in A).

occurrence was highly dependent on channel geometry with the greatest proportion of variance attributed to channel gradient on a given river section (Fig. 3). River width exhibited a comparatively weaker effect on dam likelihood and we observed a non-linear relationship between channel width and probability of dam occurrence. Our analysis suggests that the likelihood of dam building behaviour peaks with moderate channel widths of around 3.5 m and falls to negligible levels at around 8 m width. Although important, channel width appears to be less influential than channel gradient, with the GLM trained without channel width only exhibiting a ~1 % lower AUC result than the full model. We believe this estimate to be robust given that the comprehensive nature of the data sampling approach in our study (i.e. all river reaches sampled for use as background points with an equal weighting scheme) effectively accounted for any potential bias towards more numerous smaller streams in river catchments (see Section 1.3). Another key variable contributing significantly to dam probability was terrain slope, with increasing values for minimum terrain slope reducing dam likelihood (Fig. 3). As opposed to channel gradient, this variable represented the variation in local topography and its relevance to damming behaviour here is mirrored in other smaller scale studies on beaver dam locations (Sharifullin et al., 2023; Swinnen et al., 2019), providing support to our results. This likely reflects the response of beaver damming behaviour to incised channel sections and/or the existence of floodplains. In a post-glacial landscape like Switzerland, topography can vary substantially and over short distances along a river long-profile, with floodplain pockets alternating with incised channel sections (Wohl et al., 2018). High terrain slope values represent more incised river sections, often artificially modified as a flood prevention strategy, that beavers may find harder or unnecessary to dam, while lower terrain slope indicates sections with floodplains near channels.

Fig. 9. Example of local areas of opportunity and conflict (blue=opportunity; red=conflict).

Table 5
Percentage of the 1 km^2 grid cells shown in Fig. 6 for each combination of low-high opportunity and low-high conflict in this study.

Outcome	Percentage of 1×1 km cells
Low Opportunity-Low Conflict	67.91
Medium Opportunity-Medium Conflict	12.94
High Opportunity-Medium Conflict	6.88
Medium Opportunity-Low Conflict	5.92
High Opportunity-High Conflict	4.01
Medium Opportunity-High Conflict	1.45
High Opportunity-Low Conflict	0.61
Low Opportunity-Medium Conflict	0.26
Low Opportunity-High Conflict	0.01

Another important result from this study is the relatively lower explanatory power that land-cover exhibited in our analysis. Topographic (terrain) variables contributed significantly more to model performance than land-cover variables as indicated by the superior performance of the terrain-only (0.96 AUC) versus land-cover-only (0.83 AUC) models. This underlines the salience of geomorphometric properties over biotic processes for identifying landscape scale trends in the distribution of beaver-related impacts. This is a promising finding for two reasons. Firstly, it means that the method described here should be highly generalizable to other areas and, secondly, it should be possible to apply such models in hindcasting and forecasting studies to understand the impact of beavers on past and future landscapes within which topographic conditions can be viewed as relatively stable across meaningful human time-scales. In addition, this result brings into question the merit of attempting to incorporate vegetation types into ideas around preferred habitat for this species (e.g. Graham et al., 2020) and adds weight to the notion that terrain, as a key constraint on the ability of beaver to engineer suitable habitat, is the key driver in beaver distributions in temperate climates.

Our study, therefore, brings new insights into the key drivers of beaver dam distribution. This adds to the body of recent work developing a picture of likely beaver expansion in a European context (Mori et al., 2024; Serva et al.,2023; 2024). In contrast to other studies however, our model provides information specifically on expected localised impacts through damming and their potential distribution at the national scale. Therefore, given the importance of managing potential conflict for successful beaver conservation, our model represents an essential tool in the suite of options available to land managers and conservation practitioners. It should be noted, however, that our model did not include an estimate of increasing beaver population density over time, which may lead to higher levels of damming behaviour in increasingly sub-optimal habitats. Given the spatially and temporally extensive nature of the BMC data, it is likely that our distribution modelling results reflect this behaviour, but this effect was not formally quantified. Such a trend would have implications for beaver management strategies and its parameterisation would be a useful addition to future modelling work.

4.1. Spatial distribution of beaver floodplain impacts

Land-use for the study region was also primarily determined by topographic conditions, with the location of productive agricultural land limited to large, low-elevation floodplains. As such, the spatial distribution of potential conflicts was closely tied to elevation and constrained to specific regions in the landscape. This implies that the majority of Switzerland should see either no effect or net positive outcomes in terms of total area in receipt of potential benefits (Fig. 6 & 7, Table 5). Predicted areas of beaver influenced floodplains were often concentrated in low-lying areas of high-productivity arable land-use, reflecting potentially high conflict (Fig. 6). There may, therefore, be easily identifiable topographic thresholds related to the overall impacts of beaver in modern cultural landscapes. In the case of Switzerland, such a threshold would seem to occupy an elevation window approximately 400–600 m a.s.l, after which the total area reflecting conflicts rapidly declines. This same window however also suggested a high degree of opportunity (Fig. 7), largely outweighing the number of areas where conflicts were greater. The role of topography was also underlined by inspection of cumulative impacts along a single river profile (Fig. 8) which met our expectations that the most upper and lowest sections should contribute little to observed impacts (Section 1.3; Fig. 1) and that moderate-to-high zones of elevation should see the clearest gains in terms of opportunities outweighing conflicts from beaver engineering. Though the cumulative frequency of conflicts was greater in the example given in Fig. 8, the general principle that opportunities present themselves in areas of moderate elevation was observed. This may explain the higher levels of opportunity over conflict at very broad scales, given the naturally higher frequency of lower order channels (occurring at moderate elevations) over higher order channels (occurring lower in the catchment). The ability to work with such principles will be of great use to managers of individual river catchments and highlights the potential practical value of our model. At broad scales, the distribution of predicted dams suggests that, of Switzerland's ~40,000 square kilometre land area, only 5 of these implied high-conflict-low-opportunity scenarios compared to 246 suggesting high-opportunity-low-conflict situations. Therefore, despite the undeniable occurrence of significant potential conflict, the presence of beavers in the landscape is predicted to have an overwhelmingly positive outcome in a purely area-based assessment at the national scale.

Notwithstanding the identification of potential thresholds for social-ecological processes relating to beaver impacts, the complex nature of cultural landscapes implies the co-occurrence of both opportunities and conflict as a result of local variation in land-use patterns. For example, Fig. 9 shows an area with a predicted beaver floodplain representing both opportunity and conflict (blue areas denote opportunity and red areas potential conflict). The model thereby facilitates the assessment of zones of opportunity in local conservation planning and the identification of areas where mitigation (e.g. the use of preventative or compensatory measures) should be considered (e.g. within a public consultation process) or, alternatively, where conflicts outweigh implied opportunities.

Such locations highlight the importance of the comprehensive mapping of potential outcomes, integrating a range of relevant characteristics, and the need for local knowledge and surveying to be able to interpret, on the ground, the results of spatial models. For example, beaver floodplains that, in an area-based assessment, imply greater opportunities than conflicts, may be desirable if mitigation of those conflicts is acceptable to decision-makers in light of the implied potential benefit. Conversely, opportunities, regardless of their total implied area, may be undesirable if the potential conflicts imply high economic, cultural, ecological or physical cost (e.g. damage to buildings, monuments or local road access, or disturbance of otherwise protected habitats). Hence, the outcome of any local assessment will be dependent on the relative weight (beyond a simple measure of area) assigned by land managers to the potential opportunity and conflict implied through use of the model. Though an area-based approach therefore comes with some limitations, a key strength of the method is its spatially comprehensive nature, which means that decision-making can be carried out at a number of relevant scales and organisational levels such that multiple spatial contexts can be consider simultaneously. We acknowledge also that non-damming behaviours such as burrowing and tree-felling, which represent other potential sources of human-beaver conflict, will also have implications for beaver management. The potential for these behaviours to impact site-level opportunities and conflicts should therefore be considered wherever possible in local assessments.

4.2. Implications for management

Our method represents a blueprint for conflict management that could be used in a range of contexts in nations tasked with managing beaver populations. The need to identify zones of potential conflict will be an important consideration for planning and allocation of resources for beaver management and the identification of new sites for translocation where conflict does occur. Above all, though our assessment suggests a positive net outcome from an area-based view of beaver impacts, local context can and should be investigated through our model. Although our overall results present a picture of net benefit from beaver expansion, our use of a single scheme for anticipating opportunities and conflicts cannot capture entirely the variation in local perceptions of opportunity and conflict. As identified by others (Holmes et al., 2024) the emergence of perceived opportunity and conflict can differ significantly between stakeholder groups. Hence, in the same way that individual sites may imply both opportunities and conflict as a function of land-use (Fig. 9), socio-cultural factors may likewise lead to contradictory views being held simultaneously by local stakeholders. Therefore, the full social-ecological context of sites should be taken into account before designating areas as suitable for restoration through the presence of beaver. As such, our model represents a blueprint for identifying and excluding areas for potential beaver-led restoration that can be further assessed and qualified through a public consultation process. A template exemplifying how the process of capturing local site suitability might proceed is given in Fig. 10.

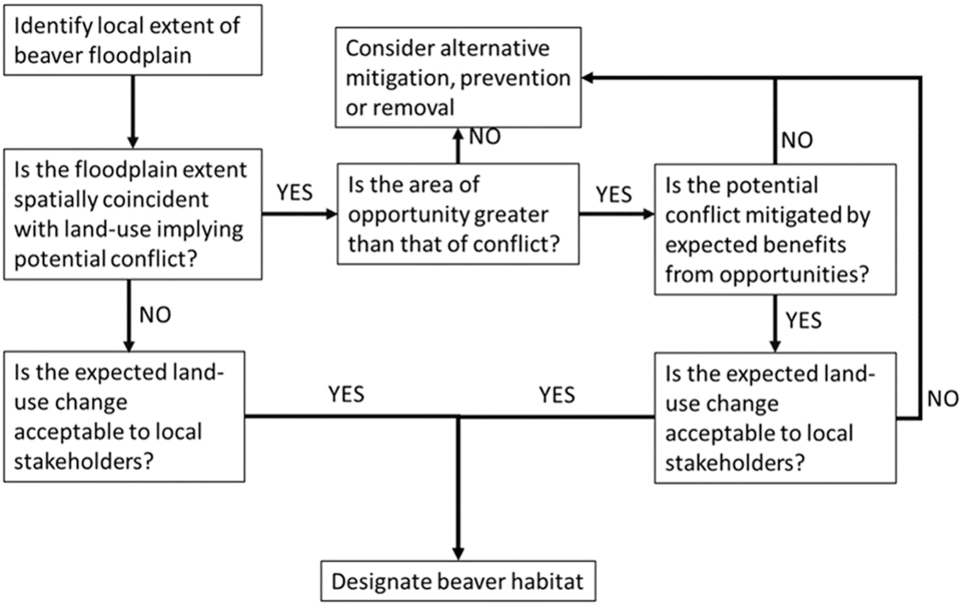

Fig. 10. Suggested decision tree for use with the beaver floodplain model.

5. Conclusion

This study describes the first comprehensive model of beaver dam likelihood and associated impacts on floodplains, filling a gap in previous research by clarifying the role of physical processes and likely conflict distribution. The use of a large comprehensive database allowed us to identify key constraints of dam occurrence. Our results revealed the relatively low influence of channel width compared to channel gradient on dam construction probability. This suggests that the approach should be highly transferable to other locations given that channel gradient is more accessible from available secondary data whereas channel width is generally much more challenging to acquire, especially for smaller rivers. Similarly, though we observed a spectrum of opportunities and conflict related to land-use, this was also principally constrained by topographic conditions. The delineation of areas reflecting overall opportunities and conflict revealed that the reintroduction of *Castor fiber* into Switzerland and its future colonisation of small rivers implies a net benefit from a landscape restoration perspective. Although this is the case measured at the national-scale, we identified concentrated regions of potential land-use conflict where mitigation and management could be focussed. Our approach is relevant to other contexts where beaver management is becoming increasingly important. For example, recent evidence suggests that beaver populations are expanding or have the capacity to expand into landscapes throughout Italy, Spain and Portugal (Serva et al., 2024). In combination with local knowledge, our method could help to maximise landscape restoration goals in these regions whilst minimising undesirable land-use conflicts that may diminish conservation efforts.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.

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Declaration of Competing Interest

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

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03304.

Data availability

The authors do not have permission to share data. Code for reproducing the analysis described will be hosted on the corresponding author's GitHub page.

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