Quantifying the impact and expansion of Eurasian beaver in Great Britain.

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I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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ii. Abstract

Eurasian beavers (Castor fiber) were extirpated from Great Britain (GB) ca. 400 years ago. Harvested for their meat, pelts and castoreum, their numbers across Eurasia were reduced to a few isolated populations. In recent years, beavers have been reintroduced in GB and their numbers have increased across Europe due to conservation efforts. However, the landscapes that beavers are now returning to have been significantly altered by anthropogenic landuse. This land use change has had hugely detrimental impacts for natural riverine and riparian processes, with respect to their structure and function. Beavers are well known for their industrious behaviours: building dams and lodges, excavating burrows and canals, and felling trees. Beavers therefore act as a significant ecological and hydrological disturbance, creating dynamic, structurally heterogeneous wetland ecosystems. Not only do the impacts of beaver enhance biodiversity through the provision of diverse habitats, but they also help to restore natural hydrological, geomorphic and ecological processes that are all but lost across intensively-farmed, densely populated European landscapes. Beavers may therefore play an important role in restoring this ecosystem function and could potentially help to mitigate the harm caused by anthropogenic landuse. However, we now rely on agriculture and infrastructure; the expansion of beaver populations can consequently result in conflict where their impacts intersect anthropogenic activity. As such, there is a requirement to better understand the impact of beavers on the structure and function of natural processes, to inform their management and conservation. Further, there is a need to develop methods that can allow us to predict the spatial and temporal changes in beaver populations across modern landscapes to underpin the recovery of the species in such a way that their benefits can be maximised whilst minimising the risk of potential conflict. This thesis presents four papers to advance our scientific understanding in this regard, as follows:

The hydrological mechanisms that cause storm event peak flow attenuation in beaver wetlands were explored at a beaver dam complex on a third order stream. Data from 612 discrete flow events were measured at a flow gauge, downstream of a beaver dam complex, seven years before and three years after it was constructed; 634 events from a neighbouring control catchment, over the same time period, were also extracted from the time series. A selection of general linear models were fitted between event peak flow and total event rainfall. The differences in the slope of the regression, before and after beavers, indicate that flow attenuation, due to beaver activity, increases with greater rainfall. This increasing attenuation effect is attributed to floodplain flow diversion and transient storage because the observed attenuation volumes greatly exceed the available storage capacity of the beaver ponds alone.

Drone-derived structure from motion photogrammetry surveys were carried out, providing a high-resolution understanding of changes in woodland canopy structure, over a one-year period. Riparian woodland has a complex structure and uncertainty in estimated point elevations can be spatially patchy and locally high. The adoption of robust error propagation methods to accurately estimate canopy height change was found to be

very important. Beaver foraging slightly reduced mean canopy height but significantly increased the variability in canopy height change. Quantile regression was used to quantify the difference in canopy elevation change across two regions of riparian woodland: with and without evidence of beaver foraging. The rates of canopy growth and height decline were greater in regions where beavers were actively foraging, indicating that beaver foraging may increase canopy height variability which could have varying implications for riparian/aquatic species and woodland management.

In order to better predict the landscape scale impact of beavers on ecosystem structure and function, it is necessary to develop methods to accurately predict their potential habitat distribution and where dams, which have the largest environmental impact, are likely to occur. To address this, we developed a modelling approach using high resolution, nationally-available datasets to create a Beaver Forage Index (BFI) model – a raster dataset describing the suitability of landcover for beaver forage and; a Beaver Dam Capacity (BDC) model which describes the density of dams that could be supported within a given reach. Beaver preferentially foraged in regions with higher BFI values and are more likely to dam (and build more dams) in reaches with higher BDC. Using these models, it is possible to estimate the number of dams that might occur at the catchment scale at beaver population capacity.

Though beavers have only been living in the wild in GB for a short period of time, their populations are growing rapidly. It is essential to build a stronger understanding of how beaver populations expand, at what rates and how management interventions, such as translocations or lethal control, might impact population dynamics. To gain this insight, we conducted annual beaver feeding sign surveys to map the distribution of beaver impacts throughout the River Otter catchment, SW England. Using a semi-automated approach, that combines kernel density estimates and expert knowledge, the number of territories in the River Otter catchment was estimated over a 5-year period. A spatially explicit method for predicting the catchment population carrying capacity was developed which uses BDC and BFI models in combination with empirical understanding on territory sizes from across Europe. Adopting the assumption of logistic growth in beaver populations, we use the observed rates of population increase, constrained by the estimated carrying capacity range to model the expansion rate of the beaver population. A range of theoretical management scenario simulations were carried out revealing that, even low-moderate management interventions may have very uncertain outcomes for population viability and therefore any management plan, involving translocation or culling of animals, should be carefully designed.

The findings presented in this thesis advance our understanding on the impacts of beaver on hydrological function, riparian woodland structure and provide methods for understanding the spatio-temporal distribution of beavers and their impacts. This understanding has already been used to inform management policies within national agencies and non-governmental organisations across GB and has the potential to inform the management of beavers across Europe.

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Term	**Definition**
Beaver Dam Capacity (BDC)	The number of dams that could be supported within a given section of river based on forage resource availability and hydrometric controls.
Beaver dam	A structure, constructed by beavers, built across a river, stream, lake/pond outflow, spring, seepage, or canal to raise upstream water depth. Constructed from a range of substrates that may include, woody material, fine sediment/gravel and rocks. These structures often extend tens to hundreds of meters into the floodplain and may result in the formation of entirely new flow pathways seemingly distinct from the originally diverted source. Impounded water behind dams provides protection from predators and access to forage.
Beaver lodge	A beaver dwelling constructed from sediment and woody material that is visible above the ground as a mound. Beavers dwell in chambers within these structures.
Beaver wetland/ complex/sequence	All terms used interchangeably to describe a wetland ecosystem, created by one or multiple beaver dams.
Beaver Forage Index (BFI)	A metric that describes the suitability of vegetation for beaver forage.
DEM/DTM/DSM	Digital Elevation Model / Digital Terrain Model / Digital Surface Model.
DOD	Digital Elevation Model of Difference: the difference between the elevation of two different elevation models measured at the same location on different epochs.
Beaver canal	A typically narrow channel, excavated by beavers to improve access, via water, to parts of territory. These structures typically extend laterally into the floodplain.
Catchment / sub-catchment	The area upstream of a given location that contributes hydrological flow. Sub catchments are smaller catchments, contained within a catchment.
Hydrograph	A graph depicting the rate of river flow and rainfall over time. In this thesis, it can be considered to refer to a hydrological event where flow increases in response to rainfall (i.e., a storm hydrograph).
IUCN	International Union for the Conservation of Nature
LoD	Limit of Detection: A threshold within which measured change cannot be considered statistically reliable.
Natural flood management (NFM)	The alleviation of flood flows by reinstating natural hydrological processes by, for example, building wood debris dams or creating floodplain ponds, etc.
Orthomosaic	A single image produced from the mosaicking of multiple images. In this thesis, the term refers to aerial imagery with a nadir (downward) facing perspective.
Territory	An area occupied and defended by one or more beavers.
Population carrying/territory capacity	The maximum number of beavers/beaver territories that can be supported by a given environment (e.g. a catchment).
Python	A scientific programming language: https://www.python.org/
R	A scientific/statistical programming language: https://www.r-project.org/
Riparian area/zone	The transitional area between freshwater and terrestrial ecosystems where fluvial and terrestrial processes interact.

ROBT	River Otter Beaver Trial: Extending from 2015-2020, this was the first legal release of wild beavers in England.
SfM	Structure from Motion Photogrammetry: a photogrammetric method for estimating 3D structure from overlapping 2D imagery.

Contents

Chapter 1. Introduction

Beavers are semi-aquatic rodents, capable of transforming riparian ecosystems with their various industrious behaviours including felling trees, building dams and lodges, and excavating burrows and canals; all to meet their ecological needs (Brazier et al., 2020b; Gurnell, 1998; Larsen et al., 2021). Across much of Europe and North America, beaver populations were greatly reduced and, in many locations, extirpated due to hunting (Halley and Rosell, 2002; Kitchener and Conroy, 1997).

Beavers help to restore many natural processes and create wetland habitats (Brazier et al., 2020b) which have been greatly diminished during the Anthropocene with Europe having lost an estimated 45% of its wetlands (Hu et al., 2017). The wetlands created by beavers are 'messy' with heterogeneous morphology and diverse ecological communities contributing substantially to the structural complexity of landscapes (Gurnell, 1998; Naiman et al., 1986) which enhances both ecosystem and hydrological function (Brazier et al., 2020b; Law et al., 2019; Puttock et al., 2017). Therefore, there is a strong interest in conserving and expanding beaver populations to reinstate these natural processes and benefit biodiversity as well as to reintroduce and/or reinforce the populations of this once native species, in line with the International Union for the Conservation of Nature (IUCN) guidelines (IUCN and SSC, 2013; Larsen et al., 2021). However, in our now intensively managed landscapes, beaver activity can lead to human-wildlife conflicts, particularly where their engineering behaviour impacts key infrastructure or agricultural land (Auster et al., 2019; Auster et al., 2021; Hood et al., 2018; Schwab and Schmidbauer, 2003). Therefore, there is a need to better understand this species so that management strategies can maximise benefit whilst mitigating potential conflicts.

The River Otter Beaver Trial (ROBT) was the first licensed release of free-living (unfenced) beavers in England (Brazier et al., 2020a). The trial spanned five years from 2015-2020. The inception of this PhD was imbedded in the trial and formed a large contribution to the science and evidence underpinning the understanding of physical impacts of beaver upon the River Otter catchment. Therefore, this thesis focuses on the River Otter catchment with a view to informing on the potential impacts of beaver in comparable landscapes, comprising widespread anthropogenic landuse. Further, the methods, models and software, developed from this thesis, provide tools that are generalisable and may be adopted across a range of landscape types and scales both within Great Britain (GB) and Eurasia. The ROBT governance structure, discussed in Auster et al. (2022), was designed to ensure that both the management of the beavers themselves, their impacts and the scientific research, undertaken as part of the trial, met the needs of the numerous stakeholders and organisations involved. The concerns and research needs/knowledge gaps raised by the ROBT steering group, and the science and evidence forum played a role in outlining potential research areas to be considered herein, ensuring that pertinent questions were co-created, answered and critical understanding to the future management of beaver in Great Britain was delivered. To address a wide range of key questions, it was necessary to adopt a broad transdisciplinary approach, comprising both empirical field-based research and modelling across the hydrological, ecological, biological and geospatial sciences, to answer a range of key questions at multiple scales to fill these evidence gaps.

This thesis has two overarching aims, each answering two key questions:

1. To advance our understanding of the structural and functional impacts of beaver at the site scale. Specifically, we consider the impacts of beaver on hydrological regime and riparian woodland structure to answer the following questions:
    - ***a.*** *To what extent and by what mechanism are hydrological regimes altered by beaver? (**Chapter 2**)*
    - ***b.*** *What impact do beavers have on riparian woodland canopy structure and how can it be measured in a robust manner? (**Chapter 3**).*

2. To develop modelling approaches that further our understanding of the spatial distribution of beaver habitat, their impacts and population dynamics to inform conservation, management and reintroduction, by answering the following questions:
    - ***a.*** *What is the distribution of beaver habitat, where are dams likely to be constructed and at what densities might they occur? (**Chapter 4**)*
    - ***b.*** *How rapidly have populations increased and how will this change into the future under varying management scenarios? (**Chapter 5**)*

This chapter presents the key background and literature that contextualises the data chapters in this thesis (Chapters 2-5). I have also co-authored a literature review, published in WIREs water (Brazier et al., 2020b), which is included in Appendix 3 providing contemporary understanding of the environmental and societal impacts of beaver, complementing the work herein.

1.1 Beaver *(Castoridae)*

1.1.1 Eurasian (C. fiber) and North American (C. Canadensis) beaver

The Pre-historic species within the *Castoridae* family were highly varied in both their behaviour and appearance. Up to 40 different pre-historic beaver species have been identified including the giant beaver genus (*C. Castoroides spp) and* a terrestrial species (*C. Paleocastor spp)* which dug spiralised burrows (Brazier et al., 2020b; Martin and Bennett, 1977; Martin, 1969).

Today, there are two remaining species of beaver: *C. canadensis*, the North American beaver, and *C. fiber*, the Eurasian Beaver. The two species have differing numbers of chromosomes and therefore cannot interbreed (Kuehn et al., 2000; Lahti and Helminen, 1974). *C. canadensis* is native to North America and Northern Mexico (Naiman et al., 1988); there are now invasive (non-native) populations present in Patagonia (Pietrek and Fasola, 2014; Skewes et al., 2006), Finland and Russia (Halley et al., 2020; Petrosyan et al., 2019). *C. fiber*'s former range extended longitudinally between GB and Eastern Siberia, stretching from the steppe of south-eastern Europe and Siberia and into the northern Tundra (Halley and Rosell, 2002). Beavers were widely harvested for their fur, meat and castoreum (Coles, 2006; Kitchener and Conroy, 1997; Manning et al., 2014; Nolet and Rosell, 1998). Consequently, their range was significantly reduced to a small number of isolated communities (Figure 1-1) (Halley et al., 2012, 2020; Halley and Rosell, 2002). Following widespread conservation efforts and a reduction in the intensity of beaver harvest across Eurasia, *C. fiber* populations have expanded rapidly, with the number of individuals estimated at 1.5 million in 2020 (Halley et al., 2020) (Figure 1-1). With the invasion of *C. canadensis* in Finland and Russia, there has been an opportunity to monitor the relative impacts of the two species (Danilov, 1995; Danilov and Fyodorov, 2015; Petrosyan et al., 2019; Rosell et al., 2005). It was initially considered that *C. canadensis* constructed dams and lodges more frequently and of a greater size than *C. fiber*; but it has since been shown that landscape characteristics likely play a bigger part in any observed differences in building behaviour and, under the same environmental conditions, their impacts are highly comparable (Brazier et al., 2020b; Danilov and Fyodorov, 2015). However, fecundity rates appear to be higher in *C. canadensis* than *C. fiber* and have been found to displace the native Eurasian species (Parker et al., 2012; Petrosyan et al., 2019; Rosell et al., 2005).

That the impacts of the two species are comparable, is significant from the perspective of those researching *C. fiber* because the amount of literature that considers *C. canadensis* is far greater than for *C. fiber* (Larsen et al., 2021) and therefore, with consideration of differing geographies, much can be learned from the study of both species. Throughout this thesis, literature considering both species is therefore drawn upon.

With populations of *C. fiber* now expanding rapidly across Europe, beavers are returning to many regions that have changed substantially since their extirpation. In 2017, Agricultural landuse covered approximately 39% of Europe and urban areas had expanded by 24.5% since 1950 (European Environment Agency, 2017). Therefore, the frequency of conflict between landowners and beaver activity will continue to increase. Already, there is significant lethal control of beavers, for example: in Poland, between 2009 and 2017, an estimate 34,870 animals were culled (Janiszewski and Hanzal, 2021); in Scotland a reported 87 and 115 animals were culled in 2019 and 2020, respectively (Scottish Natural Heritage, 2021, 2020). In many regions, these management approaches are perhaps unavoidable. However, given the numerous documented benefits afforded by beaver, it is imperative that we further our understanding of the species and develop ways to inform management practices so that their benefits may be maximised, whilst mitigating conflicts and the requirement for lethal control.

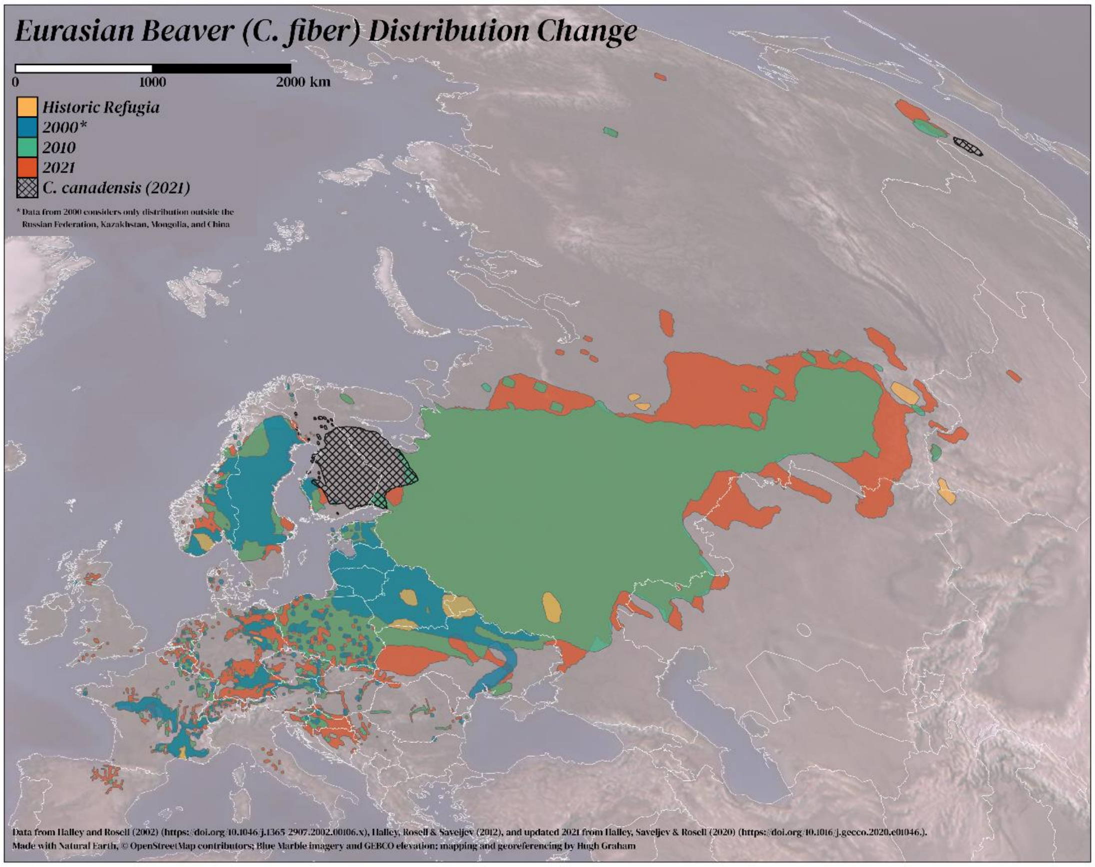

Figure 1-1: The distribution change of beaver across Eurasia. Data from: Halley et al. (2012 and 2020), and Halley and Rosell (2002). Data from 2000 considers only the distribution outside of the Russian Federation, Kazakhstan, Mongolia and China. Substantial increases in the distribution of Eurasian beaver have occurred since 2000. The North American beaver (C. canadensis) has a large population in Finland and Russia, but its expansion is relatively small compared with the Eurasian beaver (likely due to management practice).

1.1.2 Beavers in Great Britain (GB)

Though remnant populations survived across Europe, beaver were extirpated from Great Britain (GB) ca. 400 years ago (Coles, 2006; Kitchener and Conroy, 1997). They have only recently been reintroduced in the wild; in Scotland, England and Wales in 2005, 2008, and ca. 2018, respectively (Brazier et al., 2020a; Campbell-Palmer et al., 2020; Crowley et al., 2017; Gaywood, 2017; Halley et al., 2020). Beaver populations are therefore at a nascent stage of their expansion.

The Scottish Beaver Trial concluded in 2014 and the two populations of the species, in Argyll and Tayside, were granted permission to remain in 2016 (Gaywood, 2017). Beginning in July 2022, beaver may be legally translocated to parts of Scotland outside of the Tay catchment to support their conservation and reduce the requirement for lethal control (Nature Scot, 2022). The ROBT concluded in 2020 and beavers have been given permission to remain within the catchment and expand naturally from it (Howe and Crutchley, 2020). A public consultation on beaver reintroduction in England has recently concluded which will inform the national strategy for beaver management; the outcomes from this consultation are currently pending (Natural England, 2021).

In Campbell-Palmer et al. (2021), we estimated that the population of beavers within the Tay and surrounding catchments comprised a minimum of 251 territories. The methods used to estimate these territory numbers were developed as part of this thesis and are presented in Chapter 5. These methods were also used for an earlier survey of the Tayside beaver population, published in *River Research and Applications* (Campbell-Palmer et al., 2020), provided in Appendix 5, which found an estimated minimum of 141 territories in 2018. In 2019, in the River Otter catchment, the total number of territories was estimated between 7 and 13 (Brazier et al., 2020a). In Chapter 5 we use data, collected during the ROBT, to estimate the rate of population growth and how it might change in the future, under a range of management scenarios.

1.2 Hydrological Impacts

1.2.1 Structural Impacts

Beaver dams locally reduce the longitudinal connectivity of river systems. In so doing, they form ponds on their upstream side, which increases wetted area and thus enhances lateral connectivity (Puttock et al., 2021, 2017; Westbrook et al., 2006). This upstream expanse of water and the flow pathways and wetlands that form around and downstream of dams alter the movement and storage of water flowing through what is described as a beaver pond complex (Figure 2-2). Such a pond complex might comprise multiple dams in sequence and connecting canals that together form wetlands that extend far into a floodplain and downstream of the dam (Brazier et al., 2020b; Grudzinski et al., 2020; Larsen et al., 2021; Westbrook et al., 2006). The local reduction in stream gradient, caused by the beaver dam and pond system, results in higher fine and coarse sediment accumulation/aggradation (Butler and Malanson, 1995; Pollock et al., 2014, 2007; Puttock et al., 2018). Over time, this aggradation, in combination with enhanced bank erosion around the edges of beaver dams due to increased lateral flow, can lead to the formation of complex, multi-threaded river systems that have strong floodplain connection (Gorczyca et al., 2018; Pollock et al., 2007). This multi-threaded, structurally heterogeneous river form would have been commonplace across Europe prior to anthropogenic interference in riverine processes through activities such as dredging, weir construction, realignment, floodplain disconnection and landuse change (Brown et al., 2018).

1.2.2 Functional Impacts

The increase in wetland area and therefore surface water storage afforded by beaver pond complexes affects hydrological regimes in multiple ways. The total amount of surface water created by beaver can be very large and, even once territories are abandoned, the modified landscape can still retain more surface water than landscapes where beaver are absent (Johnson-Bice et al., 2022). The presence of more open water and wetland areas increase evapotranspiration (Correll et al., 2000; Fairfax and Small, 2018; Larsen et al., 2021; Meentemeyer and Butler, 1999) and groundwater losses (Westbrook et al., 2006), the rates of these processes will be strongly controlled by local geology, topography, landcover and climate (Brazier et al., 2020b; Larsen et al., 2021). However, the increased water residency times, afforded by beaver dams, has been found to offset these losses by maintaining baseflows during dry periods (Majerova et al., 2015; Nyssen et al., 2011; Smith et al., 2020) which could provide perennial wetlands in drylands, where flow is ephemeral (Gibson and Olden, 2014). Critically, this hydrological stabilisation has been shown to increase resilience to wildfire and climate change by providing important wetland refugia for many species (Fairfax and Whittle, 2020).

Hydrological stabilisation also manifests during periods of high flow. There is considerable evidence to show that beaver pond complexes slow the flow of water as it passes through them. Reduced and delayed peak flows have been observed across multiple studies (Nyssen et al., 2011; Puttock et al., 2021, 2017) and are attributed to an increase in the availability of storm water storage. This flow attenuation effect has also been found to persist even during the largest of hydrological events (Westbrook et al., 2020). In Puttock et al. (2021), we presented further evidence, across four sites in GB, that beaver wetlands have a significant impact on the peak flows of hydrological events, with reductions of between XX and YY across the sites. This work has been published in *Hydrological Processes* and is provided in Appendix 4.

With growing support for nature-based solutions to climate change and interest in beavers' ability to support/enhance flood and drought resilience via hydrological stabilisation (BBC, 2017; Larsen et al., 2021; Ngai et al., 2021), it is crucial that we build understanding on both hydrological responses to beaver dams and the hydrological mechanisms/processes that underpin the modified flow regimes. Whilst the processes that control hydrological stabilisation during dry periods are quite well understood (at least qualitatively), those that control high flow events are less well described (Brazier et al., 2020b; Larsen et al., 2021). Chapter 2 adds to this understanding by discussing how the differing response in river flow to rainfall events, before and after the construction of a beaver pond complex, can explain what hydrological processes and mechanisms contribute to the flow attenuation effect.

There is a need to understand the cumulative impact of many dam complexes, within a catchment, on hydrological regime. In the short term, the most effective way to achieve this is with hydrological runoff modelling; a mechanistic understanding of the hydrological process is crucial for this. The information provided in Chapter 2, in combination with an understanding of the potential spatial distribution of dams provided in Chapter 4, provides a basis from which to begin this line of research. Over the longer term, it is vital that empirical monitoring be continued to support the validation of hydrological models and to improve management.

1.3 Ecological Impacts

1.3.1 Structural Impacts

Beaver impact ecological structure in two overarching ways. Firstly, they alter the physical structure of the locations they inhabit. This occurs both due to the construction of dams and lodges, the creation of ponds and wetlands, the geomorphic reworking of river planform and bed sediments, and due to the felling of trees and other vegetation. Secondly, they alter the structure of ecological communities. Riparian habitats, once dominated by terrestrial fauna and flora are replaced by wetlands. This disturbance increases not only alpha (local) diversity but also enhances beta diversity (the ratio between regional and local diversity) (Law et al., 2019). This occurs due to ecosystem disturbance; unlike in non-beaver wetlands, beavers continually change the areas they inhabit through their engineering and eventual abandonment, which leads to a higher turnover in ecological composition (Law et al., 2019; Willby et al., 2018). This patch-scale disturbance results in the increase in landscape (Gamma) diversity and ultimately maintains ecological stability at landscape scales (Johnson-Bice et al., 2022).

In respect to the physical alteration to habitat structure, most research has focussed on the changes in wetland structure that occur following beaver pond complex creation. The impacts to physical vegetation structure are less well documented and, where they are, the focus is primarily on the how community structure is affected by beavers. It has often been suggested that, through felling riparian trees, beaver create a more open canopy structure (Donkor and Fryxell, 1999; Nolet et al., 1994; Peinetti et al., 2009). This may benefit a range of other species by increasing structural heterogeneity and increasing light penetration (Broadmeadow and Nisbet, 2004; Gao et al., 2014; Seavy et al., 2009). However, the change in physical riparian woodland structure in response to beaver foraging has never been quantified. The felling of trees is also widely reported to be a key source of conflict where the felling of trees, particularly in public locations, is perceived as destructive and potentially harmful to the local environment and/or aesthetic (Auster et al., 2020; Yarmey and Hood, 2020). As such, management measures to protect trees are frequently adopted, such as protecting tree trunks with wire mesh or a sand-gravel paint mix (Brazier et al., 2020a). There is, therefore, a need to better understand how beaver impact riparian woodland structure to inform both effective conservation and management. In Chapter 3 we address this by using drone-based photogrammetry to detect changes in vegetation structure over the course of a year and consider how the observed changes to vegetation structure are relevant to beaver management in GB.

1.3.2 Functional Impacts

In many respects, the functional impacts of beaver on ecology are some of the best documented aspects of beaver science. The wetlands created by beavers are typically more productive than the habitats that they replace; increases in plant and invertebrate biomass and diversity are widely documented (Law et al., 2019; Osipov et al., 2018) . This increased productivity occurs alongside the provision of novel habitats including the wetlands themselves but also vital deadwood habitats such as, instream and standing dead wood (Thompson et al., 2016), beaver dams and lodges (Rolauffs et al., 2001). This forms the foundation for supporting a greater diversity of life, supporting mammals (Nummi et al., 2019), amphibians (Dalbeck et al., 2020), birds (Nummi et al., 2021; Stringer and Gaywood, 2016), invertebrates (Brazier et al., 2020b; Willby et al., 2018) and fish (Kemp et al., 2012). At the landscape scale, this represents a significant improvement in terms of biodiversity but, in our now anthropogenic landscapes, we must consider the local scale impacts of beavers (Law et al., 2019). In most cases, the habitats replaced/modified by beaver are widespread and common at the landscape scale. However, it is possible, therefore, that beaver may have an undesired impact where they interact with isolated or rare ecological species or communities with specific requirements that are not provided by beaver-modified landscapes. Consequently, their impact in such regions may detract from beta diversity (Law et al., 2019). Whether or not such an effect may occur and to what degree it would be offset by the many biodiversity benefits afforded by beaver will be spatially variable.

The functional response of ecosystems to beaver activity is generally well described. However, interactions will vary temporally and spatially. Therefore, there is a need to improve our structural understanding of how beavers impact ecosystems across space and time so that we may be able to more effectively quantify and predict the landscape scale impacts of beaver on ecological communities. This will prove particularly important in regions where species of high conservation importance are at risk due to habitat disturbance or transformation. To achieve this, an understanding of the potential spatiotemporal distribution of beavers is required; we present tools to build this understanding in Chapters 4 and 5.

1.4 Habitat Requirements and modelling

Beavers have some very specific habitat preferences. They preferentially seek out areas with deciduous riparian woodland, with a strong preference for species such as willow *(Salix spp)* and poplar *(Populus spp)* (Mahoney and Stella, 2020; Nolet et al., 1994). Beavers also require deep water to facilitate access to forage, transporting resources and protection/evasion from potential predators. Where deep water is unavailable, beavers will construct dams to increase the suitability of a given location. However, despite these specific requirements, beavers are generalists and are highly adaptable (Nolet et al., 1994; Vorel et al., 2015). They can inhabit (though do not preferentially settle in) woodland which is dominated by coniferous trees (Hartman, 1996; Pinto et al., 2009). They have even been found to colonise areas with little or no woody vegetation; recent northward advances of beaver in the North American tundra indicate that beaver habitat selection can be extremely flexible (Tape et al., 2018).

This brings both opportunity and challenges from the perspective of modelling beaver habitat. There are a great many different habitat suitability indexes (HSIs) that show strong predictive performance locally (Barnes and Mallik, 1997; Curtis and Jensen, 2004; Hartman, 1996; Hartman and Tornlov, 2006; Howard and Larson, 1985; McComb et al., 1990). However, these models often do not generalise well when applied to regions where they were not developed (Baldwin, 2013; Barnes and Mallik, 1997; Cox and Nelson, 2008; Graham et al., 2020; Suzuki and McComb, 1998). This is because, as beaver populations expand, preferred habitats become rapidly occupied; beavers adapt to these conditions by exploiting sub-optimal habitats (Fustec et al., 2001; Graham et al., 2020; Nolet et al., 1994; Vorel et al., 2015) and the nature of this adaptation will be strongly dependent on local geographies. To address this, researchers have developed models which generalise more effectively than the classical regression-based approaches used to create most local HSIs (Dittbrenner et al., 2018; Graham et al., 2020; Macfarlane et al., 2017). This has been achieved by adopting expert rule-based based models with broader confidence ranges that offer a more generalised but pragmatic description of beaver habitat (Dittbrenner et al., 2018; Macfarlane et al., 2017). In Chapter 4 we adapt these modelling approaches for British landscapes to produce a generalisable model that can predict the distribution of beaver forage habitat and the potential distribution of dams and their density at the catchment scale (Graham et al., 2020). Critical to this modelling work were enhancements that could appropriately consider the often narrow and discontinuous woody vegetation present along many GB streams (and indeed those of other countries where intensive agriculture is prevalent in the lowlands). Further, we show that beaver dam capacity can be used to estimate the probability of damming at the reach scale and the number of dams that may occur at the catchment scale. The development of such a tool is a crucial step for creating spatially coherent management strategies.

1.5 Population Dynamics

Because fecundity rates in *C. canadensis* differ from *C. fiber* it is important to discriminate between the two species when considering population dynamics. Conveniently though, *C. fiber* population change has been well described (Barták et al., 2013; Brommer et al., 2017; Halley et al., 2012, 2020; Halley and Rosell, 2002; Hartman, 2003; Petrosyan et al., 2016). What these studies highlight is that the rates of population growth and spatial expansion are strongly influenced by the regional habitat and climate. Across different ecotones, different growth models can explain observed changes. For example, under optimal conditions where forage resource regrowth exceeds beaver harvest rate, the population growth conforms to the logistic model (Barták et al., 2013; Brommer et al., 2017; Petrosyan et al., 2016), where population increases exponentially up to the point where available habitat is limiting and the expansion rate slows. Alternatively, where forage regrowth rates are lower than beaver consumption, eruptive growth can occur which is characterised by an initial rapid expansion, followed by a sudden decline and eventual stabilisation of the population (Hartman, 2003). These and other growth models have been derived based on long term observation, which is crucial for establishing empirical understanding. What is lacking is the ability to predict at what rate beaver populations might expand within British landscapes to support the forward planning of management. We seek to address this requirement in Chapter 5 where we use field sign survey data, collected annually during the 5-year ROBT, to estimate the change in territory expansion and use growth models, observed elsewhere in Europe in similar climatic regions, to predict how the beaver population in the River Otter catchment might change under differing management scenarios. This type of modelling is needed to support longer term planning and resource allocation that will inevitably be required if beaver reintroduction and expansion continues in GB.

1.6 Rationale

On balance, the scientific literature overwhelmingly shows that the impacts of beaver are a force for positive change by reinstating natural processes. In landscapes stripped of much of their natural structure and function, beaver reintroduction and expansion has the potential to significantly benefit natural hydrological, geomorphic and ecological processes. However, the rapid expansion of the species across riparian zones, dominated by anthropogenic landuse, will continue to result in management conflicts and challenges. There is a need to pursue novel lines of research and improve current understanding of the structural and functional impacts of beaver at the site scale, so that we can accurately describe the effect and importance of beaver as ecosystem engineers, particularly in intensively-managed landscapes. This is key for supporting local decision making where beaver impacts intersect anthropogenic landuse (particularly where it is of economic importance).

Given the observed rates of population expansion across Europe (Figure 1-1) and recent governmental support for beaver translocation and reintroduction in GB, there is a pressing need to understand beaver behaviour at the landscape scale. We therefore must continue to enhance our ability to predict the impact of beaver, as they return to our landscapes in greater numbers, by developing new tools and methods to model their spatiotemporal distribution and impact at the landscape scale. Empirical understanding must underpin this work to ensure that both predictions and associated uncertainty are robustly quantified.

This thesis provides novel insight into the structural and functional impact of beaver at the site scale, providing empirical understanding regarding the mechanisms that underpin peak flow attenuation in beaver wetlands Chapter 2 and the impact of beaver foraging on riparian vegetation structure (Chapter 3). Methods for predicting the spatial distribution of beaver habitat and dam density (Chapter 4) are presented alongside modelling approaches to predict future population dynamics, under varying management scenarios (Chapter 5). Therefore, this research builds on both our empirical understanding of beaver impacts and offers novel ways to upscale this understanding in both time and space.

1.7 Thesis structure

The Primary research of this thesis is presented as four individual papers/chapters (2-5). Chapter 4 is published and presented in its typeset format. Chapters 2 and 3 each address critical knowledge gaps in terms of the site-scale impacts of beaver on the landscape to build our understanding of the structural and functional impacts of beaver. Chapters 3 and 4 seek to bridge the gap between local and landscape scale understanding by advancing what we know about the spatial and temporal distribution of beaver habitat, dam distribution and population dynamics.

1.7.1 *Chapter 2 - Exploring the causes of flow attenuation in a beaver dam sequence.*

In this chapter, the functional hydrological response of a 3rd order stream, following the formation of a beaver pond complex, is investigated. Using a Before After Control Impact (BACI) experimental design we compare hydrological event responses before and after the pond complex was constructed and against a neighbouring control catchment. We also use flow duration curve analysis to consider other potential impacts to hydrological regime. This chapter builds on the work published in Puttock et al. (2021), which is included in Appendix 4. In Puttock et al. (2021), we measured the difference in peak flow events before and after dam construction across multiple sites of varying scales; this was imperative to build a stronger empirical understanding of how beaver pond complexes alter hydrological responses at different locals. This chapter builds on this work by considering one site from the River Otter catchment in detail, where we have the longest flow record and a control site. With this richer dataset, we consider in greater detail the hydrological mechanisms which underpin the observed attenuation of peak flows.

1.7.2 *Chapter 3 - Using aerial photogrammetry to detect significant canopy height change resulting from beaver foraging.*

Previous work focusing on changes to ecological structure has primarily focused on alterations to wetland and freshwater habitats (Hood and Bayley, 2008; Larsen et al., 2021; Puttock et al., 2017). Changes in vegetation structure are less frequently studied, although changes to riparian tree community structure, in response to beaver foraging and wetland expansion, are documented (Hood and Bayley, 2009; Nummi and Kuuluvaine, 2013). This chapter seeks to describe the structural change in riparian canopy, within a beaver territory, over the course of a year. The structure of any woodland canopy is complex; however, riparian woodland presents an additional challenge in that it typically comprises multiple tree species of heterogeneous age and size classes. To accurately quantify change in such a system, it is typical to use either terrestrial or aerial light detection and ranging (LiDAR). These technologies are, however, very costly and lower cost methods would therefore be preferable to increase the temporal resolution of repeat surveys. In this paper we test the efficacy of drone-based Structure from Motion (SfM) photogrammetry to quantify change in the woodland structure. And, through the testing of a range of error propagation approaches, we present cost-effective methods that may be used by future researchers across a greater range of sites to help build our understanding on the structural impacts of beaver on riparian vegetation structure.

1.7.3 *Chapter 4 - Modelling Eurasian beaver foraging habitat and dam suitability, for predicting the location and number of dams throughout catchments in Great Britain*

To inform any beaver management or reintroduction plan, it is imperative to know the availability of suitable beaver habitat and where beaver impacts are likely to occur. Therefore we adopted the Beaver Dam Capacity (BDC) modelling approach of Macfarlane et al., (2017), now widely used across North America, because it uses a pragmatic fuzzy inference system to make estimates of beaver dam capacity which intrinsically incorporates uncertainty in predictions and generalises well across different landscape types. In order to deploy the model in GB a new Beaver Forage Index (BFI) was developed from a range of high resolution, nationally-available, landcover datasets which could appropriately capture the complex and often fragmented riparian vegetation that is pervasive across GB. The model was also re-factored and re-parametrised to account for differing geomorphic and hydrological properties of British river systems.. Using beaver field sign data from across three different catchments, containing beaver, we undertook a statistical analysis to make predictions as to the likely number of dams that might occur within a catchment at population carrying capacity. This will facilitate valuable future work to construct empirically based simulations on the impact of dams at the catchment scale. This chapter is published in Graham et al., (2020).

1.7.4 Chapter 5 - Monitoring, modelling and managing beaver populations at the catchment scale.

The River Otter Beaver Trial has afforded a unique opportunity to monitor the expansion of a nascent beaver population. Using annual feeding sign survey data, we estimated the changing number of territories present in the catchment over the course of the trial. We then used a spatially explicit simulation approach to estimate the territory capacity of the catchment, with consideration of habitat quality and territory size. By combining the understanding from the field sign surveys and the estimated maximum number of territories that can be supported in the catchment, we adopt the logistic growth model to predict potential changes in population under a range of lethal control/translocation management scenarios. The methods and tools provided in this chapter can be applied to catchments beyond the River Otter. Thus, providing a valuable tool which can help inform effective management of future beaver populations and potentially support the sustainable translocation of beavers to other regions.

1.7.5 Chapter 6 - Synthesis and Conclusions

The final chapter of this thesis consolidates the findings presented herein and discusses their relevance both within the scientific literature but also for advancing our understanding of the impacts of beaver in a British landscape, much changed since their extirpation. The ways in which the findings from this paper have already contributed to beaver management in GB are discussed and research areas that deserve further attention are proposed.

1.8 Statement of Contribution

I am the lead author of this thesis and the four papers, included herein as chapters 2-5. In all these papers, I led the writing, data analysis, model development and data visualisation. Multiple co-authors are included in these papers for contributing their time and expertise in reviewing the work, carrying out field work, securing funding for the project and supervising the project development.

I have also contributed to five other relevant papers as a co-author. These papers are highly relevant to this thesis and, though I did not lead on this work, I made significant contributions to writing, reviewing and data/statistical analysis. These papers are cited in text throughout this thesis and included in Appendices 1-5; the citation and a brief description of each paper is given below:

Appendix 1:

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

This was the first study on the impact of beavers on peak flows during storm events in GB. The discharge of a first order stream was measured at the inflow and outflow of a beaver enclosure, containing 13 dams, between October 201 and January 2016. Discrete hydrological events were extracted; peak flows were found to decline by 30% (±19% SD) and lag times increased by 29% (±21% SD). Water samples were collected during storm events, up and downstream of the enclosure; suspended sediment, nitrogen and phosphate concentrations were found to be lower downstream of the dam, indicating a reduction in diffuse pollutant loading. Conversely, dissolved organic carbon concentrations increased between the up and downstream sampling locations.

Appendix 2:

Puttock, A., Graham, H.A., Carless, D., Brazier, R.E., 2018. Sediment and nutrient storage in a beaver engineered wetland. Earth Surface Processes and Landforms 43, 2358–2370. https://doi.org/10.1002/esp.4398

This study was conducted at the same location as Puttock et al., (2017) (Appendix 1). The depth and extent of fine sediment, deposited in the bottom of the 13 beaver ponds was surveyed. In total, an estimated 101.53 ± 16.24 t of sediment had accumulated within the ponds. Sediment samples were analysed for nitrogen and carbon content; when extrapolated for the estimated total sediment volume, 15.90 ± 2.50 t of carbon and 0.91 ± 0.15 t of nitrogen were predicted to be stored within the pond sediment. Approximately 70% of the sediment stored within the pond was shown to originate from upstream sources (intensively-managed grassland) and the remainder was likely to have been remobilised from within the site by beaver engineering activities.

Appendix 3:

Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H., Brown, C.M.L., 2021. Beaver: Nature's ecosystem engineers. WIREs Water 8, e1494. https://doi.org/10.1002/wat2.1494

This review paper provides an up-to-date summary of the current state of our scientific understanding regarding the impacts of Eurasian beavers. The paper addresses five different research areas: "Ecosystem structure and geomorphology", "hydrology and water resources", "water quality", "freshwater ecology", and "humans and society". Future research and management considerations are discussed, particularly in regard to the effect of beaver in landscapes which are frequently dominated by anthropogenic landuse. The work presented, in this review is highly relevant to this thesis as it helps to contextualise the results presented in Chapters 2-5.

Appendix 4:

Puttock, A., Graham, H.A., Ashe, J., Luscombe, D.J., Brazier, R.E., 2021. Beaver dams attenuate flow: A multi-site study. Hydrological Processes 35, e14017. https://doi.org/10.1002/hyp.14017

In this paper, we demonstrated that beaver wetlands attenuated peak flows at four different locations across GB. Discrete hydrological events were extracted from the time series data at each site. Additive General Linear Models were used to estimate the change in the relationship between total event rainfall and peak event flow. Across all sites, peak flows displayed a statistically significant decline following the construction of beaver dams. Reduced peak flows alongside increased lag times resulted in an overall reduction in “flashiness”. The attenuation effect was found to be largest during higher magnitude storm events. The paper identifies the need for an improved understanding of the hydrological mechanisms that control changes in hydrological function. This is addressed in Chapter 2 where we re-analyse data from one of the sites from Puttock et al. (2021) using a range of different models, that consider the potential interaction between increased storm magnitude and the presence of a beaver wetland, to discuss the most likely mechanism that could be driving the observed flow attenuation.

Appendix 5:

Campbell-Palmer, R., Puttock, A., Wilson, K.A., Leow-Dyke, A., Graham, H.A., Gaywood, M.J., Brazier, R.E., 2021. Using field sign surveys to estimate spatial distribution and territory dynamics following reintroduction of the Eurasian beaver to British river catchments. River Research and Applications 37, 343–357. https://doi.org/10.1002/rra.3755

Field sign surveys were undertaken during winter 2017 and 2018 in the Tay (Scotland) and Wye (England and Wales) catchments, respectively. Using methods developed as part of this thesis and presented in Chapter 5, the field sign observations were used to carry out a semi-automated classification of beaver territories, to support the estimate of beaver populations. The number of territories in 2019 for the Tay was 114 (In Campbell-Palmer et al. (2021), the estimated figure was 251). No stable territories were located in the Wye catchment, with low densities of isolated and/or dispersing animals. The survey and semi-automated territory modelling demonstrated considerable value as a potential management tool, that may be used to monitor beaver population change. In Chapter 5, we use these methods to estimate the potential rate of beaver territory expansion and how this might be affected by territory translocation and/or lethal control.

Chapter 2. Exploring the dynamics of flow attenuation at a beaver dam sequence.

This chapter builds upon our previous work (published in Hydrological Processes (Puttock et al., 2021) and provided in Appendix 4) by interrogating hydrological time series data, from a beaver impacted study site (where a control catchment was also available), in detail to explore the mechanisms that control flow attenuation in beaver pond sequences. By generating averaged hydrographs for all events before and after beaver dam construction, using general additive models, we compared the changes in hydrograph geometry with the control site, finding a more attenuated response after beaver dam construction. Using a suite of different general linear models, we considered the importance of the interaction between increased storm magnitude and peak event flow, which showed that flow attenuation increased with storm magnitude. We consider the potential causes of this phenomenon and attribute the effect to transient floodplain storage; providing a conceptual model to support these conclusions.

As noted by a recent and comprehensive review of the impacts of beaver (Larsen et al., 2021); with an increasing number of studies demonstrating flow attenuation in beaver dam sequences, there is a requirement to develop a stronger understanding of the hydrological process that underpin observed flow attenuation. This work seeks to contribute to this knowledge gap in the literature and may provide essential information for modelling studies that seek to extrapolate beyond site scale findings.

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RESEARCH ARTICLE

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Exploring the dynamics of flow attenuation at a beaver dam sequence

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Abstract

Beavers influence hydrology by constructing woody dams. Using a Before After Control Impact experimental design, we quantified the effects of a beaver dam sequence on the flow regime of a stream in SW England and consider the mechanisms that underpin flow attenuation in beaver wetlands. Rainfall-driven hydrological events were extracted between 2009 and 2020, for the impacted ($n = 612$) and control ($n = 634$) catchments, capturing events 7 years before and 3 years after beaver occupancy, at the impacted site. General additive models were used to describe average hydrograph geometry across all events. After beaver occupancy, Lag times increased by 55.9% in the impacted site and declined by 17.5% in the control catchment. Flow duration curve analysis showed a larger reduction in frequency of high flows, following beaver dam construction, with declines of Q5 exceedance levels of 33% for the impacted catchment and 15% for the control catchment. Using event total rainfall to predict peak flow, five generalized linear models were fitted to test the hypothesis that beaver dams attenuate flow, to a greater degree, with larger storm magnitude. The best performing model showed, with high confidence, that beaver dams attenuated peak flows, with increasing magnitude, up to between 0.5 and 2.5 $m^3\ s^{-1}$ for the 94th percentile of event total rainfall; but attenuation beyond the 97th percentile cannot be confidently detected. Increasing flow attenuation, with event magnitude, is attributed to transient floodplain storage in low gradient/profile floodplain valleys that results from an increase in active area of the floodplain. These findings support the assertion that beaver dams attenuate flows. However, with long-term datasets of extreme hydrological events lacking, it is challenging to predict the effect of beaver dams during extreme events with high precision. Beaver dams will have spatially variable impacts on hydrological processes, requiring further investigation to quantify responses to dams across differing landscapes and scales.

KEYWORDS
beaver, beaver dams, *Castor fiber*, ecosystem engineers, floodplain storage, flow attenuation, hydrology, natural flood management

1 | INTRODUCTION

Where beavers construct dams, there can be a transformative impact on the fluvial landscape. Beaver dams reduce stream longitudinal connectivity, simultaneously increasing lateral connectivity (Brazier, Puttock, et al., 2020; Puttock et al., 2021). This often results in the reinstatement of channel-floodplain interactions, enhancing hydrological connectivity and driving the creation of dynamic, structurally complex wetlands (Brazier, Puttock, et al., 2020; Gurnell, 1998; Larsen et al., 2021). The enhancement of biodiversity, through the re-establishment of such wetland environments, is well known (Law et al., 2016; Stringer & Gaywood, 2016). However, the coincidental impacts of beaver dams on hydrology are less well understood from a process-based perspective.

Beavers construct dams to increase local water depth so that they can: (i) enhance security from predation by raising water levels above burrow/lodge entrances (Gurnell, 1998); (ii) improve access to foraging resources and reduce terrestrial movement, which is higher risk and greater effort (Campbell-Palmer et al., 2015); (iii) to prevent freezing of water during the winter; and (iv) to store food resources, in the form of a woody cache, beneath the water surface (Campbell-Palmer et al., 2015). Typically, dams are constructed in small rivers <6 m wide and <0.7 m deep (Hartman & Tornlov, 2006). Other factors that influence dam construction and density are building material availability, stream power, stream gradient and stream width (Dittbrenner et al., 2018; Graham et al., 2020; Macfarlane et al., 2017). It is typical for dams to be constructed in low-medium gradient headwater streams ≤5th order (Graham et al., 2020; Gurnell, 1998; Rosell et al., 2005; Stevens et al., 2007). In larger rivers, where water is suitably deep, beavers are unlikely to build dams in the main channel (Brazier, Puttock, et al., 2020; Gurnell, 1998; Hartman & Tornlov, 2006).

Dams exert strong controls over hydrological processes during both high and low flows. The retention of more water within catchments has been shown to maintain base flows mediating the impacts of drought conditions (Majerova et al., 2015; Nyssen et al., 2011; Smith et al., 2020). It has also been shown that, in small headwater streams, beaver dam complexes can contribute to the attenuation of peak flows during hydrological events (Nyssen et al., 2011; Puttock et al., 2021, 2017), reduce mean flow velocity (Green & Westbrook, 2009) and provide significant stormflow storage which increases water-residence times (Grygoruk & Nowak, 2014; Gurnell, 1998; Westbrook et al., 2020; Woo & Waddington, 1990). This flow attenuation effect has been attributed to the following causes:

i. Beaver ponds provide a reservoir in which stormflow can be temporarily or transiently (Westbrook et al., 2020) stored before being released more slowly from the pond than it entered. The contribution of this mechanism is debated (Devito & Dillon, 1993; Larsen et al., 2021; Westbrook et al., 2020) because the available storage/freeboard behind dams is typically very small (Larsen et al., 2021) as pond depth is normally controlled by dam crest height; The effect of this attenuation mechanism is likely to be largely controlled by dam structure and flow state (Ronnquist & Westbrook, 2021; Woo & Waddington, 1990)
ii. Beaver dams, their wetlands and associated canals increase hydraulic roughness slowing flow and increasing water depth. Though these functional processes have been discussed (Grudzinski et al., 2020; Gurnell, 1998; Puttock et al., 2017; Puttock et al., 2021; Westbrook et al., 2020), their relative contribution is not known and is most likely variable (Larsen et al., 2021).
iii. Beaver dams enhance floodplain activation; water is therefore more readily stored within and on the floodplain. This effect was documented by Westbrook et al. (2006, 2020) and modelled by Neumayer et al. (2020), who predicted attenuation only in a stream situated in an unconfined low-profile floodplain valley (Nanson & Croke, 1992).
iv. Some attenuation may also occur through groundwater and evapotranspirative losses (Larsen et al., 2021; Westbrook et al., 2006). Whilst the contribution of these mechanisms has not been quantified in beaver wetlands, it is likely that, following dry antecedent conditions or in arid locations, the effect of groundwater flow could exceed that of evapotranspiration.

With the assumption that transient storm water storage is limited to beaver ponds alone, like a flood storage basin, it can be assumed that a beaver pond sequence has a finite storage volume which will be reached quite rapidly during a storm event. A greater volume of storage may be available where the freeboard behind dams is large (Larsen et al., 2021) and or dam flow state is classified as underflow; that is, where water flows through holes in the dam structure below the of dam crest; Ronnquist and Westbrook (2021). Such observations have also been described for man-made leaky wooden dams which, in many respects, aim to mimic the natural processes created by beaver dams; Norbury et al. (2021) note the importance of porosity in man-made structures for regulating peak flows. Several studies have now reported increasing attenuation with higher flows (Nyssen et al., 2011; Puttock et al., 2021; Westbrook et al., 2020) which cannot be explained by pond storage alone. A key factor that may help to explain these processes is the structural heterogeneity of beaver wetlands which is not limited to the dam structures themselves but includes the often dense and expansive canal networks that beavers create across floodplains (Grudzinski et al., 2020). This structural complexity likely plays a crucial role in controlling numerous hydrological and floodplain processes. This study aims to explore further the dynamics of flow attenuation and discuss what mechanisms might be driving these observed increases in attenuation.

Land use intensification and channel modification are responsible for widespread fluviogeomorphic degradation such as channel incision and floodplain disconnection (Brown et al., 2018; Kondolf, 1997). In combination with projected intensification of storm events, flooding is likely to become more acute (O'Briain, 2019). Restoring natural processes and promoting water retention in catchments may help to ameliorate such impacts (Ellis et al., 2021).

This research analyses the mechanisms by which beaver dams impact stream hydrology using a Before After Control Impact (BACI) experimental design (Bilotta et al., 2016; Smith, 2014). A companion piece of analysis is also published as part of a multi-site comparison in Puttock et al. (2021) that demonstrated flow attenuation across sites. Herein, focusing on one site in detail, we expand on these findings to consider the causes of observed changes to hydrological regime.

Puttock et al. (2021) demonstrate the effect of flow attenuation across multiple sites containing beaver dams. This was done using additive regression models comparing total event rainfall and peak event discharge with beaver presence as an additive covariate. In this context, a simple, parsimonious model enabled clear comparison between geographically disparate locations. These models assume an equal magnitude of attenuation with increasing rainfall intensity. This assumption may be appropriate if beaver dams behave as storage ponds; but, as mentioned above, given the small freeboard upstream of many dams, this mechanism cannot explain the increased attenuation for subsets of larger magnitude events observed by Puttock et al. (2021). This suggests that there is an interaction effect between total event rainfall and beaver dam presence, that is, with increasing storm magnitude, more attenuation occurs, and the slopes of the regression diverge for events before/after beaver. Therefore, an alternative or additional mechanism of flow attenuation to pond storage is required to explain this phenomenon.

This study tests the following hypotheses to advance our process-based understanding of the functional impact that structural change, brought about by beaver dams, delivers during hydrological storm events.

> **H1.** *Flow entering the beaver dam complex is slowed, resulting in increased lag times between peak rainfall to peak flow.*

> **H2.** *Storm event peak flows are lower following the construction of a beaver dam sequence and the amount of attenuation increases with total event rainfall.*

Based on the outcomes of hypotheses one and two, a conceptual model is proposed describing the mechanisms of flow attenuation at the beaver dam complex and consider how this may form the basis of future work across a wide range of landscape types.

2 | METHODS

2.1 | Site descriptions

Two catchments are considered in this study; Budleigh Brook, the impacted site that contained a beaver complex and Colaton Brook, the control site, which had no evidence of beaver activity throughout the entire monitoring period (Figure 1).

2.1.1 | Budleigh Brook

Beavers have been active in the Budleigh Brook catchment since January 2017. The catchment is located within the wider River Otter Catchment (Brazier, Elliott, et al., 2020) and was colonized naturally (as opposed to being the site of beaver release). The precise time of colonization is unknown, though beaver signs, including damming, were observed on February 1st, 2017, therefore the period August 2016 to January 2017 (possible time of colonization) was excluded from this study.

Approximately 1 km of 3rd order channel is contained within the occupied beaver territory (ca. 3 ha); up to six dams had been constructed, within this reach, during the monitoring period. The contributing catchment area is 6.3 km^2 and has mixed land use comprising: managed grassland, outdoor pig farming, arable farming, heath, and woodland. Climatic conditions at Budleigh Brook are temperate, with a mean annual maximum temperature of 12.6°C and a mean of 1065 mm of rainfall annually (Met Office, 2020).

Beavers have significantly modified the site via the construction of dams as shown in Figure 2. The first and largest dam is located at the downstream end of the complex. This dam extends ca. 75 m across the floodplain and has caused the formation of numerous flow paths through the floodplain downstream of the structure. The pond, generated by this dam, has a surface area of ca. 1900 m^2 and contains the beaver lodge. Several other dams have since been constructed upstream; presumably to improve mobility for accessing alternative food resources. A second pond with an area of ca. 300 m^2 has been constructed further upstream. Some of these dams have been managed (removed or height reduced) to prevent surface water flooding of a nearby road (Brazier, Elliott, et al., 2020). Several other small dams exist but are not large enough to form a floodplain pond, but still impound water within the channel and push water onto the floodplain at high flows. The largest dam was constructed before February 2017 and has remained relatively stable since; upstream dams have collapsed and been rebuilt multiple times throughout the study period.

The Hayes Lane gauging station is located ca. 700 m downstream from the beaver dam complex (lat., long.: 50.6561, −3.3249) with no other channels entering the stream between the beaver dams and the gauging station. This gauging station is owned and maintained by the Environment Agency. The gauge is set within a stilling pond upstream of a weir which comprises a double-trapezoidal channel profile along its crest (SI 1). The gauging station was constructed to provide an early flood warning system to the residents of East Budleigh, a community with properties at risk of flooding (Brazier, Elliott, et al., 2020).

Further information about the site can be found in Brazier, Elliott, et al. (2020) and Puttock et al. (2021).

2.1.2 | Colaton Brook

The neighbouring catchment, to the north of Budleigh Brook is Colaton Brook (Figure 1). Colaton Brook is also a 3rd order stream with a contributing catchment area of 5.5 km^2 upstream of the flow gauge.

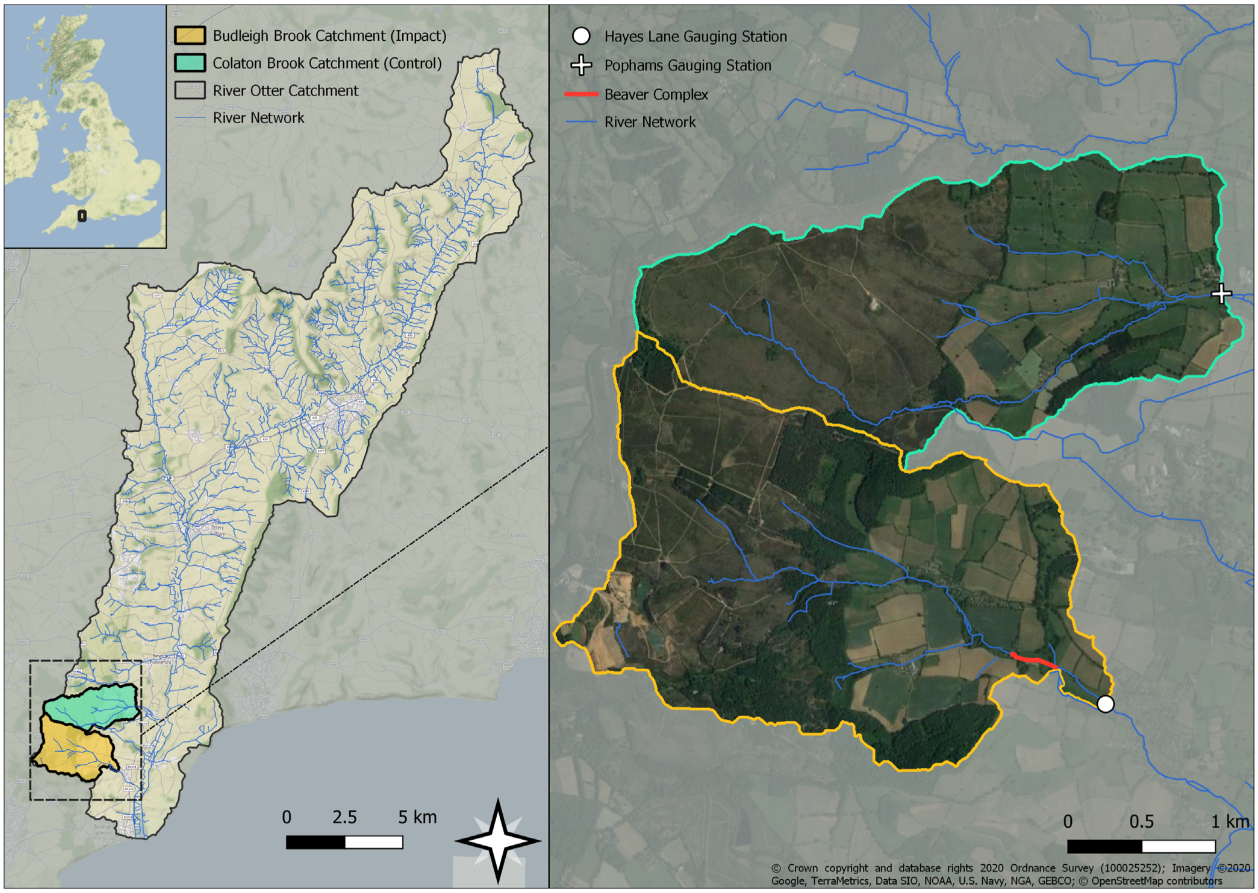

FIGURE 1 Left—Budleigh Brook (yellow) and Colaton Brook (green) catchment locations; right—location of EA gauging stations for the two catchments and the beaver complex on Budleigh Brook. Budleigh Brook has a catchment area of 6.3 km^2 comprising managed grassland, outdoor pig farming, arable farming, heath, and woodland. The Colaton Brook catchment has an area of 5.5 km^2 with dominant land uses including: Heathland, managed grassland, arable farming, and woodland

The land use includes heathland, managed grassland, arable farming, and woodland. Pophams gauging station (Lat., Long.: 50.68125, −3.314561), also owned and maintained by the EA, provides 15-min interval flow measurements. Beavers were not resident in this catchment during the study period and no beaver signs have been located upstream of the gauging station (Brazier, Elliott, et al., 2020; Brazier, Puttock, et al., 2020; Graham et al., 2022). This, the comparable size, stream order, distribution of land use and proximal location of the Colaton Brook catchment make it a highly suitable control.

2.2 | Data processing/cleaning

The Hayes Barton gauge on the Budleigh Brook (impact) has not been rated for discharge measurement by the Environment Agency and reports only depth. The gauging station measures depth at 15-min intervals and a record exists from July 2009 to present. Flow was estimated from this depth record using the following procedure. An area-velocity flow meter (NivuFlow Mobile 750, Nivus, Germany) was installed for 2 months (December 2019–February 2020), 50 m upstream of the gauge/weir crest, within a stable, uniform trapezoidal channel (SI 1). Depth at zero flow was calculated by surveying the depth of flow over the weir crest and subtracting this from the gauged depth. A flow-depth rating equation (SI 2) between measured flow and depth at the gauging station was generated using piecewise spline regression, as described in Fenton (2018), using the splines package (R Core Team, 2020). The depth at zero was used to anchor the rating curve through zero at this point. The rating equation was then applied to the full time series: from July 2009 to March 2020 (excluding the period August 2016 to January 2017 when the presence of beavers was uncertain).

Data from both the impact (Budleigh Brook) and control (Colaton Brook) sites were cleaned to remove visibly erroneous sections of the time series. These sections occurred during periods of maintenance where the stilling pond was drained. Further cleaning of the data was required to remove noise occurring at low flows. This step was necessary in advance of the automated event extraction to prevent the misidentification of events. An automated cleaning strategy was used:

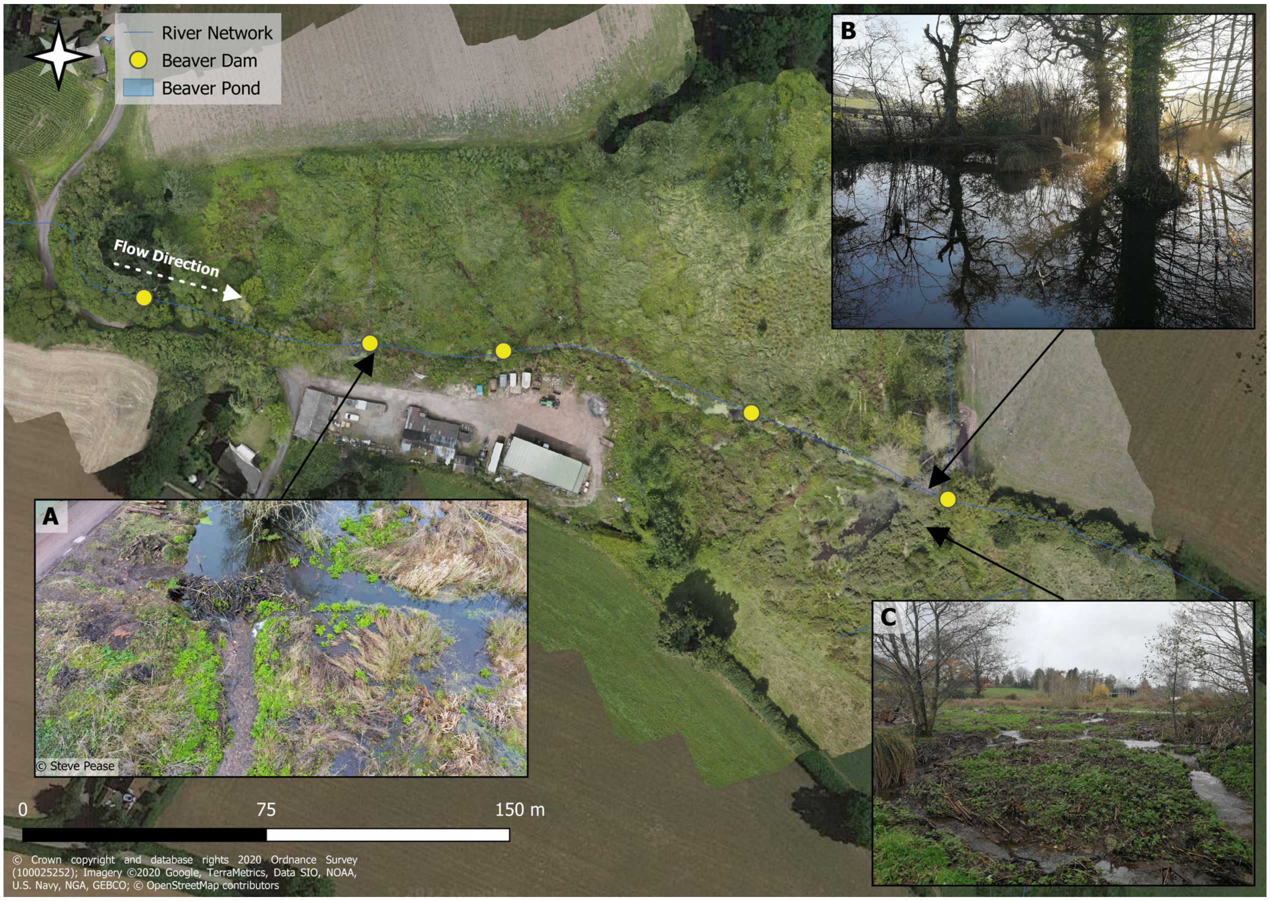

FIGURE 2 Budleigh Brook beaver dam complex showing dam and pond locations. (a) Diversion of water out of bank into the floodplain; (b) the main lodge pond; (c) development of multithread complex channel planform. The base map shows a drone-derived orthomosaic of the site overlain on Google Earth Imagery

quantiles, for a specified time window (in this instance 12.5 h) at the 25th and 75th percentile, were calculated (termed *Q25*th and *Q75*th, respectively); a rolling quantile for the 70th percentile, for a one-month period, was also calculated (*MQ70*). Where (*Q75*th – *Q25*th) > *MQ70*, the flow was considered elevated and any fluctuation in flow driven by precipitation; therefore, measured discharge was used. Where (*Q75*th – *Q25*th) < *MQ70*, the flow was considered to be low and not responding to a flow event; therefore a 7.5 h rolling mean for *Q* was used in place of measured *Q* to smooth out sensor noise occurring during low flows. The aim of this cleaning was to remove common noise associated with low flow measurement. No cleaning was therefore applied to flow event peaks, which was the dominant focus of this analysis.

2.3 | Rainfall calculation

A rainfall record was required alongside the flow data to understand the precipitation volume and rate that contributes to each flow event. There were no historic rainfall gauges within either impact or control catchments that cover the full flow record used in this study. Further, rainfall is spatially variable and data from a single rain gauge can be problematic (Younger et al., 2009; Zeng et al., 2018). Therefore, rainfall radar data, derived from the NIMROD system (Met Office, 2003) were used. NIMROD data are provided as gridded total rainfall with spatial and temporal resolutions of 1 km and 5 min, respectively. Total rainfall for each time step was extracted for each site's contributing catchment area and converted to mean rainfall rate, before aggregating to 15-min intervals to align with the temporal resolution of flow data, as per Puttock et al. (2021). Data download and conversion was conducted using Python (Python Software Foundation, 2019) and raster statistics were extracted with R (R Core Team, 2020) using the exactextractr package (Baston, 2020). The full hydrological time series is provided in SI 3.

2.4 | Event extraction

The extraction of rainfall-runoff events and corresponding metrics was undertaken using a semi-automated rule-based approach for the identification and pairing of rainfall and flow features from sub-hourly observations (Puttock et al., 2021). Slow flow/fast flow was estimated by implementing flow separation on the padded time series (2880 reflected values, i.e., 2 days) with five passes of a single parameter recursive digital filter (alpha value of 0.98) after Ladson et al. (2013).

Rainfall events were classified as periods of rainfall over the median, categorized as either continuous (rainfall occurring on consecutive time steps) or isolated (SI 4). The span for minimum permitted gap between continuous periods was set through visual inspection and rainfall event periods separated by less than this span (90 min) were merged. To adapt thresholds for interannual variation and seasonality, while retaining a consistent approach, flow events were delineated using the digitally filtered fast flow (Ladson et al., 2013; Puttock et al., 2021). By default, the first timestamp in the event window was set to the start of the rainfall event ongoing at the beginning of the response event; or if no rainfall event was ongoing, the preceding rainfall event was used. Where a response event was paired with the same initiating rainfall as the previous event, it was assumed that contributing rainfall for the new event occurs during the falling limb, and the event window was bounded by the peak of the previous flow response.

All classified events were checked via visual inspection; erroneous/implausible events were removed from the analysis when, for example, the hydrograph geometry is angular and likely results from a sensor error or draining of the stilling well for maintenance; 91 and 13 events were removed for impact and control catchments, respectively. Event peak flow and total rainfall were calculated for each retained event window; with total event numbers of 612 and 634, for impact (Budleigh Brook) and control (Colaton Brook) catchments, respectively.

2.5 | Data/statistical analysis

All statistical analysis and data visualization was undertaken using R (4.0.2) (R Core Team, 2020). the following packages were used: tidyverse (v1.3.1) (Wickham et al., 2019), lubridate (v1.8.0) (Grolemund & Wickham, 2011), stats (v4.1.0) (R Core Team, 2020), broom (v0.7.10) (Robinson et al., 2021), glm2 (v1.2.1) (Marschner, 2011), performance (v0.8.0) (Lüdecke et al., 2021), mgcv (v1.8.35) (Wood, 2017, 2011, 2004, 2003), gt (v0.3.1) (Iannone et al., 2020), gridExtra (v2.3) (Auguie, 2017), and ggpattern (v0.3.2.1) (FC & Davis, 2021).

To address H1, that the beaver dam complex slowed flow and increased lag times, a hydrograph averaging technique was adopted. Hydrograph data, including flow, rainfall and time were extracted for all events across both sites; events with a duration >95th percentile (36.75 h) were removed as these longer events were too few in number to model robustly with this approach. For each site, two general additive models (GAM) were fitted to compare both rainfall intensity and stream flow change with time since event start. Each GAM was fitted using the form below:

$$Response \sim s(Time, by = Beaver\ Presence, k = i) + BeaverPresence,$$

where *Response* is either rainfall rate or stream flow depending on which model is fit, *Time* is the time since event start and *Beaver Presence* is the presence/absence of beaver. The ***s*** function defines the smoother used within the GAM where *Beaver Presence* is included as a covariate, such that the smoother is fit independently for each factor level (i.e., for events where beavers were present and absent). The *k* argument is the basis dimension of the smoother term (approximating the degrees of freedom); values of 5 and 10 (the default, i.e., $k - 1$) were used for stream flow and rainfall models, respectively. A *k* value of 5 was required to reduce overfitting of the stream flow model. A cubic regression spline smoother was used for all models. The GAMs provide an approximation of the mean hydrological event response before and after beaver, providing important insight into changes in event geometry. However, as rainfall and flow are not explicitly used in the same model, comparison between the before/after beaver responses must be considered alongside changes in mean rainfall and the response at the control site. All GAMs were fitted using the mgcv package (Wood, 2017, 2011, 2004, 2003). Herein these models are referred to as GAM hydrographs. Average lag times before and after beaver were calculated by differencing the predicted peak times of rainfall and flow.

To evaluate the impact of beaver dams on overall hydrological regime, flow duration curves (FDC) (Vogel & Fennessey, 1995) were generated for both control and impacted sites. FDC metrics including R2FDC and Q5:Q95 ratio were also calculated to evaluate the changes to the FDC. R2FDC describes the slope and the variability of flow in the middle third of the FDC in logarithmic scale (Ochoa-Tocachi et al., 2016); a value closer to zero therefore indicates increased hydrological stability in the central flow range. Q5:95 ratio is used as a flashiness index (Jordan et al., 2005) to describe the range in flow conditions; lower values indicate that a system is less flashy, having a slower response to rainfall.

Given that meteorological effects, precipitation in particular, normally exert strong control over the flow regime of temperate perennial river systems, it is important to consider this when investigating the effect of a non-meteorological disturbance on a river system (such as a beaver dam). Therefore, following the methods in in Puttock et al. (2021), General Linear Models (GLM) were used to consider how peak flows were related to total event rainfall, with beaver presence included as an additive covariate and site as an interactive covariate (M1 in Table 1). Site was included as a model term to compare the difference between the control and impacted locations. We extend this analysis and compare this model alongside four alternative models as shown in Table 1. All models were fitted using a Gamma error distribution because small hydrological events were far more common than large events and therefore a Gaussian (normal) error distribution is not appropriate. Models were fitted with increasing complexity; M2 and M3 included beaver presence as an interactive covariate, enabling freedom in the regression slopes between the two factor levels; M2 and M3 were fitted using identity and log link functions, respectively. M4 and M5 use the second-degree orthogonal polynomial of total event rainfall as the continuous control variable in addition to beaver presence and site as interactive covariates; M4 and M5 were fitted using identity and log link functions, respectively. Polynomial regression was adopted following the inspection of normalized residual plots for M1:M3 (SI 6) which indicated the potential existence of a

TABLE 1 A description of the fitted general linear models. The model number is the reference used in this paper, its form is presented as pseudo code in line with R syntax and the link function denotes the relationship between the linear predictor and the mean of the distribution. Models 1 and 2 were fitted using he glm2 package (Marschner, 2011) and Models 3:5 were fitted with the glm function from R's stats package (R Core Team, 2020)

Model ID	Model form	Link function
M1	$Event\ Max.\ Flow \sim Total\ Rainfall + Beaver\ Presence \times Site$	Identity
M2	$Event\ Max.\ Flow \sim Total\ Rainfall \times Beaver\ Presence \times Site$	Identity
M3	$Event\ Max.\ Flow \sim Total\ Rainfall \times Beaver\ Presence \times Site$	Log
M4	$Event\ Max.\ Flow \sim Poly(Total\ Rainfall,\ 2) \times Beaver\ Presence \times Site$	Identity
M5	$Event\ Max.\ Flow \sim Poly(Total\ Rainfall,\ 2) \times Beaver\ Presence \times Site$	Log

TABLE 2 Model performance metrics for the GLMs presented in Table 1 and Figure 5; used to help with model selection. *K* denotes the number of terms used for fitting the model, Akaike information criterion (AIC) and Bayesian information criterion (BIC) are a descriptor of model quality where a lower value indicates a better fit. R^2 was derived according to Nagelkerke (1991). Estimates of model precision are given by root mean square error (RMSE) and sigma

Model ID	K	AIC	BIC	Nagelkerke's R^2	RMSE	Sigma
M1	5	−12.35	18.41	0.64	1.24	0.97
M2	8	−146.49	−100.34	0.69	1.17	0.93
M3	8	−200.10	−153.95	0.70	1.77	0.91
M4	12	−244.04	−177.38	0.72	1.10	0.90
M5	12	−226.72	−160.06	0.72	1.09	0.90

nonlinear response due to a trend in residual plots. M1 and M2 were fitted using the glm2 package (Marschner, 2011); M3:M5 were fitted using the glm function from the stats package (R Core Team, 2020).

Total event rainfall was chosen as the main control variable, rather than other rainfall metrics, as it was found to have a strong correlation with peak flow across the sites in Puttock et al. (2021) and therefore allowed for comparison with multiple other locations. The Pearson's r correlation values between peak flow and total event were 0.483 and 0.595 for impact and control catchments, respectively; similar values were given for mean rainfall and rainfall rate. The inclusion of site and its interaction with beaver presence/absence is crucial for determining whether any effect of beaver was coincidental or not. Where the interaction between beaver presence and site is significant, it can be deduced that the impact of beaver, at the impacted site, on peak flow is significantly different from the control site. This well-established Before-After-Control-Impact (BACI) design offers robust inference for systems where all influential variables cannot be known or measured (Bilotta et al., 2016; Smith, 2014).

Following the evaluation of model diagnostic plots (SI 6), produced using the performance R package (Lüdecke et al., 2021), Model performance metrics (Table 2) including Akaike information criterion (AIC), Bayesian information criterion (BIC), R^2 (Nagelkerke, 1991), Root Mean Square Error (RMSE) and Sigma, and qualitative plausibility, the M5 model (Polynomial model with log link) was selected as the best model. Though it did not produce the lowest AIC value or highest R^2 (second best of the tested models), it was found to most effectively capture the uncertainty in the data distribution; particularly so for large events with >40 mm total rainfall where only three events of this magnitude were captured post beaver. This was particularly evident in the residual diagnostics plots where there was lower deviance in residuals for larger predicted values indicating a greater reliability for predictions during larger storm events, which is of key interest herein. Using M5, the peak flow attenuation was calculated across the total rainfall range by calculating the difference between predictions with and without beaver. Attenuation was then plotted against the percentile total rainfall to understand how beaver dams attenuate flow across the observed event total rainfall range.

3 | RESULTS

3.1 | (H1) Flow entering the beaver dam complex is slowed, resulting in increased lag times

Figure 3 shows the GAM hydrographs; in the control site (Colaton Brook), a slight reduction in the mean peak flow and lag time is observed between the periods before and after beaver occupancy at the impact site. Differences in the shape of the GAM hydrograph before and after beaver are subtle indicating that, whilst mean event magnitude may have declined, the hydrological response to these events is relatively unchanged. In contrast, for the beaver-impacted site (Budleigh Brook), there is a larger reduction in event magnitude but also a considerable deviation in hydrograph shape after the construction of the beaver dam complex. Most notably, the delayed event peak and reduced gradient of the rising limb; this increase in lag times (55.9%), in contrast to the decrease (17.5%) at the control site, is a

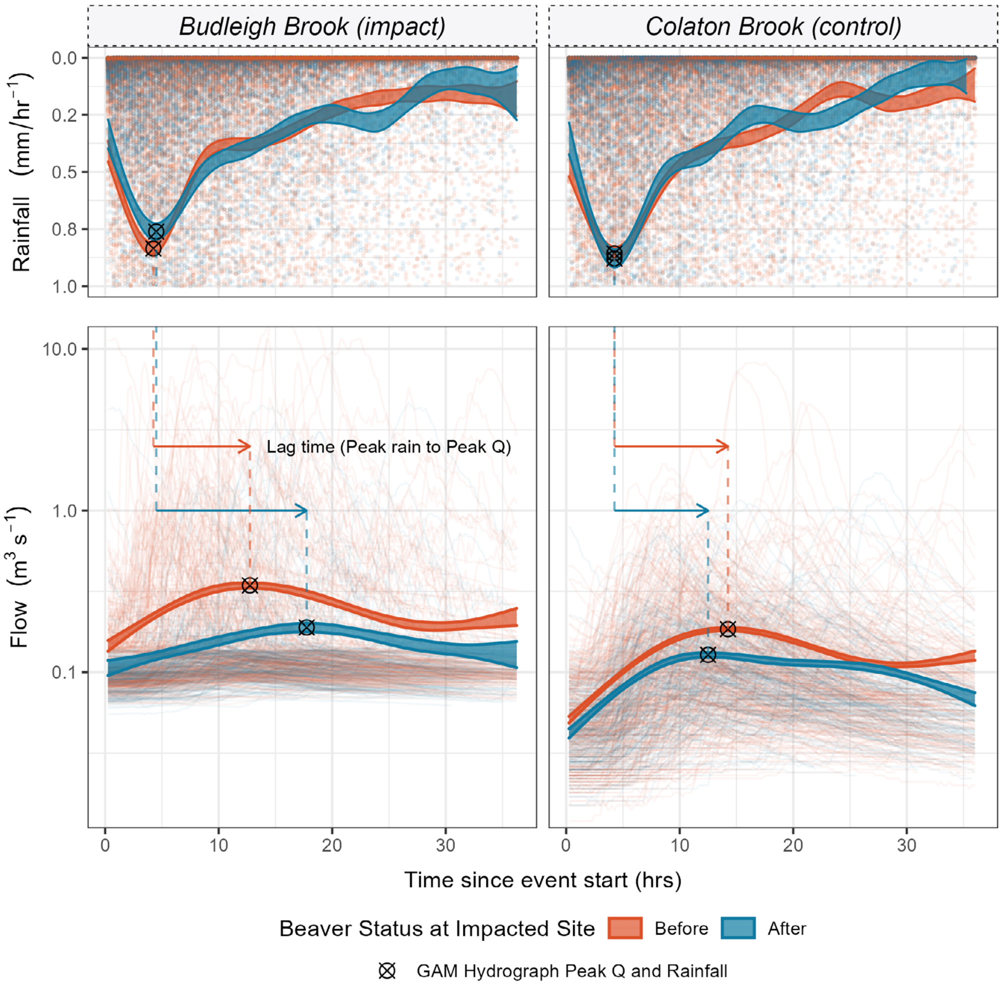

FIGURE 3 The 95% confidence limits of the general additive model (GAM) hydrographs are presented as the shaded ribbons; individual rainfall records are presented as points and individual event hydrographs are presented as lines. The plot enables semi-quantitative assessment of changes in average hydrograph response following beaver dam complex construction. Average event peaks are shown as crosses; these demonstrate that an increase in lag times has occurred at the impacted site whilst a slight decrease in lag times occurred at the control

strong indication of flow attenuation. GAM hydrograph slope gradient, during the lag-time period, decreased at both sites by 67% CI [64, 72] and 29% CI [26, 33] for the impacted and control sites, respectively. Mean event rainfall intensity at the control site remained similar after beaver dam construction. This is the case too for the impacted site, although a slight decrease in peak rainfall following beaver colonization may explain, to some extent, the larger peak flow reduction observed at Budleigh Brook.

3.2 | (H2) Storm event peak flows are lower following the construction of a beaver dam sequence and the amount of attenuation increases with larger rain events

The FDC curves (Figure 4) and metrics (Table 3) clearly show that, at the impacted site, higher flows were less frequently observed; highlighted by a 33% decrease in the Q5 exceedance value at the impacted site and only a 15% reduction at the control. The results for low flows, at the Q95 exceedance limit, also differ; in the control catchment, an increase in Q95 of 12.5% was observed in contrast to the impacted site which experienced a 10% decline in Q95, following beaver colonization.

Changes to the Q5:Q95 ratio flashiness index were comparable across both sites. R2DFC decreased in both sites with a 21% and 14% decrease in the control and impacted sites, respectively. Larger differences in Q5 and Q95 values, alongside a smaller reduction in R2DFC, at the impacted site indicate that the effect of the beaver dam sequence was particularly evident during the hydrological extremes, and less change was observed for intermediate flows, relative to the control site, which experienced larger changes in the central region of the FDC.

Models M1, M4 and M5 (Table 1 and Figure 5) found a significant ($p < 0.05$) interaction between beaver presence and site, indicating

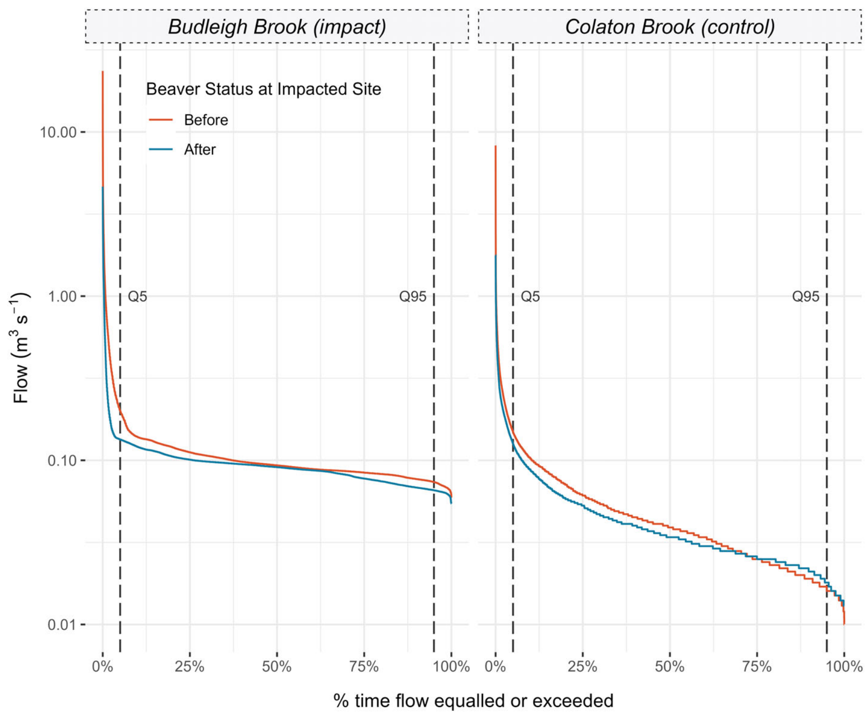

FIGURE 4 Flow duration curves (FDC) for Budleigh and Colaton Brook. These plots represent the proportion of time that a given flow is equalled or exceeded. Q5 and Q95 lines indicate the proportion of time the flow was greater or equal to the 95th and 5th flow percentiles, respectively

TABLE 3 Flow duration curve (FDC) metrics for the two sites, including: Mean and median flow; R2FDC which describes the slope and the variability of flow in the middle third of the FDC in a logarithmic scale (Ochoa-Tocachi et al., 2016); Q5 and Q95 exceedance limits, and the Q5:Q95 ratio which is used as a descriptor of system flashiness

	Mean	*Median*	*R2FDC*	*Q5*	*Q95*	*Q5:Q95 ratio*
Budleigh Brook (impact)						
No Beaver	0.13	0.09	−0.23	0.20	0.07	2.72
Beaver	0.10	0.09	−0.20	0.13	0.07	2.04
% Change	−21.58	−2.49	−14.40	−33.29	−10.86	−25.16
Colaton Brook (control)						
No Beaver	0.06	0.04	−0.72	0.15	0.02	9.38
Beaver	0.05	0.03	−0.56	0.13	0.02	7.06
% Change	−15.18	−12.82	−21.25	−15.33	12.50	−24.74

that there was a significant difference between the peak flows before and after beaver at the impacted site. Models M2 and M3 showed a significant ($p < 0.05$) interaction between beaver presence, site and event total rainfall which indicated that the slope of the relationship between total rainfall and peak flow is significantly different after beaver occupancy at the impacted site. Model summary tables are presented in SI 7. Raw data, and data density distributions for peak flows across each site are presented in Figure 6.

Nagelkerke's R^2 (Nagelkerke, 1991) values indicate that models M4 and M5 provide the best fit (Table 3). Although M4 has a better model fit than M5, based on AIC and BIC (Table 3), there is deviation in the residuals for the upper limits of fitted values (as shown in residual diagnostics plots given in SI 6 and fractionally lower RMSE (Table 3)); therefore, M5 was adopted, despite its marginally poorer fit, as we can have greater confidence in its inference for larger events.

Flow attenuation change with percentile total event rainfall is presented in Figure 7. For much of the total rainfall distribution, it was observed that 95% confidence intervals of the model (M5) were greater than zero; this region is highlighted in Figure 7 as a green hatched region. Peak flow attenuation was found to increase up to the 94th percentile with a magnitude of between 0.5 and 2.5 $m^3 s^{-1}$ (95% CI) equivalent to a peak flow reduction of between 23.4 and 76.5%. Beyond the 97th percentile, attenuation was estimated to be between 0 and 5.2 $m^3 s^{-1}$ and therefore could not be identified with confidence. No such attenuation was observed for Colaton Brook.

4 | DISCUSSION

4.1 | (H1) Flow entering the beaver dam complex is slowed, resulting in increased lag times

Increases in lag times and reduced rising limb slopes were three and two times greater, respectively, at the impacted site following beaver dam complex construction, than the control site (Figure 4). Given the significant interaction term between beaver presence and site in the selected

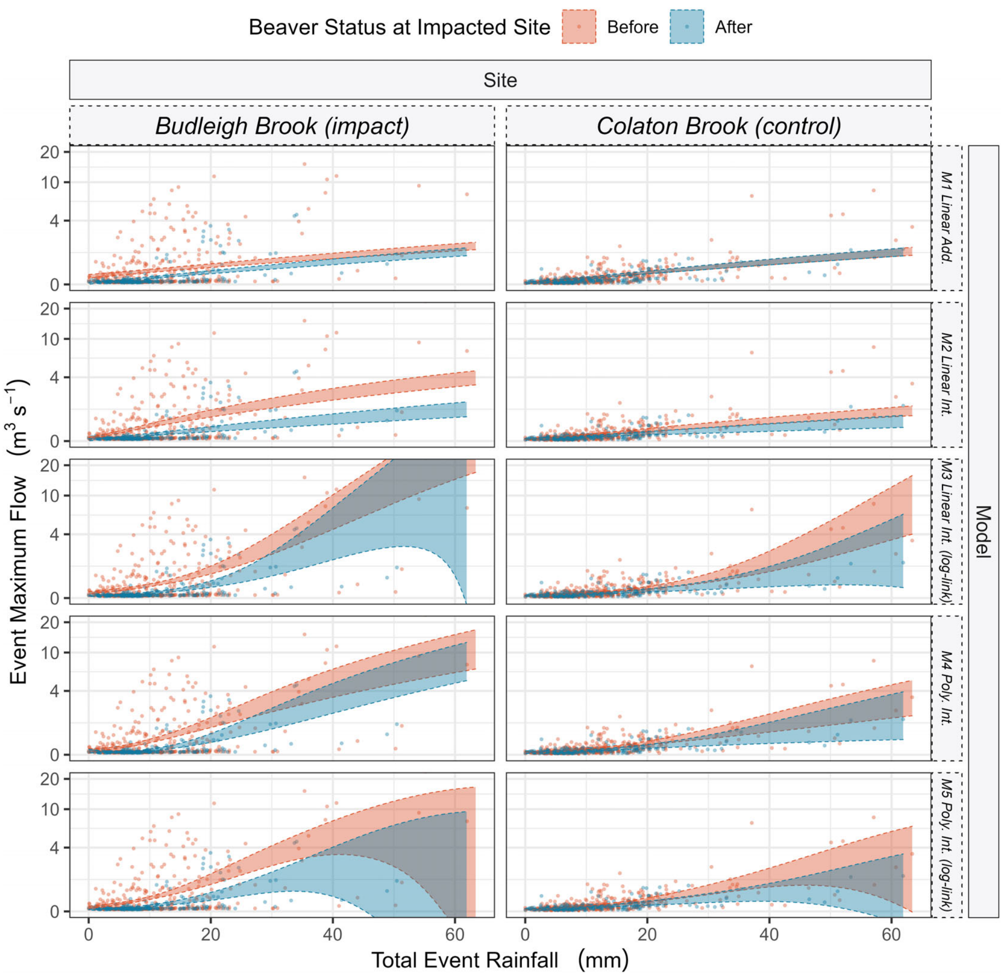

FIGURE 5 The general linear models fitted to determine the impact of a beaver dam sequence on the relationship between total hydrological event rainfall and peak event discharge. Shaded areas represent the 95% confidence intervals of the fitted models. Model IDs correspond to Table 1. *Add*. Indicates that beaver presence is included as an additive term, *Int*. indicates that it was included as an interactive effect. Where log-link is not specified, an identity link was used. All models show that peak flows, for a given total event rainfall, decreased following beaver presence; for models M3:M5 there may only be confidence in this effect up to a given limit (where confidence intervals intersect)

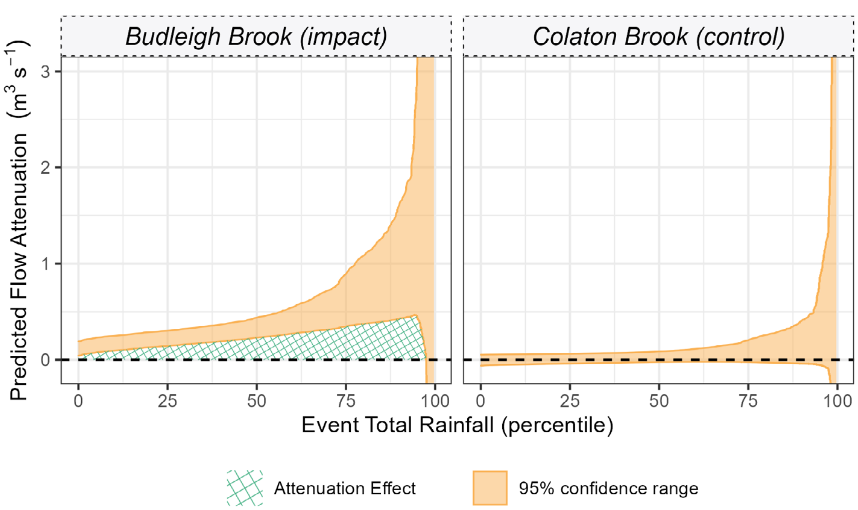

FIGURE 6 The predicted flow attenuation derived from the polynomial regression with log link (M5: Table 1, Figure 5). This is the difference between predicted flows pre and post beaver. Orange shaded regions describe the 95% confidence limits of the model. Where confidence limits are above the zero (dashed) line, there can be >95% confidence in attenuation—this area is shown by the green crosshatched area. Where the zero-line falls within the confidence limits there is low confidence of observing flow attenuation

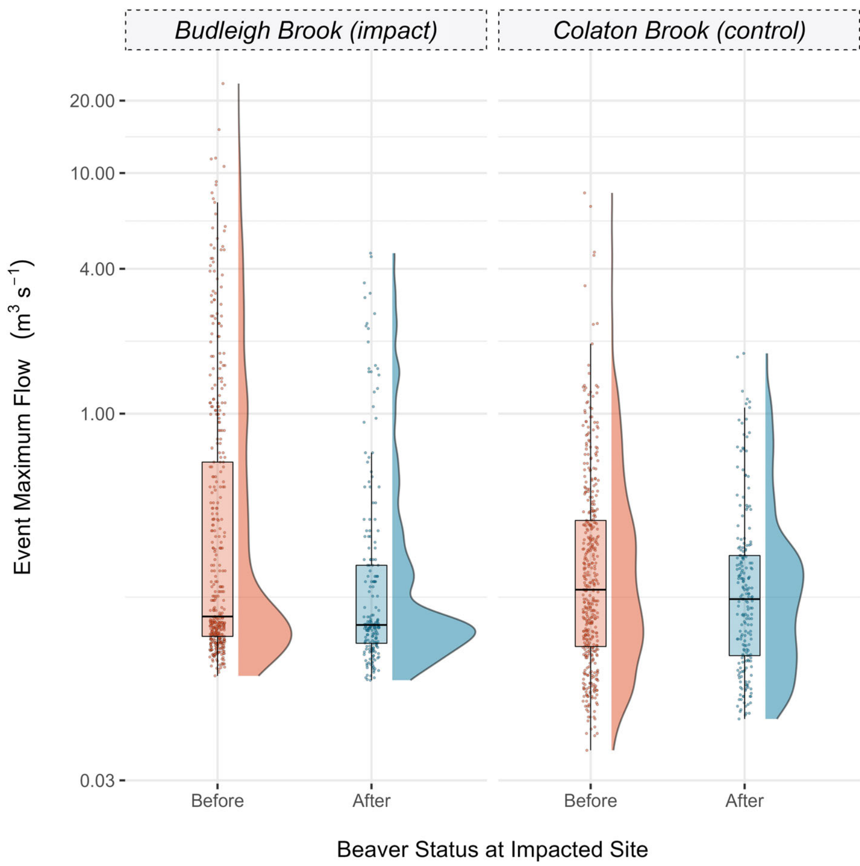

FIGURE 7 Raincloud plot showing the raw data, boxplot statistics and density distribution of peak flows for hydrological events in both Budleigh Brook and Colaton brook, before and after beaver the complex was established in the impacted site

GLM model (M5), there can be confidence that this change resulted from the creation of the beaver dam complex. The potential for beavers to increase lag times has been both observed (Burns & McDonnell, 1998; Larsen et al., 2021; Nyssen et al., 2011; Puttock et al., 2021, 2017; Westbrook et al., 2020) and modelled (Neumayer et al., 2020; Stout et al., 2017) in other studies. This flattening of the curve is a clear demonstration of the theory underpinning natural flood management (NFM) interventions, where the desired goal is to mediate the flow response, extending the duration of events such that the peak flow is reduced (Ellis et al., 2021; Lane, 2017; Norbury et al., 2021).

Key reasons for this attenuated hydrograph geometry are likely to include, the increased effective storage capacity (Gurnell, 1998; Larsen et al., 2021; Puttock et al., 2021, 2017; Westbrook et al., 2006; Woo & Waddington, 1990) and reduced flow velocities (Butler & Malanson, 1995; Green & Westbrook, 2009; Parker et al., 1985), driven by an increase in roughness (Larsen et al., 2021; Puttock et al., 2017).

4.2 | (H2) Storm event peak flows are lower following the construction of a beaver dam sequence and the amount of attenuation increases with larger rain events

Attenuation estimates presented herein for Budleigh Brook and in Puttock et al. (2021), across three other sites in England, illustrated an attenuation effect for larger storm events. Increased attenuation with larger events was also reported by Nyssen et al. (2011), for a dam complex in Belgium, where a dam sequence was found to lower peak flows and increase flood flow return intervals. Westbrook et al. (2020) demonstrate that flood attenuation still manifests for even the largest of hydrological events; the authors found that, in Alberta during largest recorded flood in the Canadian Rocky Mountains, the majority (68%) of dams within the research area were resilient to high flows providing important storm-water storage and increased water retention times both in ponds and laterally across adjacent floodplains.

The location considered herein and those others in (Puttock et al., 2021), sit within unconfined, low-profile flood plain valleys. Modelling by Neumayer et al. (2020) demonstrated increased lag times due to beaver dams but only in valleys with wide and low gradient floodplain profiles. Local topography and channel/floodplain geomorphology are therefore likely to exert a strong control on attenuation processes (Brazier, Puttock, et al., 2020; Larsen et al., 2021; Westbrook et al., 2006). Available storage within ponds is also very likely to affect flow attenuation (Westbrook et al., 2020); however, it is highly variable. Where ponds are less full, prior to an event, they have greater capacity to store/attenuate flow due to the available freeboard (Larsen et al., 2021; Ronnquist & Westbrook, 2021; Westbrook et al., 2020). This mechanism will largely be controlled by the flow state of dams within a complex (Ronnquist & Westbrook, 2021; Woo & Waddington, 1990). As ponds

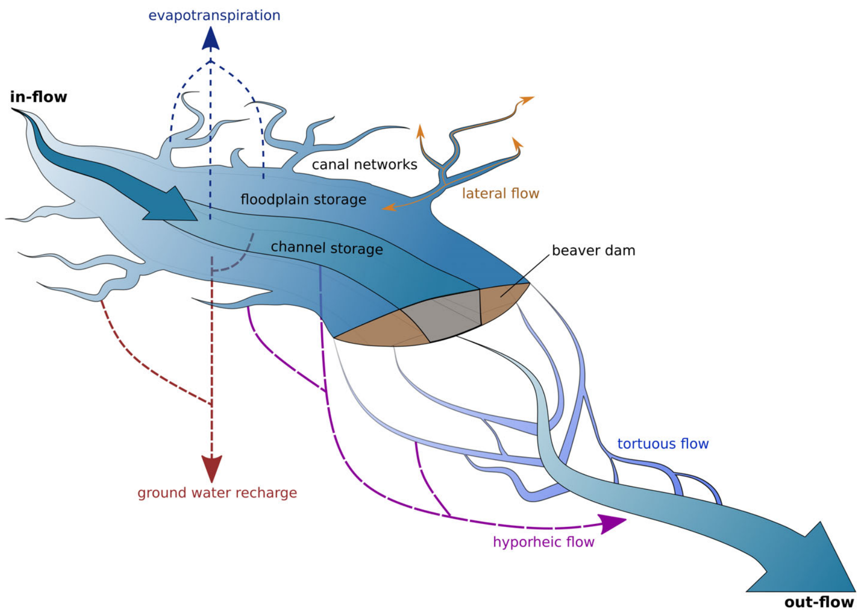

FIGURE 8 Conceptual model describing the mechanisms of flow attenuation within a beaver wetland with an unconfined floodplain. As flow and therefore the depth of water behind the dam increases, the area of activated floodplain also increases; this results in the formation of new flow, infiltration and evapotranspiration pathways. These pathways become longer and more tortuous as the flooded area expands during a flow event. Canals likely play an important role in transporting water laterally into the floodplain further enhancing floodplain connection

fill during an event, water is stored in the pond during the transition between underflow/gap flow to overflow (i.e., overtopping) (Butler & Malanson, 1995; Devito & Dillon, 1993; Ronnquist & Westbrook, 2021). In addition to dam structure, antecedent conditions will also play a critical role in controlling pre-event pond levels/flow state (Neumayer et al., 2020; Puttock et al., 2021, 2017). However, the largest dam in the Budleigh Brook pond complex is typically in a full or near to overflow state (Ronnquist & Westbrook, 2021), even after dry weather, and therefore the available freeboard, that is, pond storage is rarely more than 5 cm. This would approximate to ca. 95 m^3 of available transient storage across the 1900 m^2 pond. Though not insignificant, this volume cannot explain the continued increases in attenuation that were observed as this storage capacity would be rapidly filled during a large event. Therefore, additional attenuation mechanisms must have taken place.

4.3 | Conceptual model of flow attenuation

We suggest that, in a low-profile floodplain valley, not confined by steep valley sides or impeded by man-made features such as levées (Nanson & Croke, 1992), beaver dams will readily reconnect channel-floodplain flow pathways, forcing water horizontally onto the floodplain as flows, and therefore pond levels behind the dam, increase. With increasing flow, water is diverted around/over/through the dam structure with ever increasing flow pathway length, tortuosity, roughness and depth. Simply put, beaver dams and their associated wetlands increase the active area of floodplain and therefore the surface area over which floodplain process can occur. This was observed by Westbrook et al. (2006) who documented large flow diversions extending up to 930 m downstream of the beaver dams. To reach a floodplain flow depth equivalent to the post beaver inundated extent, a flood with a >200-year return interval would have been required. A conceptual diagram of these processes is presented in Figure 8 which highlights the multitude of hydrological pathways that are activated in a beaver wetland, when the channel and floodplain are reconnected by damming; these include surface processes but also subsurface flow both into the shallow hyporheic zone, and deeper aquifer storage, depending on the local soil and geological properties. Beaver canals further enhance these processes by diverting water to more distant regions of the floodplain yet again increasing the active floodplain area (Grudzinski et al., 2020); canals will provide both new flow pathways but also act as temporary storage areas during storm events.

The diverted flow increases water storage, but it is transient and dynamic; as noted by Westbrook et al. (2020) who found that the flood extent, during a very large flow event, was up to 20 m from the pond edge. This supports the idea that wider dams, that enhance floodplain connection, may exert a greater effect on peak flow due to the increased availability of floodplain storage, in addition to pond storage (Puttock et al., 2021). At some threshold discharge, the attenuation effect must plateau (though it is noted here that long, tortuous and high roughness flow paths will persist); this threshold approximates the point where floodplain inundation before beaver is equal to the inundation extent post beaver. In a confined valley, the area over which new flow pathways can form and water can be transiently slowed, stored and infiltrated/evaporated is substantially reduced and therefore this threshold/plateau will be reached more rapidly. Consequently, it is likely that beaver dams have the strongest effect in reducing peak flows in low-profile valleys (Neumayer et al., 2020), where the structures are more likely to persist (Graham et al., 2020; Green & Westbrook, 2009; Macfarlane et al., 2017; Westbrook et al., 2020) and they can activate the floodplain rapidly and over larger areas enhancing transient storage and reducing overland velocities. The effect of beaver dams on high flows, therefore, varies spatially in response to topography, geomorphology, dam structure and dam density (Gurnell, 1998; Puttock et al., 2021; Ronnquist & Westbrook, 2021; Westbrook et al., 2020) but also temporally in response to antecedent climatic conditions. Further investigation in the hydrological effects of beaver dams in steeper river systems would be valuable though to understand the importance of lateral subsurface infiltration and its potential contribution to attenuating peak flows; such processes are likely to be highly dependent on local soil types.

These mechanisms of flow attenuation have important ramifications for where beaver dams may be desirable from a flood mitigation perspective and where projects replicating beaver dam processes, such as the use of beaver dam analogues (Bouwes et al., 2016; Munir & Westbrook, 2021), should be placed in order to yield flow attenuation benefits. These factors will need to be considered, alongside other potential impacts of dams, on biodiversity and economically valuable land/infrastructure. Beavers preferentially dam streams with wider floodplain extents (Dittbrenner et al., 2018) and with lower stream gradients (Dittbrenner et al., 2018; Graham et al., 2020; Hartman & Tornlov, 2006; Macfarlane et al., 2017) where available, often at locations immediately downstream of tributary confluences (Baskin et al., 2011). Therefore, it is possible that the greatest attenuation benefit will accrue during the initial stage of beaver population expansion as these preferred locations are occupied.

As beaver populations expand, family groups will abandon territories, leaving dams unmaintained. Where these dams have previously persisted for some time, they are often stabilized by vegetation (Johnson-Bice et al., 2022; Pollock et al., 2014). Many of these dams can therefore remain in the landscape and continue to exert strong controls over surface water storage/flow routing at catchment and regional scales after the abandonment of territories (Johnson-Bice et al., 2022). Abandoned dams may also influence storm event dynamics; so their impact on peak flow attenuation, and indeed low flow conditions, warrants further investigation.

The anthropogenic modifications of rivers systems globally, primarily through the intensification of land use, combined with dredging, drainage and the construction of permanent barriers like weirs/dams, that starve rivers of coarse sediment, have led to the widespread incision of river channels within their floodplains (Brown et al., 2018; Kondolf, 1997). For a floodplain to be activated, in an incised channel, a far greater flow is required (Pollock et al., 2014). It is likely therefore that the attenuation effect of beaver dams will be most substantive in these modified systems, where the ratio between the flow required for floodplain activation, pre/post beaver dam construction, is greatest. Where incision is not an issue and floodplains are (still) activated readily, the potential increase in attenuation, due to beaver may well be less pronounced as the river's hydrological response is likely to already be more natural and attenuated. This could explain why Burns and McDonnell (1998), who monitored the impacts of a large beaver dam complex and associated wetland on the hydrological regime of a forested catchment in New York State, observed flow attenuation but only to a very limited extent for large events.

4.4 | Low flow considerations

Several studies report the amelioration of drought conditions downstream of beaver dam complexes (Majerova et al., 2015; Nyssen et al., 2011; Smith et al., 2020). This effect manifests because the water stored in beaver ponds leaks slowly, maintaining an elevated base flow. In contrast, it is suggested that increased evapotranspiration rates can lead to a decline in base flow discharge (Correll et al., 2000; Larsen et al., 2021; Meentemeyer & Butler, 1999; Woo & Waddington, 1990). FDCs for the impacted site appear to show no maintenance of base flow with low flows (<Q95) decreasing following beaver dam complex construction. Streamflow losses may have therefore increased following beaver reintroduction. This may have resulted from either increased evapotranspiration in the beaver wetland (Burns & McDonnell, 1998; Fairfax & Small, 2018), and/or increased groundwater recharge, following increased water residence time (Westbrook et al., 2006). The spatial extent of this effect is unknown, though it is conceivable that, due to the porous pebble bed geology of both catchments (Sherrell, 1970), that local groundwater losses may enhance low flows further downstream. Spatial variability in hydrological responses to beaver dams, during high flows, is frequently discussed (Brazier, Puttock, et al., 2020; Larsen et al., 2021); spatial and temporal variability, in the response to low flows, may also be significant and warrants further investigation.

4.5 | Implications for future work

This study demonstrates that there are likely to be multiple mechanisms by which beaver dams attenuate high flows, most likely occurring simultaneously during flood events. There is strong evidence to suggest that this attenuation will increase with greater flows. However, given the large uncertainty for predicted attenuation during the largest of events, further work is required to understand the potential impact of beaver dams on flow, both at the site and catchment scale (Brazier, Puttock, et al., 2020; Larsen et al., 2021). Hydraulic modelling, such as that demonstrated by Neumayer et al. (2020) and Stout et al. (2017) is a vital step in understanding the effect of beavers at these extreme flows. The representation of beaver dams in such models is complex and challenging though, currently requiring dam structures to be defined by the limitations of software. For example, Neumayer et al. (2020) represent the interstitial gaps in the dam as a set number of small pipes; this pragmatic simplification is understandable, but no doubt could be improved with further empirical observation. A stronger dialogue between such empirical data and model development would help to refine parameters such as hydraulic roughness across beaver wetlands, rates of dam under/through flow, and when floodplain activation occurs during large storm events. It is also crucial to capture the variability in dam structure and dimension as demonstrated by Ronnquist and Westbrook (2021) and Hafen et al. (2020)—these factors, in addition to variable dam densities, are likely to exert strong controls on flow attenuation (Beedle, 1991). Therefore, further hydraulic modelling is required, to build on the work of Neumayer et al. (2020) to consider dams of different dimensions, densities and locations. This is crucial as the numbers, densities and size of dams represented by Neumayer et al. (2020) are relatively small at the catchment scale in comparison to those observed or predicted elsewhere (Graham et al., 2020; Macfarlane et al., 2017; Zavyalov, 2014). Once greater confidence in estimating flow attenuation at extreme flows is gained, it will be important to consider how to extrapolate these findings to the catchment scale. By combining our understanding of where beavers build dams and in what densities (Dittbrenner et al., 2018; Graham et al., 2020; Hartman & Tornlov, 2006; Macfarlane et al., 2017; Swinnen et al., 2019), alongside an estimate of the inundated area that may occur (Karran et al., 2016), and an understanding of how flow attenuation manifests across varying event magnitudes (Neumayer et al., 2020; Nyssen et al., 2011; Puttock et al., 2021; Westbrook et al., 2020), flow states (Ronnquist & Westbrook, 2021; Woo & Waddington, 1990) and hydrometric conditions (Majerova et al., 2015; Westbrook et al., 2020), it will be possible to build a much stronger understanding of the catchment scale hydrological impacts of beaver.

Multiple studies now demonstrate the local scale impact of beaver dams on hydrology (Nyssen et al., 2011; Puttock et al., 2021, 2017), but there is a lack of empirical work that considers hydrological change at the (sub)catchment scale. Modelling that attempts landscape-scale extrapolation of local impacts would greatly benefit from empirical work also conducted at this scale (Brazier, Elliott, et al., 2020; Brazier, Puttock, et al., 2020; Larsen et al., 2021). Dam sequences have already been shown to exert a larger effect on hydrology than single dams (Beedle, 1991), it is therefore reasonable to assume that this cumulative effect may also prevail when considering the impact of multiple dam complexes within a catchment, though it is not yet proven to what extent this may manifest. As shown for woody debris dams (Dixon et al., 2016; Lane, 2017), there is likely to be a cumulative effect, but this is unlikely to simply equate to the sum of the impact of individual dam complexes (Larsen et al., 2021). This understanding will prove key for informing future policy on beaver management but also effective approaches for human-engineered NFM projects that seek to replicate beaver dam processes (Auster et al., 2022; Munir & Westbrook, 2021).

5 | CONCLUSION

This study provides further evidence that beaver dam sequences attenuate peak flows during hydrological events. Peak flow attenuation increased with total event rainfall but there was considerable uncertainty for events where total rainfall was >97th percentile. The process of attenuation was demonstrated through the analysis of GAM hydrographs which showed clear changes in hydrograph geometry, following beaver dam complex construction, with increased lag time and reduced rising limb slope. Transient floodplain storage is likely to play a more significant role in contributing to the observed attenuation in addition to pond storage, groundwater losses and reduced velocity, resulting from an increase in roughness and decrease in channel slope and an increase in the area over which hydrological floodplain processes may occur. It is suggested that substantive transient floodplain storage may only occur in streams with low-profile floodplain valleys and therefore these stream reaches are likely to yield the most substantive attenuation effect. The impacts on hydrological regime were most apparent during hydrological extremes—both high and low flows; changes to the frequency and magnitude of intermediate flows were negligible. Spatial, geographic, and meteorological variability will play a major role in determining the relative importance of attenuation mechanisms at play in beaver wetlands.

This research has important implications for beaver reintroduction and management. Beavers may contribute to flood resilience strategies such as natural flood management and catchment restoration, where dams occur in landscapes that support the transient flow attenuation mechanisms discussed herein. In these locations, beaver dam complexes may offer some low-cost flood resilience to small, at-risk communities, especially of value where conventional flood-risk solutions may not be financially justified. The potential cumulative effect of many hundreds of dams could also have significant implications for catchment scale hydrological processes and thus flood-risk reduction, but a stronger understanding of the spatio-temporal variability in beaver dam-hydrological interactions is needed to quantify such effects.

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DATA AVAILABILITY STATEMENT

All code and data to reproduce this analysis is available from the following repository https://doi.org/10.5281/zenodo.6034308 (Graham, 2022). The code used to download and extract The Met Office NIMROD rainfall radar time series (Met Office, 2003) can be found in this repository: https://github.com/exeter-creww/Rainfall_radar.

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SUPPORTING INFORMATION

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Chapter 3. Using aerial photogrammetry to detect significant canopy height change resulting from beaver foraging.

This chapter presents findings from a study on the impact of Eurasian beaver foraging on canopy height change in a riparian woodland using drone-based Structure from Motion (SfM) photogrammetry. Using SfM photogrammetry for change detection in vegetated systems is challenging due to the difficulties of differentiating real change from measurement error. We therefore compare three different methods for error propagation and discuss their implications for our observations.

This study shows that beaver increase variability in canopy height change which may have implications for riparian woodland structure. Further, it highlights the significance and variation in error propagation techniques for SfM change detection.

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Using aerial photogrammetry to detect significant canopy height change resulting from beaver foraging.

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Abstract:

Drone-based structure-from-motion photogrammetry (SfM) is widely used in geomorphology to detect changes in topography over time. SfM has been less frequently adopted for detecting change on complex surfaces, such as vegetation canopies, because of the difficulties of differentiating true change from measurement error in derived elevation models.

Beavers (*Castor fiber)* were reintroduced to a 10 ha site in Devon, UK comprising structurally complex riparian woodland. We assessed the impact of beaver activity on woodland canopy elevation, over a one-year period, using three different methods for generating digital elevation models of difference (DoD). Each method varied in how two error sources (SfM precision and rasterisation uncertainty) were used to define a limit of detection (LoD). These methods included: (i) DoD with no error propagation (No LoD); (ii) a weighted LoD method (LoD_{95}) which proportionately adjusted elevation change based on the local LoD and; (iii) a minimum LoD (LoD_{min}) approach which reported elevation change only beyond a spatially explicit LoD value.

The no LoD method failed to account for measurement uncertainty and therefore offered limited confidence in observations. LoD_{min} was likely too conservative, discarding information due to natural roughness in ecosystem

surfaces. We consider LoD_{95} to be most suitable for assessing canopy change because it preserves more information whilst still accounting for measurement uncertainty. The adoption of such methods is significant as it enables practitioners of SfM change detection to better distinguish real signals from noise (resulting from measurement error) in complex vegetated systems.

All methods demonstrated that beaver activity increased the areal extent of low stature vegetation and reduced mean canopy height by c.a. 0.05 m CI [0.04, 0.06]. Spatially filtered Quantile regression revealed that the magnitude of larger positive and negative canopy height changes increased in woodland containing beaver activity. Relative to woodland without beaver, canopy height decreased by 0.05-1.0 m and increased by 0-0.15 m, for quantiles of 0.05 and 0.95, respectively. Beaver activity therefore increased the variability of canopy height change, which could enhance the structural heterogeneity of riparian woodland.

Keywords:

beaver; structure-from-motion photogrammetry; drone; ecosystem engineers; vegetation change

1 Introduction:

Riparian woodlands are globally important ecosystems (Broadmeadow and Nisbet, 2004; Singh et al., 2021). At the interface of terrestrial and riverine systems, riparian woodlands provide important habitats (Glass and Floyd, 2015; Naiman et al., 1993; Santos et al., 2011). They also play an essential role in riverine processes: reducing floodplain flow velocity (Dixon et al., 2016; Leyer et al., 2012; Thomas and Nisbet, 2007), increasing bank stability (Singh et al., 2021; Vigiak et al., 2016), regulating stream temperatures (Dugdale et al., 2020; Garner, 2017), acting as a nutrient/food source for riverine food webs (Broadmeadow and Nisbet, 2004; England and Rosemond, 2004), controlling nutrient source-sink dynamics (Cole et al., 2020), and provide sources of in-stream woody material which drive local-scale geomorphic processes (Sear et al., 2010) and form important habitat (Wohl, 2017).

Eurasian beaver (*Castor fiber*) are ecosystem engineers. Beaver modify river and riparian systems by building dams and lodges, digging burrows and canals, and grazing on vegetation (Brazier et al., 2020; Gurnell, 1998; Larsen et al., 2021). The impacts of these behaviours can be profound; particularly in catchment headwaters where beaver are more likely to construct dams to create deep water refugia and improve access to food resources (Campbell-Palmer et al., 2016). The main component of most beaver dams is woody vegetation (Haarberg and Rosell, 2006). The effect of foraging for food and building materials can have pronounced effects on riparian vegetation (Goryainova et al., 2014; Peinetti et al., 2009).

Beaver wetlands provide vital habitat for many species (Law et al., 2019; Stringer and Gaywood, 2016). Their impact on vegetation also influences biodiversity; by felling trees beaver can increase functional and structural heterogeneity (Donkor and Fryxell, 1999; Nolet et al., 1994; Peinetti et al., 2009). Stratified or semi-open areas of woodland support a greater diversity of plant/tree species (Gao et al., 2014) and associated bird communities (Seavy et al., 2009), in addition to a range of other terrestrial and aquatic species (Broadmeadow and Nisbet, 2004). Where beaver activity coincides with anthropogenic land use, management is often required to either limit damage or enable the shared use of a riparian area (Brazier et al., 2020; Schwab and Schmidbauer, 2003) . Eurasian beavers are expanding across much of Europe, with populations estimated at a minimum of ~1.5 million (Halley et al., 2020). Understanding the potential impacts of beaver on riparian woodland in European landscapes, dominated by anthropogenic land use, is required to maximise benefits whilst minimising conflict (Auster et al., 2020, 2019).

In combination with lightweight drones, Structure-from-motion photogrammetry (SfM) is used across the natural sciences (Anderson and Gaston, 2013; Fawcett et al., 2019; Westoby et al., 2012) to measure structural phenomenon including, but not limited to, vegetation structure (Belmonte et al., 2020; Cunliffe et al., 2020a, 2020b; Forsmoo et al., 2018; Fu et al., 2021). SfM has also proven to be a valuable tool for elevation change detection in geomorphic settings, with applications for soil erosion (Cândido et al., 2020; Glendell et al., 2017), river planform change (Marteau et al., 2017) , landslide dynamics (Lucieer et al., 2014; Peppa et al., 2019) and coastal morphology (Duffy et al., 2018; Pikelj et al., 2018). Most examples of SfM change detection in vegetated settings have focused on differences in space; fewer studies consider differences over time (although see: (Chu et al., 2018; Dandois and Ellis, 2013; Fraser et al., 2016; Fu et al., 2021)). This scarcity of temporal change studies, particularly in natural/semi-natural settings, may be due to the challenges in reconstructing complex surfaces, such as tree canopies (Dandois et al., 2015), with appropriate quantification of model accuracy and precision to differentiate true change from measurement error (James et al., 2017; Lane et al., 2003). The potential application of SfM photogrammetry for monitoring beaver impacts, though demonstrated qualitatively (Puttock et al., 2015), has not been widely applied for quantitative measurement of canopy dynamics and therefore warrants further investigation.

In this study we set out to answer the following questions.

- **Q1.** How do different aerial SfM change detection methods compare for the quantification of canopy height change in riparian woodland?
- **Q2.** What impact does beaver foraging have on riparian woodland canopy height?

To do so, we tested three processing methods that use drone based SfM photogrammetry for canopy height change detection following the reintroduction of beaver. Firstly, a Digital Elevation Model of Difference (DoD) where no error propagation is considered (Fraser et al., 2016; Lucieer et al., 2014; Stepper et al., 2015). Then, two more robust approaches that propagated SfM precision, a spatially explicit descriptor of photogrammetric reconstruction quality (James et al., 2017), and rasterisation uncertainty, the standard deviation of the elevation of points within a given raster cell (Brasington et al., 2003; Lane et al., 2003; Wheaton et al., 2010), to derive a Limit of Detection (LoD). The LoD was used in different ways for the robust approaches; using a weighted (Lane et al., 2003) method and then a threshold approach (James et al., 2017).

2 Methods:

2.1 Site description

Clyst William Cross County Wildlife site, England has an area of 10 ha and is located on the River Tale, a 4th order stream (lat: 50.820, long: -3.313) (Figure 1). Grassland, sedge, rush, shrub and woodland are the main vegetation types. Riparian woodland is dominated by Willow (*Salix sp*.) Hazel (*Corylus avellana*), and Alder (*Alnus glutinosa*). During the study period (September 2017 – September 2018), no extreme weather events occurred that could have significantly altered the site’s condition. The site is privately owned with a very limited footfall, no hunting, livestock grazing or tree felling by people. In 2016, a pair of beavers were released at the non-enclosed site as part of the River Otter Beaver Trial, the first study of free-living beaver reintroduction in England (R. E. Brazier et al., 2020). The beavers established and maintained a territory throughout the period of monitoring, and had kits resulting in a family group of ca. 2-5 animals. The site contains high quality beaver habitat, with an abundance of feeding and building resources; our modelling classified the habitat as 'preferred’ (Beaver Forage Index = 5/5) and the streams as having a ‘frequent’ or ‘pervasive’ capacity for beaver damming (dam capacity > 4/km) (Graham et al., 2020).

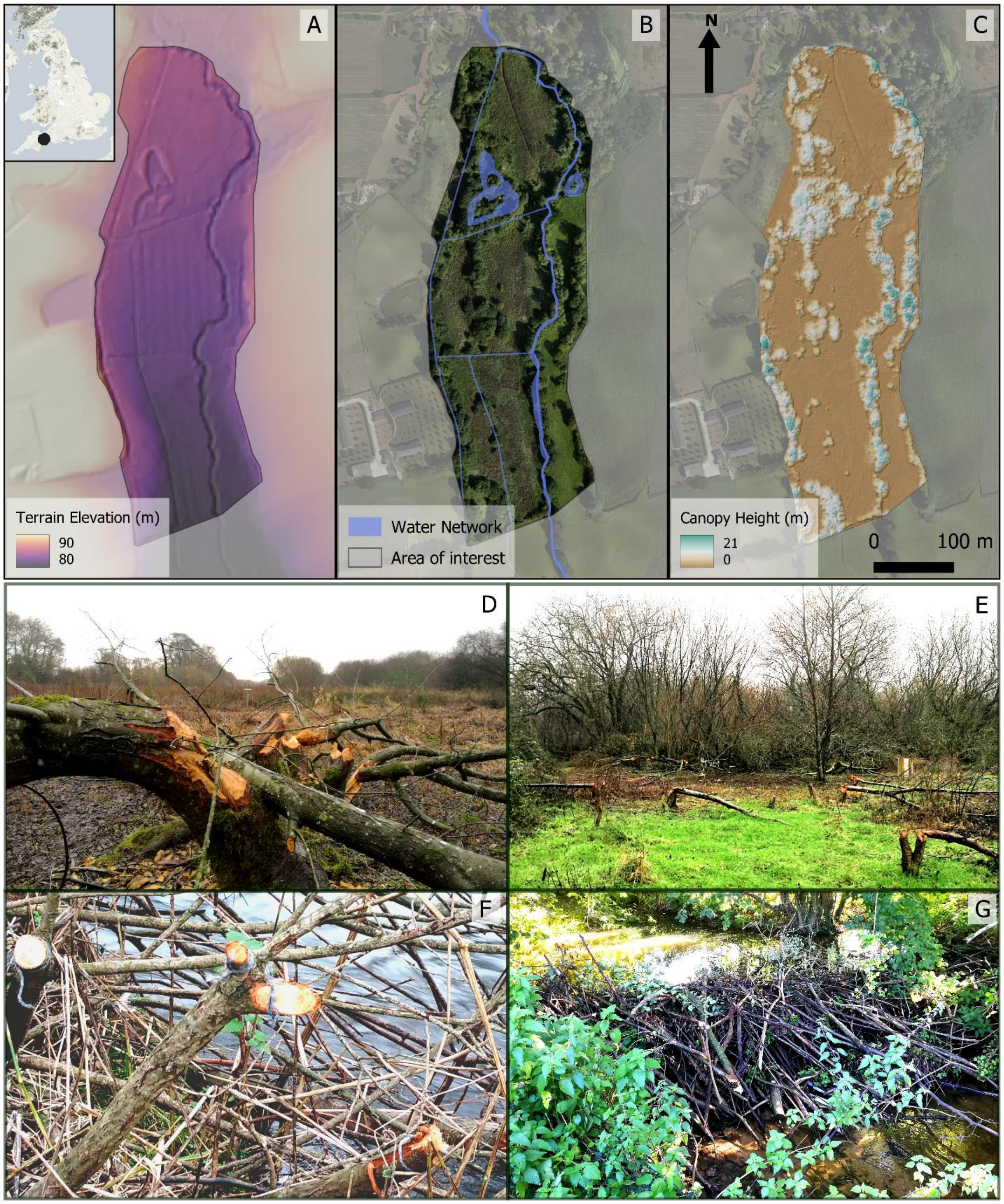

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Figure 1: ***A*** *- Clyst William Cross site location and 2m Digital terrain model from the Environment Agency 2017 composite LiDAR (Environment Agency, 2017);* ***B*** *- Orthomosaic generated from drone survey (Sep. 2017) with Google Earth imagery presented in shaded area. The river network data is from ordnance survey's MasterMap water network (Ordnance Survey, 2018). The River Tale runs along the eastern side of the site from north to south; other drains/1st order streams enter the site from the west. Ponds are located on either side of the floodplain. Beavers were released into the larger of the two ponds on*

the site. Some small islands (c.a. 600 m2), in the center of the ponds, were not accessible and were therefore not surveyed for beaver foraging signs. ***C*** *– Canopy height model generated from drone survey (Sep. 2017);* ***D*** *– Willow felled for forage to access nutritious upper branches;* ***E*** *– felled Willow/Alder, example of the clear impact of beaver foraging on canopy;* ***F*** *– smaller stems cut by beaver as forage;* ***G*** *– The main dam constructed on the River Tale (approx. 1.5 m high).*

2.2 UAV Survey design:

We deployed 40 fixed ground markers across the site, before commencing drone flights, each measuring 20 cm x 20 cm (SI 1). These markers remained in place throughout the monitoring period and were geolocated at the beginning and end of the study using a global navigation satellite system (Leica GS08) with a typical precision of ±0.02 m in the horizontal and ±0.03 m in the vertical dimension. One marker moved more than 0.1 m and was excluded from the analysis. All other marker locations remained within <0.05 m of their initial survey location. Where markers were obscured by vegetation and not visible from any images, they were not included in the model build for that survey (see section 2.3).

The site was surveyed using a 3DR IRIS drone (unpiloted quadcopter), equipped with a Ricoh GR4 camera (16.2 sensor, 28mm focal length, maximum aperture f2.8, shutter speed faster than 1/1000th sec). For each survey, two flights were undertaken: nadir imagery from 60 m above ground level (agl) and oblique (ca. 20° from nadir) images from 55 m agl, providing mean ground sampling distances ca. 16 mm. The different perspectives afforded by this approach improve the stability of the camera network (Hendrickx et al., 2019; James et al., 2017; James and Robson, 2014). Both surveys obtained 75% forward and side overlap; every part of the study area was captured in at least 32 images.

Two surveys are presented in this manuscript; the first in September 2017 (Sep 17), 15 months after beavers were released at the site, and the second in September 2018 (Sep 18). Wind speeds, measured 2 m above ground level, were low with <=1 and <=2.4 m s^{-1} for the Sep17 and Sep18 surveys respectively and therefore it was unlikely that photogrammetric reconstructions were significantly affected (Cunliffe, et al., 2021). Each survey took approximately 1.5 hours to complete; in total, three days were required to install ground control points and survey their locations before and after surveys were carried out. Results obtained from additional surveys are described in the supplementary materials (SI 4).

The same fixed ground control, sensor, drone platform and flight path (SI 7) were used for all surveys to optimise repeatability in data capture. This enabled greater confidence when comparing between derived height models by limiting potential variation in accuracy and precision due to methods/equipment (Eltner et al., 2015) .

2.3 SfM Processing

SfM photogrammetric processing was carried out using a workflow following (Cunliffe et al., 2020a, 2016). Image data and marker coordinates were imported into Agisoft Metashape (v1.5) (Agisoft, 2020). Image sharpness was assessed using Metashape's image quality tool; all retained images had an image sharpness score of ≥ 0.56. Photos were matched and cameras aligned, using the 'highest quality' setting, key point limit of 40,000; tie point limit of 8,000, generic and reference pair pre-selection enabled, and adaptive camera model fitting disabled. Reference parameters were set to: marker location accuracy = XY ± 0.02 m, Z ± 0.05 m; marker projection accuracy was set to 2 pixels; tie point accuracy was set to the greater of one or the mean root mean square re-projection error. Points that were clearly erroneous or had a reprojection error above 0.45 were removed. Geolocated markers were placed on ten projected images for 35 and 34 ground markers for Sep 17 and Sep 18 surveys, respectively. For Sep 17 and Sep 18 surveys, 25 and 26 of these markers, respectively, were used to spatially constrain the photogrammetric reconstructions (Ribeiro-Gomes et al., 2016). The same nine markers, used for accuracy assessment for both surveys, were deselected at this stage. The following lens parameters were enabled: Focal length (f), principal point (cx, cy), radial distortion (k1, k2), tangential distortion (p1, p2), aspect ratio and skew coefficient (b1, b2) before the bundle adjustment was optimised using the filtered cloud of tie points. More than 99.6% of cameras were aligned and used for the dense cloud generation for both surveys; n = 1643 and n = 1632 for Sep 17 and Sep 18 respectively. Multi-view stereopsis (dense point cloud generation) was undertaken using the 'high quality' setting, with mild depth filtering to preserve finer details of the vegetation (Cunliffe et al., 2016, 2020a; Lussem et al., 2019).

2.4 Calculating Canopy Change

Here we describe the processing steps used for change detection; this workflow is visualised in Figure 2.

Point cloud processing and change detection calculations were carried out using python (v3.8.6) (Python Software Foundation, 2019) and these key libraries: Point Data Abstraction Library (v2.2.0) (PDAL) (PDAL Contributors, 2018), numpy (v1.19.4) (Harris et al., 2020), rasterio (v1.1.8) (Gillies and others, 2019) and geopandas (v0.8.1) (Jordahl et al., 2020).

The current best practice method for change detection in geomorphic settings is in the Multiscale Model to Model Cloud Comparison (M3C2) technique (James et al., 2017; Lague et al., 2013), which directly compares the relative position of points between point clouds acquired from different times. Although M3C2 is highly effective where surfaces are simple, such as bare earth or rock, it is extremely challenging to apply in vegetated settings (although has been adopted in a semi-arid setting by Gillan, et al. (2019)) due to low tie point density resulting from the structural complexity of the vegetation and the influence of wind on its reconstruction (Cunliffe et al., 2021; Duffy, et al., 2018; Zhang, et al., 2019) and therefore most geomorphic change detection studies simply omit vegetated areas (e.g. James, et al., 2017, and Winiwarter, et al., 2021). We therefore adopted the following approach:

Point clouds were rasterised at a spatial resolution of 0.5 m by deriving the mean elevation of all points within a radius equal to the resolution multiplied by the square root of two, using PDAL, to generate Digital Surface Models (DSMs) (SI 2). If no points were present within this radius a window size of up to 10 cells (i.e. 5 m) allowed for more distant points to be used for interpolating the surface. A resolution of 0.5 m was chosen as it provided enough detail to classify the type of canopy loss that we expect to observe (i.e. the felling of trees >2 m high) and it was coarse enough to capture a suitable number of points from which to reliably describe the mean point elevation for a given cell area (mean number of points per cell: 4509 ± 3387 (SD)). This is important because SfM yields spatially variable point densities with lower point densities in vegetated areas compared with bare earth or rock. In order to minimise XY co-registration error, the same extent was used for all rasters therefore creating grids with identical dimensions and geolocations. We assumed the co-registration term, given in Equation 2, was zero when calculating the LoD.

Canopy Height Models (CHM) (SI 3) were generated, using rasterio and numpy, by calculating the difference between the DSM at each survey and a 2 m Digital Terrain Model (DTM), derived from Lidar data (Environment Agency, 2017) (Figure 1). The same DTM was used for both epochs with horizontal and vertical accuracies of ±0.4 and ±0.15 m RMSE respectively. The DTM was used to provide a datum to contextualise the absolute elevations. Because we considered relative change, between the same locations the DTM had no impact on derived results; if a comparison were made between two spatially distinct locations, the error from the DTM would require further consideration.

2.4.1 Error Sources

Two of the change detection methods we used (LoD_{95} weighting and LoD_{min} threshold) were derived after Brasington et al. (2003), James et al. (2017) and Lane et al. (2003). These authors demonstrated the need to quantify potential sources of error when creating a DoD; in SfM applications, these sources of error are, most notably; co-registration error, SfM precision error and rasterisation uncertainty.

2.4.1.1 SfM Precision

SfM processing itself is a source of uncertainty. Many studies use a single value to capture this uncertainty, typically the Root Mean Square Error (RMSE) of either the reprojection error or independent check markers (Smith et al., 2016). However, this uncertainty varies across reconstructions and therefore we used James et al.'s (2017)

Monte Carlo based approach to estimate spatially-explicit SfM precision. Iterative bundle adjustments were carried out on the internal sparse cloud model. For each iteration, pseudo random noise, from a normal-distribution, was applied as an offset to measured camera and marker locations. The standard deviations for these random offsets were derived from survey measurement precision of markers, and the RMSE of image residuals for camera locations (James et al., 2017). We computed 1000 iterations per survey; whilst less than the 4000 recommended by James et al., (2017), we were interested in z precision estimates that stabilised more rapidly than x and y (James et al., 2017). This also reduces computational time which was quite high (~16 hr per 1000 iterations). We adopted the approach by James et al. (2017) with one key difference; the standard deviation of point locations was calculated using Welch's online algorithm (Welford, 1962) which iteratively updates standard deviation values without needing to save the output from each iteration, substantially increasing performance and enabling application to the entire dataset without down sampling. The resulting sparse point cloud, including precision for each point, was converted to a 1 m resolution grid aligned with the elevation rasters. Where no points were present within a given cell, we imputed the missing values using the maximum (worst) precision value recorded for the point cloud.

2.4.1.2 Rasterisation Uncertainty

Rasterisation uncertainty is introduced when converting point clouds to a raster because multiple point elevations are summarised to a single value for each cell. Rasterisation uncertainty was captured by the creation of a roughness map (Figure 3), using PDAL, where each cell summarises the standard deviation of point elevations within a radius of the cell resolution (0.5 m) multiplied by the square root of two, from the cell centroid.

2.4.2 Error Propagation

2.4.2.1 Digital Elevation Models of Difference without limit of detection (No LoD)

This method involves the subtraction of the elevation values of the second survey from the first; no error propagation is carried out, as in Equation 1. The disadvantage of this approach is that, without the use of a LoD, it is not possible to determine if observed change is statistically significant (James et al., 2017)

$$\Delta z = z_{\mathrm{A}} - z_{\mathrm{B}}$$

Equation 1: Change detection using the No LoD method: where $\boldsymbol{\Delta z}$ *is elevation change,* $\boldsymbol{z_A}$ *is elevation at the first survey and* $\boldsymbol{z_B}$ *is elevation at the second survey.*

2.4.2.2 Calculation of Limit of Detection (LoD)

Calculating the LoD is fundamental in robust change detection with SfM due to the range of potential error sources (James et al., 2019). The LoD for the change in elevation between two surveys considers the rasterisation uncertainty and SfM precision from each survey. The aggregation of these error sources is detailed in Equation 2 which combines the error propagation methods described in (Lane et al., 2003) and (James et al., 2017). SfM precision and rasterisation uncertainties were summed for each survey because these errors cannot be assumed to be independent. However, the combined errors from each survey were included in the quadrature as it was reasonable to assume that the errors from each survey were likely to be independent and random (Brasington et al., 2003; Lane et al., 2003; Wheaton et al., 2010). Equation 2 assumes that errors are normally distributed; however, this LoD equation forms the basis of the detection of significant change using a t-statistic (Equations 3 and 4), which is reasonably robust where errors deviate from a normal distribution (Lane, et al., 2003). LoD and all other raster array calculations were undertaken using rasterio and numpy.

$$LoD = \sqrt{(P_A + \sigma z_A)^2 + (P_B + \sigma z_B)^2} + reg$$

*Equation 2: limit of detection calculation (**LoD**): where **P** is the SfM precision value, **σz** is the standard deviation of the point elevation values (rasterization uncertainty), **A** indicates the first survey, **B** indicates the second survey and **reg** is co-registration error (which, for this study, had a value of zero).*

2.4.2.3 Weighted LoD_{95}

This approach used the LoD as a weight, reducing the magnitude of change relative to the LoD as described by Lane et al., (2003). Where absolute elevation change (Δz) was greater than the LoD multiplied by 1.96, representing the 95% confidence limit, Δz was considered robust. However, any change that was less than this limit was weighted, relative to the coincident LoD. The weighting algorithm is shown in Equation 3:

$$W_{\Delta z} = \begin{cases} \Delta z - (LoD\ t) \times 0.5, & |\Delta z| > (LoD\ t) \wedge \Delta z > 0 \\ \Delta z \times \Delta z/(LoD\ t) \times 0.5, & |\Delta z| < (LoD\ t) \wedge \Delta z > 0 \\ \Delta z + (LoD\ t) \times 0.5, & |\Delta z| > (LoD\ t) \wedge \Delta z < 0 \\ \Delta z \times \Delta z/(LoD\ t) \times -0.5 & |\Delta z| < (LoD\ t) \wedge \Delta z < 0 \end{cases}$$

*Equation 3: Calculation for LoD_{95} weighted change (**$W_{\Delta z}$**) where **Δz** is elevation change between the first and second survey (as defined in Equation 1), **LoD** is the limit of detection (as defined in Equation 2), and **t** controls the confidence level of the change detection. We used a value of t=1.96 which equates to a 95% confidence level.*

2.4.2.4 LoD_{min} Threshold

For this method, where Δz was less than the LoD, no change was returned. Where Δz was greater than the LoD, the difference in elevation between the time steps was considered robust and the change in elevation, less the LoD, was returned. A more conservative threshold for change detection can be used by increasing the value of *t*, as shown in Equation 4. We use the LoD value, where *t*=1 (Equation 2) which equates to a confidence interval (CI) of 68% (Lane et al., 2003).

$$T_{\Delta z} \begin{cases} \Delta z - (LoD\ t), & |\Delta z| > (LoD\ t) \wedge \Delta z > 0 \\ \Delta z + (LoD\ t), & |\Delta z| > (LoD\ t) \wedge \Delta z < 0 \end{cases}$$

*Equation 4: Calculation for LoD$_{min}$ threshold change (**$T_{\Delta z}$**) where **Δz** is elevation change between the first and second survey (as defined in Equation 1), **LoD** is the limit of detection (as defined in Equation 2), and **t** controls the confidence level of the change detection. We used a value of t=1 which equates to a 68% confidence level.*

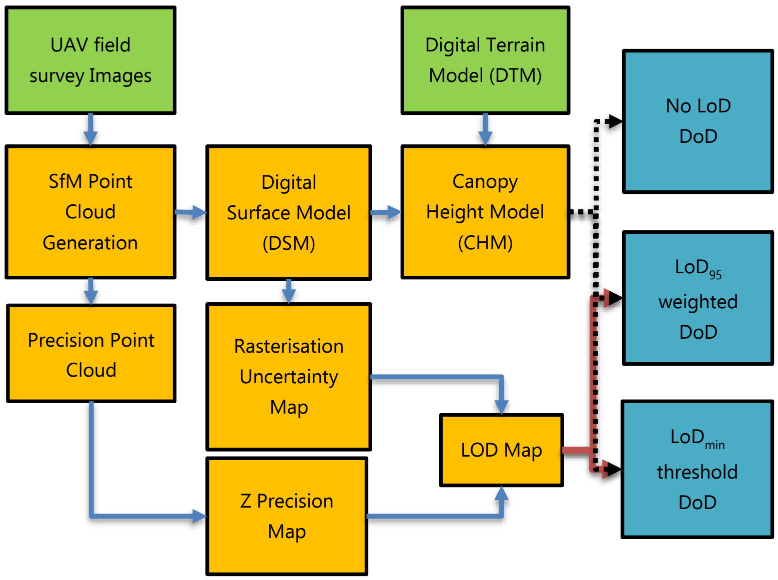

Figure 2: Data collection/processing workflow. Green boxes indicate data input sources, orange boxes show the point cloud/raster processing and blue boxes indicate the different DoD products.

2.5 Mapping Beaver signs

Beavers leave conspicuous signs where they have felled trees/shrubs (Figure 1). Each year, all accessible areas of woody vegetation were surveyed for foraging signs in the winter of 2017 and 2018 using established methods (Campbell-Palmer et al., 2020). Evidence of beaver foraging was mapped with a handheld GPS (precision: ± 10 m) (Figure 4). The CHM from September 2017 was used to classify areas with a canopy elevation > 2 m as woodland (Figure 4). Woodland areas with and without beaver foraging were defined as follows: The woodland was divided into discrete woodland units by splitting the woodland area with a 20 m grid. All observed foraging signs, recorded before the Sep 18 survey, were buffered by 10 m to account for geo-location uncertainty. Woodland units that intersected buffered foraging points were classified as 'foraging' and those that did not intersect as 'no foraging'. Woodland units were dissolved based on foraging classification. The woodland zones had an area of 4.1 and 4.2 ha for 'foraging observed' and 'no foraging', respectively. DoD cell values underlying each zone were extracted.

2.6 Data/Statistical Analysis

Statistical analysis and visualisation was undertaken using R (v-4.02) (R Core Team, 2020) and the following packages: tidyverse (v1.3.0) (Wickham et al., 2019), broom (v0.7.6.9) (Robinson et al., 2021), spmoran (0.2.2.1) (Murakami, 2021), and gt (v0.2.2) (Iannone et al., 2020).

2.6.1 Comparing areas of change

Total area for canopy elevation increase and decrease for foraging and no foraging zones was calculated for each DoD method (Figure 6) by multiplying the number of cells, with either positive or negative change, by the spatial resolution of the DoD (0.5 m).

2.6.2 Comparing magnitude of elevation change

To visualise the difference in change magnitude across each zone, density plots of canopy height change were generated for each zone and DoD method (Figure 7). Density values were scaled to allow comparison between DoD methods. The mean canopy height change and 95% confidence intervals (standard error multiplied by 1.96), were derived for each zone and DoD method (Table 1); this assumes that canopy height changes are normally distributed as demonstrated in Figure 7.

To gain a more nuanced insight into canopy height changes than are evident simply from the mean, we used spatially filtered unconditional quantile regression (Murakami and Seya, 2019) to calculate how beaver foraging zone influences the canopy change at a range of quantiles (tau =0.01 – 0.99). Quantile regression models were fitted using the spmoran R package (Murakami and Seya, 2019; Murakami, 2021), which calculates spatially filtered quantile regression estimates and confidence intervals, with consideration of spatial dependence, through the adoption of approximate random effects eigenvector spatial filtering (Murakami and Griffith, 2019).

3 Results:

3.1 Error Propagation

SfM precision and rasterisation uncertainty maps are presented in Figure 3. Rasterisation error greatly exceeded SfM precision with mean rasterisation error and SfM precision, across both surveys, being 0.62 m ± 0.9 (SD), and 0.028 m ± 0.012 (SD) respectively. Both of these error terms are larger in areas with more complex structure (e.g. woodland) (Figure 1 and Figure 4). Check/control marker RMSE values and their non-dimensional equivalents are presented in SI 6.

Error sources were combined, using Equation 2, to produce a LoD map (Figure 3). The edges of woodland zones have the highest LoD; here the change detection was less sensitive.

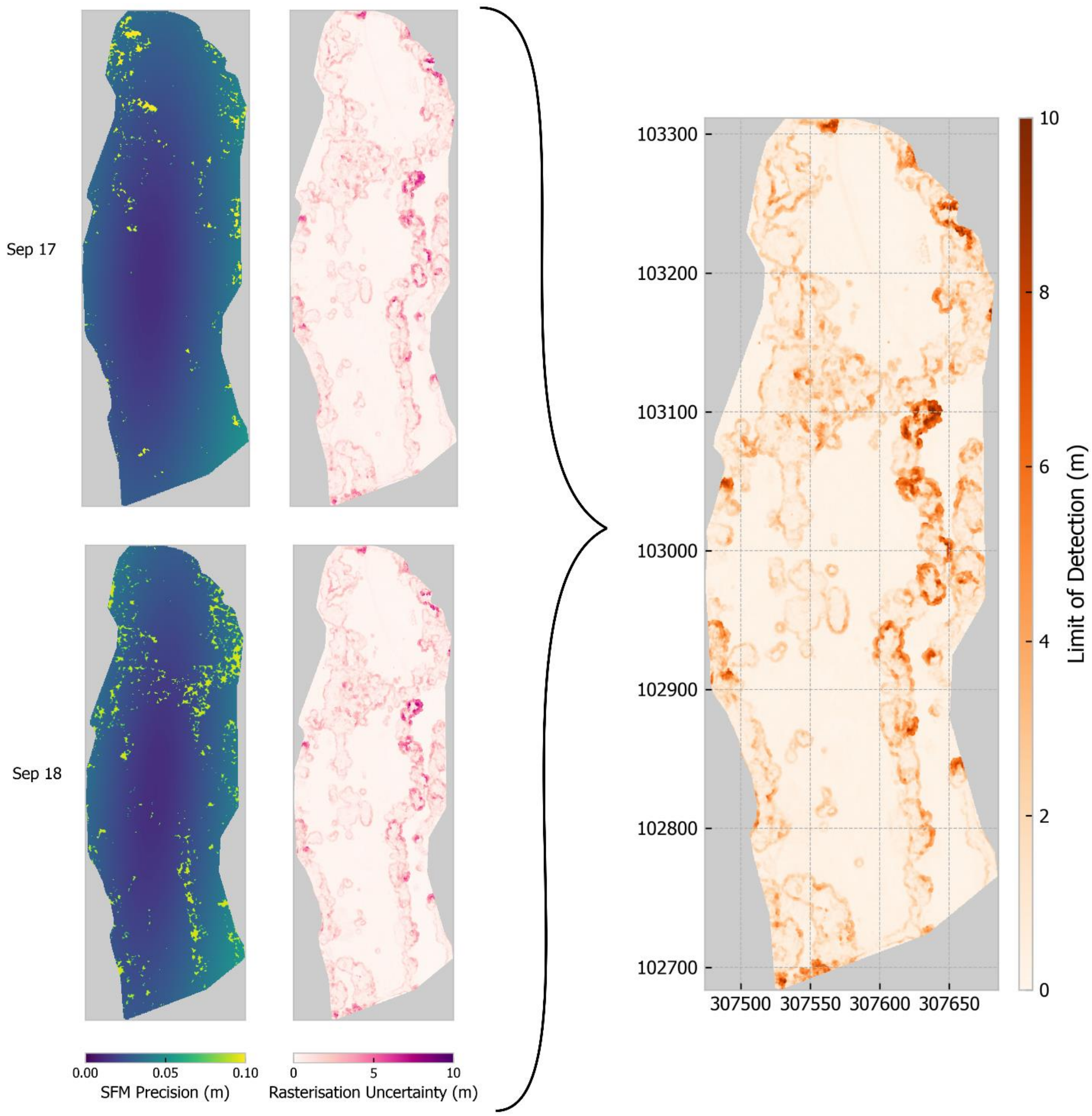

Figure 3: SFM precision maps (viridis palette – left) and Rasterisation uncertainty maps (pink palette – right) for the Sep 17 and Sep 18 surveys are shown on the left. The Limit of Detection map is shown on the right (orange palette) which is derived from the precision and rasterisation uncertainty maps using Equation 2.

3.2 Canopy Height Change Detection and Attribution

The derived foraging and no foraging zones are presented in Figure 4. Much of the activity occurred around the large pond but extended up and downstream along the River Tale (Figure 1).

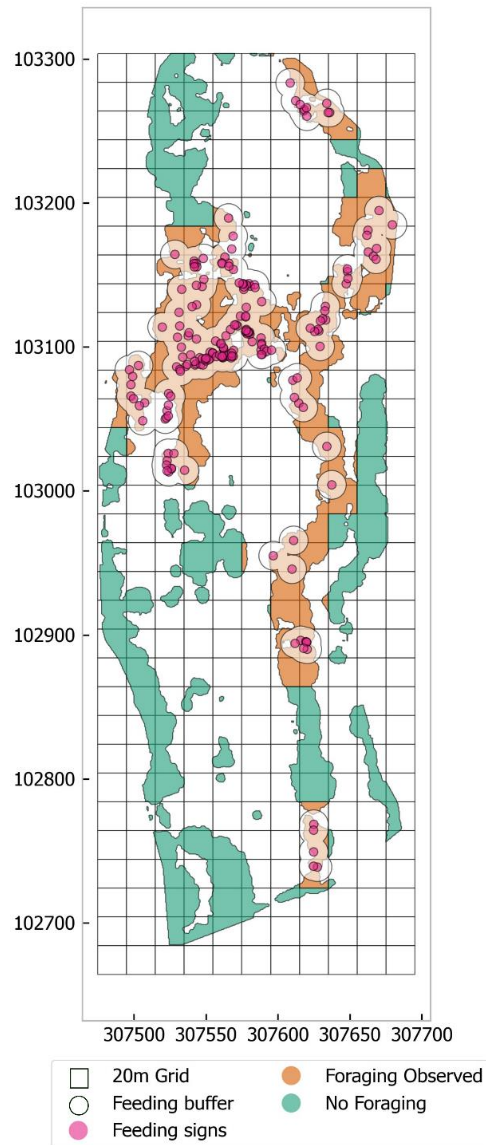

Figure 4: The locations of feeding signs and a depiction of how they were used to define woodland zones with and without foraging. Areas of woodland are defined as areas of the Sep 17 canopy height model (CHM) (SI 3) > 2 m; the woodland area was then split into multiple units, defined by the 20 m grid. Where these woodland units intersect the 10 m buffer around feeding signs, they were classified as 'Foraging Observed '.

DoD maps are presented in Figure 5 for each DoD method (DSM and CHM maps are presented in SI 2 and SI 3).

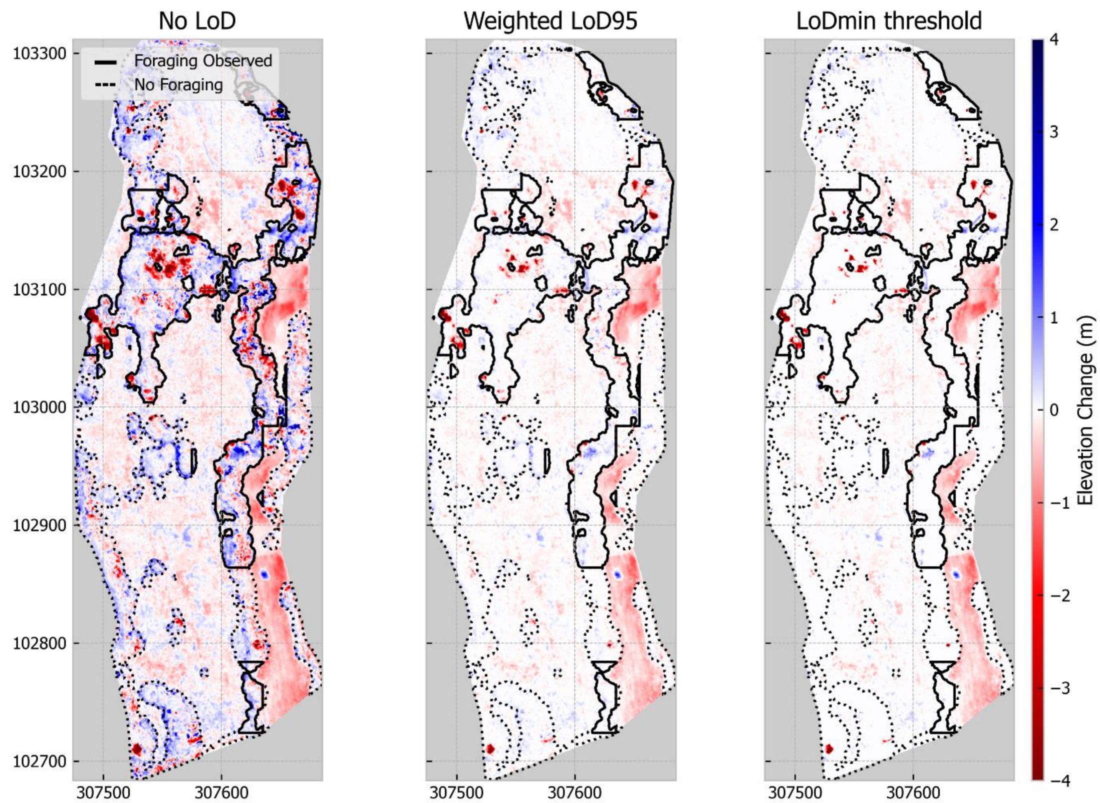

Figure 5: Digital elevation models of difference showing the change in elevation between the two survey intervals computed using three different change detection approaches. Foraging and no foraging regions are differentiated by the solid and dotted polygon areas, respectively.

The total areas of canopy height growth and decrease, derived from DoD maps (Figure 5), are presented in Figure 6. Results for the No LoD are identical to the LoD^{95}. The LoD^{min} method shows a much smaller area of canopy height change than other methods. All three methods were consistent in retrieving a larger area with decreased canopy height and a smaller area with increased canopy height in the foraging zone relative to the no forage zone.

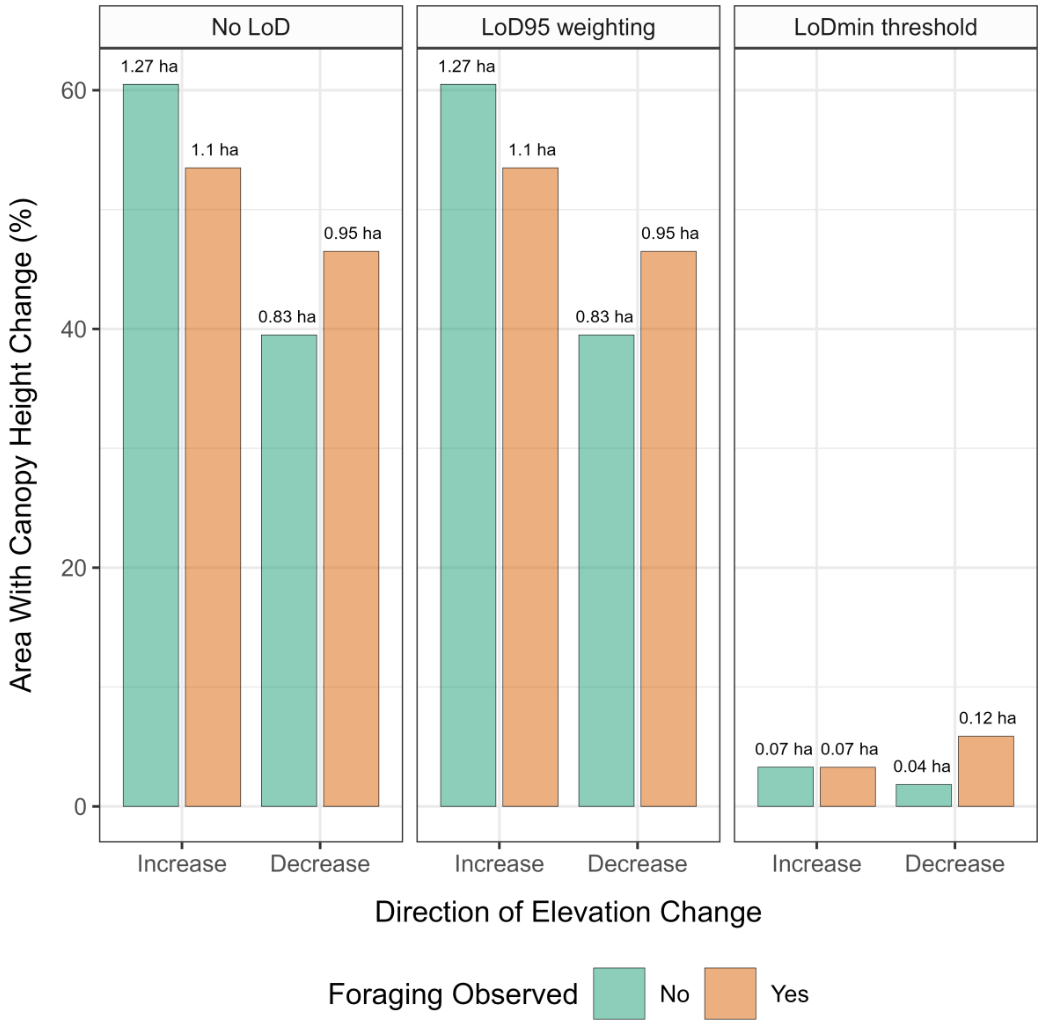

Figure 6: The areal percentage of each zone that experiences elevation increase and decrease. The total area of this change is given in the label above each bar.

Scaled density plots of canopy height change (Figure 7) revealed that larger magnitude changes were more common in the foraging zone. Figure 5 and Figure 7 also demonstrate a major difference between DoD methods; the No LoD approach shows a larger area of high magnitude change (more intense colours) in Figure 5 and a greater point density above and below zero in Figure 7 whereas both of the robust methods have a far greater concentration at or near zero.

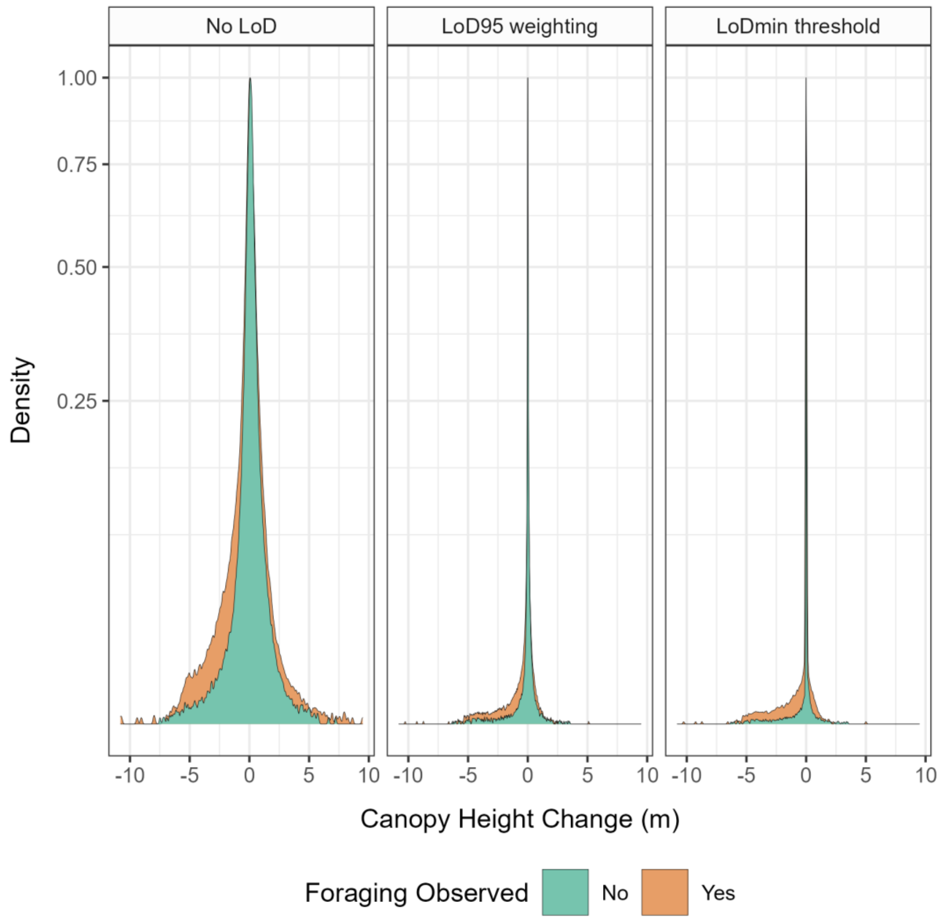

Figure 7: Density plots for canopy elevation change in zones with and without beaver foraging for each change detection method.

Table 1 shows mean changes in canopy height across foraging zones and LoD methods. All methods report similar results for mean canopy height change in the beaver foraging zone, with a 0.051 to 0.053 m reduction. There is more variation in the no foraging zone; No LoD and Lod_{95} methods report an increase of 0.1 m CI [0.098, 0.107] and 0.01 m CI [0.008, 0.011] respectively; the LoDmin method shows little to no change with a mean of -0.007 m CI [-0.008, -0.005].

Table 1: Mean canopy height change across each foraging zone: conf.low and conf.high refer to the 95% confidence intervals of the mean.

Zone	mean	conf.low	conf.high
No LoD			
No Foraging	0.102	0.098	0.107
Foraging Observed	-0.052	-0.059	-0.045
LoD95 weighting			
No Foraging	0.009	0.008	0.011
Foraging Observed	-0.051	-0.054	-0.048
LoDmin threshold			
No Foraging	-0.007	-0.008	-0.005
Foraging Observed	-0.053	-0.055	-0.050

There were marked differences between the estimated changes in canopy heights in the more extreme quantiles of the distribution (Figure 8 and Table 2). In the foraging observed zones, all three DoD methods show a greater canopy height decrease in the ≤ 5^{th} percentiles and, though the magnitude of this change differs between DoD methods, the relative differences were similar. There was also a small but noteworthy increase in canopy heights, in the foraging zone, at the 99^{th} percentile.

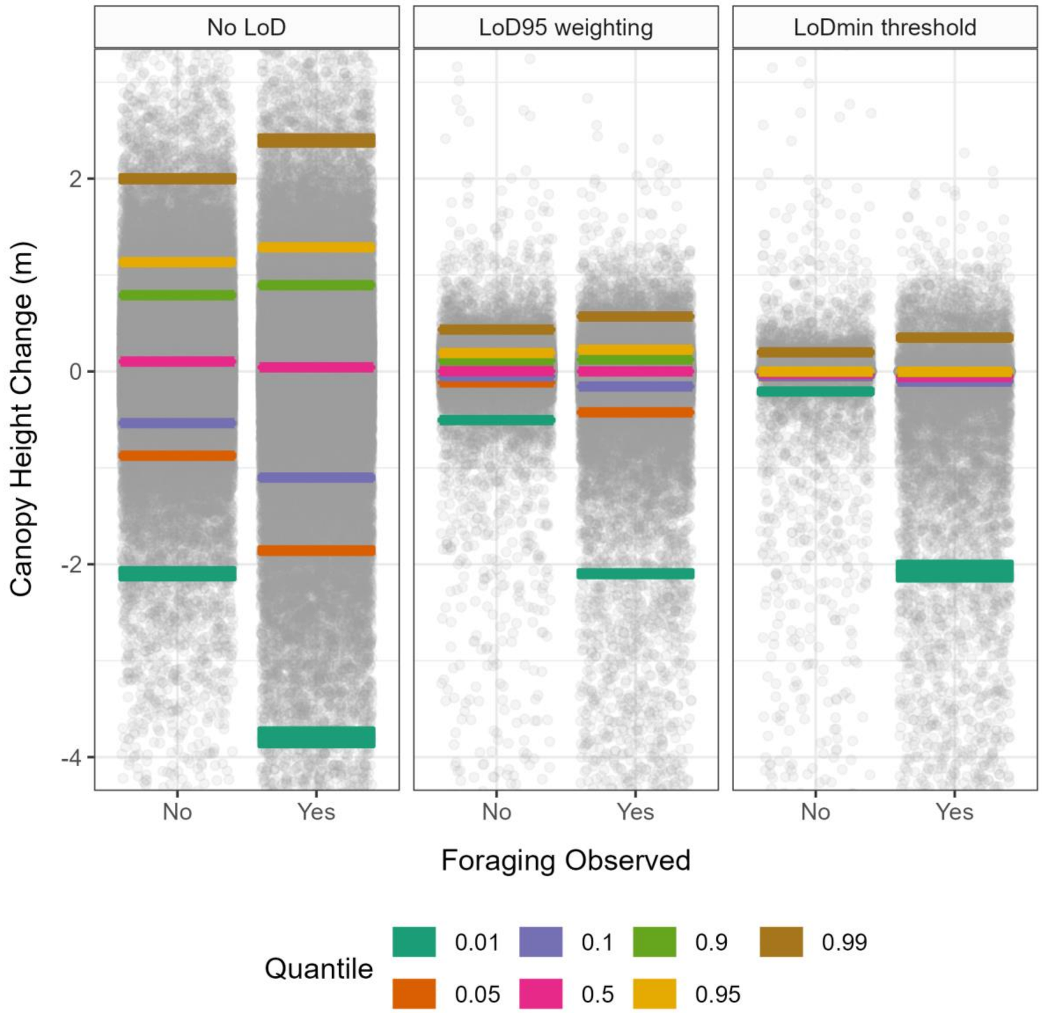

Figure 8: Spatially filtered unconditional quantile regression results showing the effect of beaver foraging on canopy elevation at different quantile levels of the canopy height change distribution. Results are presented for all three change detection methods, detailing the key differences between results derived from each method.

Table 2: Spatially filtered quantile regression summary table showing estimates and confidence intervals. Full quantile regressions table is provided in SI 5.

term	quantile	estimate	conf.low	conf.high
No LoD				
Intercept	0.05	-0.874	-0.888	-0.859
Foraging Observed	0.05	-0.987	-1.000	-0.964
Intercept	0.50	0.103	0.100	0.105
Foraging Observed	0.50	-0.060	-0.061	-0.059
Intercept	0.95	1.133	1.121	1.146
Foraging Observed	0.95	0.154	0.150	0.156
LoD95 weighting				
Intercept	0.05	-0.113	-0.115	-0.112
Foraging Observed	0.05	-0.311	-0.315	-0.307
Intercept	0.50	0.003	0.003	0.003
Foraging Observed	0.50	-0.002	-0.002	-0.002
Intercept	0.95	0.191	0.189	0.192
Foraging Observed	0.95	0.034	0.034	0.034
LoDmin threshold				
Intercept	0.05	-0.048	-0.058	-0.046
Foraging Observed	0.05	-0.048	-0.040	-0.048
Intercept	0.50	-0.024	-0.028	-0.021
Foraging Observed	0.50	-0.032	-0.030	-0.029
Intercept	0.95	-0.001	-0.001	-0.001
Foraging Observed	0.95	-0.001	-0.001	-0.001

For intermediate quantiles, the No LoD method generated estimates that diverge most widely from zero-change. Similar patterns of change are demonstrated for the LoD_{95} method but with reduced magnitude. In the case of the LoD_{min} method, the magnitude of change was lower than for the LoD_{95} method in all but the 99^{th} percentile. A full regression summary table is presented in SI 5.

4 Discussion:

4.1 (Q1) How do different aerial SfM change detection methods compare for the quantification of canopy height change in riparian woodland?

This study presents results from three different temporal change detection methods in riparian woodland using drone-based SfM. Previous applications of SfM change detection in vegetated systems mostly employ the No LoD method (Chu et al., 2018; Fraser et al., 2016; Fu et al., 2021; Stepper et al., 2015). To improve the robustness of change detection, it is preferable to account for measurement uncertainties (James et al., 2019). With increasing interest in using drone SfM to monitor changes in canopies, it is important to consider the implication of error propagation for inferred changes and to account for measurement uncertainty when quantifying ecosystem change spatially and through time.

Similar estimates of mean canopy height change in the foraging zone were observed for all DoD methods (Table 1). However, where change was subtle and spatially variable, we found greater differences in estimated canopy height change between methods (Figure 5, Figure 8 and Table 2). Therefore, researchers considering SfM change detection in vegetated systems should carefully consider the type of error propagation that will be used and the associated implications for accuracy and precision. The No LoD method is not recommended as it fails to account for the multiple sources of error that accumulate throughout SfM-DoD processing. The results in this study show that the LoD_{min} approach is the least sensitive method; the thresholds enforced by this approach were probably too conservative and disregarded real change that was small relative to estimated LoD. This occurs because real within-cell variation of the canopy surface is incorrectly assumed to be measurement uncertainty. The LoD_{95} method offers an alternative where canopy change is weighted relative to the spatially coincident LoD value, therefore the direction of change is preserved but the magnitude of the change is mediated based upon the LoD. This can be considered a compromise between the No LoD and LoD_{min} approaches in order to maximise the retention of information whilst maintaining statistical confidence in those observations.

A review by Iglhaut et al. (2019) found no studies that considered SfM precision when studying change detection in forested systems, although it has been used to evaluate SfM point cloud model quality (Fawcett et al., 2019).

We encourage future researchers to consider SfM precision where possible; however, it is worth noting that, in this study, the magnitude of error propagated from SfM precision was c.a. 22 times lower than rasterisation error. However, both the SfM precision and rasterisation uncertainty are spatially explicit and may therefore provide crucial understanding of error in those regions of the canopy with greater structural complexity. The calculation of SfM precision also does not have to follow the computationally intensive methods in this study, derived after James et al. (2017), as it is now possible to calculate sparse cloud point precision more easily in the latest version of Metashape (v.1.5.0) (James et al., 2020) with other photogrammetry software likely to follow.

Woodland ecology is highly dynamic both seasonally and inter-annually, and its structure varies over multiple temporal scales due to variation in wind, solar radiation, phenophase, growth, disease or damage. The surface of a woodland canopy is therefore in continual flux. To consider both subtle and extreme canopy change, whilst propagating potential errors that accumulate throughout data collection/processing pipelines, we suggest that, in vegetated settings, weighted approaches for LoD calculations are preferred. LoD_{95} reduces the chance of overestimating change whilst retaining as much information as possible. Results from an identical change detection approach, carried out during leaf-off conditions in winter (SI 4), showed similar patterns to those presented for summer but had much higher SfM precision and rasterisation uncertainty and consequently contained less information to evaluate change at the site. We recommend leaf-on surveys to maximise confidence in canopy change detection from photogrammetric surveys.

4.2 (Q2) What impact does beaver foraging have on riparian woodland canopy height?

Over one year, beaver foraging decreased mean canopy height by an average of between 0.045 and 0.059 m over an area of 4.1 ha. The no foraging zone did not experience such a decline in mean canopy height with mean change being between -0.008 and 0.107 m. This reduced canopy height in the foraging zone was not distributed evenly across the woodland zone (Figure 5); there were distinct areas of substantial canopy loss (> 2 m) which we attribute to beaver felling trees for forage and/or building materials such as the examples presented in Figure 1. This variability in canopy change is most clear in Figure 8 where we observed a greater magnitude of canopy height decrease in the lower extreme percentiles (1st and 5th) of the canopy change distribution which we expect corresponds with the felling of trees and increased canopy openness. The ≥ 95th percentiles, show that canopy growth may also be greater in beaver foraging zones. Possible explanations include:

(i) Canopy crown expansion into recently created openings and/or the rapid regrowth of coppice, in response to foraging (McColley et al., 2012; Peinetti et al., 2009).

(ii) Increased water availability, due to dam construction, which drives growth rates in willow (Bilyeu et al., 2008; Marshall et al., 2013)

Enhanced growth rates indicate increased annual net primary productivity (ANPP) as observed by Fairfax and Small (2018), Jones et al. (2009), and Peinetti et al. (2009). Beaver foraging at our study site increased the variability of canopy change, with greater observed rates of canopy height decrease and increase, and a net reduction in mean canopy elevation. Despite the relatively short time frame of this study, the results align with Peinetti et al., (2009) who modelled the impacts of beaver on willow woodland structure in Colorado. They too showed that beaver foraging drives an increase in willow size and ANPP and, whilst we cannot prove that increased ANPP has occurred here, it likely contributes to the observed increases in growth magnitude in the upper quantiles of the change distribution (Figure 8).

It is widely understood that structurally complex woodland, comprising a range of height and age classes, benefits biodiversity (Broadmeadow and Nisbet, 2004; Gao et al., 2014; Naiman and Decamps, 1997; Singh et al., 2021). Riparian woodlands also offer important resilience to climate change via shading, reducing peak temperatures and lowering mortality risk in species such as salmonid fish (Feld et al., 2018). Maintaining multi-layered woodland is beneficial for a range of aquatic biota (Glova and Sagar, 1994; Jusik and Staniszewski, 2019) and is recommended by the Forestry Commission for riparian woodland management (Broadmeadow and Nisbet, 2004). Beaver may offer a potential ecosystem service in respect to this.

5 Conclusion:

When seeking to quantify change in vegetation canopies using SfM it is critically important to account for measurement error. For complex surfaces, such as vegetation canopies, we recommend weighted approaches to error propagation to retain as much information as possible whilst allowing confidence in the observations. The work presented herein, highlights the importance of spatially explicit error propagation for SfM change detection in vegetated systems and provides a reproducible approach that may be adopted to more effectively differentiate between noise (from measurement error) and true signals.

This study shows that beaver activity increases the variability of canopy height change in riparian woodland with increases in the magnitude of canopy height decrease and growth in beaver foraging areas. By improving our ability to quantify change in complex riparian woodlands, this study will help inform the management of riparian woodlands and the impacts that beaver may have upon them as their range continues to expand across Europe.

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7 Statement of Contribution

HG, PB, AC, AP, RB and KA developed the experimental design; HG, AP and AC conducted drone surveys; JC, ME and HG carried out beaver sign surveys; HG, AC and PB undertook data processing and analysis; HG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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9 Data Accessibility Statement

Drone-derived photographs, along with derived point cloud and raster, have been submitted to PANGAEA for archiving, subject to their curation process – a DOI will be provided here once this process is completed. The Python scripts used for SfM processing in Agisoft Metashape can be found here: https://doi.org/10.5281/zenodo.5500199. All code to reproduce the processing of SfM outputs and data analysis can be found is located here: https://doi.org/10.5281/zenodo.5760603.

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Chapter 4. Modelling Eurasian beaver foraging habitat and dam suitability, for predicting the location and number of dams throughout catchments in Great Britain

The fourth chapter of this thesis is presented in its published format. All accompanying references are included in their published, type-set format at the end of the paper.

This paper presents modelling approaches to predict the distribution of beaver forage habitat and dams. These models are used to make predictions about the potential number of dams that could be constructed within three different catchments from across Great Britain.

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I am the primary author of this paper. I led the writing, model development, statistical analysis and data visualisation. I also contributed to field work which was led by ME, JC and RCP. Support from WM, JW and JG, at the Ecogeomorphology and Topographic Analysis Lab (Utah State University), was given during the model development and during manuscript editing phases. AP, KA, ME and RB supervised this work, contributing to model design and manuscript edits.

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ORIGINAL ARTICLE

Modelling Eurasian beaver foraging habitat and dam suitability, for predicting the location and number of dams throughout catchments in Great Britain

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Abstract

Eurasian beaver (*Castor fiber*) populations are expanding across Europe. Depending on location, beaver dams bring multiple benefits and/or require management. Using nationally available data, we developed: a Beaver Forage Index (BFI), identifying beaver foraging habitat, and a Beaver Dam Capacity (BDC) model, classifying suitability of river reaches for dam construction, to estimate location and number of dams at catchment scales. Models were executed across three catchments, in Great Britain (GB), containing beaver. An area of 6747 km^2 was analysed for BFI and 16,739 km of stream for BDC. Field surveys identified 258 km of channel containing beaver activity and 89 dams, providing data to test predictions. Models were evaluated using a categorical binomial Bayesian framework to calculate probability of foraging and dam construction. BFI and BDC models successfully categorised the use of reaches for foraging and damming, with higher scoring reaches being preferred. Highest scoring categories were ca. 31 and 79 times more likely to be used than the lowest for foraging and damming respectively. Zero-inflated negative binomial regression showed that modelled dam capacity was significantly related ($p = 0.01$) to observed damming and was used to predict numbers of dams that may occur. Estimated densities of dams, averaged across each catchment, ranged from 0.4 to 1.6 dams/km, though local densities may be up to 30 dams/km. These models provide fundamental information describing the distribution of beaver foraging habitat, where dams may be constructed and how many may occur. This supports the development of policy and management concerning the reintroduction and recolonisation of beaver.

Keywords Eurasian beaver · *Castor fiber* · Beaver dams · Dam capacity · Modelling · Management · Habitat

Introduction

Beaver reintroduction and recolonisation across Europe provides opportunities for conservation and provision of ecosystem services (de Visscher et al. 2014; Law et al. 2016; Puttock et al. 2017, 2018). However, for the species to coexist with humans, particularly in densely populated and intensively managed landscapes, informed policy and management is required (Auster et al. 2019; Crowley et al. 2017; Gaywood et al. 2015). This should be based on a strong understanding of where beaver are likely to be active, where dam impacts/opportunities occur and how many dams may be expected in a catchment. Such understanding is vital to ensure that benefits that beaver offer be maximised, whilst minimising negative impacts on land and infrastructure. Herein, we provide a modelling framework that contributes to this understanding which describes beaver foraging habitat and river reaches suitable for dam construction.

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The Eurasian beaver (*Castor fiber*) was extirpated from mainland Great Britain (GB) approximately 400–600 yBP (Kitchener and Conroy 1997; Manning et al. 2014), and populations were significantly reduced throughout Eurasia as a result of hunting (Halley et al. 2012). The species is now expanding throughout mainland Europe alongside an increasing number of enclosed and free-living populations in Scotland and England. Their ability to significantly modify fresh water habitats through dam building, lodge constructing, tree felling and excavating canals and burrows has earned beavers the title of ecosystem engineer (Gurney and Lawton 1996). Dam construction has a profound effect on the landscape, often forming complex wetlands (Gurnell 1998). Beavers construct dams to (i) increase water depth, reducing predation risk (Gurnell 1998), (ii) access food resources (Campbell-Palmer et al. 2016) and (iii) create deep water for food caches (Campbell-Palmer et al. 2016). Dams are typically built on rivers < 6 m wide and < 0.7 m deep (Hartman and Tornlov 2006). Beaver dams vary in size and structure (see examples in SI.11) depending on purpose, environmental setting, channel geometry, age and hydrological regime.

Riverine and riparian systems across Europe have changed significantly since the Holocene because of agricultural intensification and urbanisation (Brown et al. 2018). This is particularly evident in GB where agriculture and sub/urban areas account for 52.9% and 7.4% of land use respectively (Rowland et al. 2017). Such change has diminished the natural functioning of river systems and contributed to an intensification of flood discharges, soil erosion and diffuse pollution (Bilotta et al. 2010), with concomitant impacts on biodiversity and society. Beaver dams can help restore natural function via (i) attenuation of peak flood flows and extension of lag times by increasing storage capacity and surface roughness (Nyssen et al. 2011; Puttock et al. 2017); (ii) increased drought resilience by maintaining base flow, storing water during dry periods and raising ground water tables (Gibson and Olden 2014); (iii) capturing fine sediment and storing nutrients (de Visscher et al. 2014; Puttock et al. 2018); (iv) aggrading incised channels (Pollock et al. 2014); (v) enhancing channel complexity (John and Klein 2004) and (vi) increasing habitat heterogeneity and biodiversity (Stringer and Gaywood 2016).

Beaver activities can also cause human-wildlife conflict where valuable infrastructure or land use is impacted (Auster et al. 2019; Crowley et al. 2017; Gaywood et al. 2015). Many conflicts can be managed to minimise damage whilst addressing animal welfare considerations and delivering aforementioned benefits (Campbell-Palmer et al. 2016). Understanding where dams are likely to be constructed is therefore important for the effective management of conflicts and benefits, especially with rapidly increasing beaver populations across Europe.

Expanding populations of beaver are known to settle a landscape in a way that approximates the ideal despotic distribution hypothesis (Fustec et al. 2001; Nolet and Rosell 1994), where established populations exclude unsettled individuals, as opposed to the ideal free distribution, where animals can move freely between habitats (Ens et al. 1995; Fretwell and Lucas 1969). This hypothesis assumes that, at low population densities, animals will select optimal habitats but, due to their territorial behaviour, animals will sequentially settle in more marginal habitats as population density increases and the availability of preferred habitats decreases (Fretwell 1972; Fretwell and Lucas 1969). The stage of population expansion will also play a role in habitat choice. Hartman (1996) suggests that the search for a mate may lead to the wider distribution of individuals within a catchment. Spatial scale also plays a role in habitat selection, with both the overall availability of woody resources and their distribution within home ranges determining the suitability of a given habitat (Zwolicki et al. 2019).

Existing models, describing beaver habitat or locations suitable for dams, are available. Many are statistical and derived from field measurement (Barnes and Mallik 1997; Curtis and Jensen 2004; Hartman 1996; Hartman and Tornlov 2006; Howard and Larson 1985; McComb et al. 1990; Pinto et al. 2009), providing the basis for understanding beaver habitat preference. However, these models can prove less effective when extrapolated spatially to landscapes with different characteristics (e.g. from arid shrub-dominated landscapes to boreal forest (Barnes and Mallik 1997)) from where the models were derived (Baldwin 2013; Barnes and Mallik 1997; Cox and Nelson 2008; Howard and Larson 1985; McComb et al. 1990; Suzuki and McComb 1998). Some geographic information system (GIS)-based models have used detailed data inputs not widely available or acquired through rigorous digitising or fieldwork campaigns (John et al. 2010; St-Pierre et al. 2017; Swinnen et al. 2017). Whilst providing accurate and locally valuable information, the application of these models at regional/national scales may be costly or infeasible. Other approaches use coarser resolution spatial data, such as rasterised environmental descriptors > $50 m^2$ (South et al. 2000; Stevens et al. 2007), that allow for the development of landscape or national-scale understanding, appropriate to policy, but have limited application for local management due to the coarse spatial resolution of results.

When faced with the task of selecting a modelling framework to understand the distribution and number of beaver dams in Great Britain, three recent modelling frameworks were considered:

(i) A recent and novel approach for identifying areas in a catchment that can support beavers was developed by Dittbrenner et al. (2018) who created a Beaver Intrinsic Potential model based on topographic parameters and discounting contemporary land use cover.

(ii) Stringer et al. (2018) developed a habitat model for Scotland; the most recent for a GB landscape. It locates woodland areas (> 0.5 ha) within 50 m of streams with a gradient < 15% to identify suitable beaver habitat; reaches containing woodland and wider than 6 m are classed as unlikely to be dammed. The authors acknowledge that the spatial distribution of dams is complex and therefore limit their predictions to areas likely and unlikely to be dammed. Additionally, they state that the 15% gradient cut-off used in the habitat model would be improved by a gradual classification rather than an absolute one. Stringer et al. (2018) state that, in most instances, the model effectively identifies suitable territory locations; however, the model occasionally fails to identify signs of beaver activity resulting from dispersing animals or where it occurs in discontinuous habitat containing patchy woodland < 0.5 ha.

(iii) Macfarlane et al. (2017) developed the Beaver Restoration Assessment Tool for North American landscapes to determine the capacity for river systems to support beaver dams. Macfarlane et al. (2017) used a rules-based fuzzy inference system which allows for the uncertainty associated with generalist beaver behaviour. Furthermore, when working across large areas with GIS, the datasets used are often either classifications or less precise than field observation. Therefore, traditional statistics, which require high precision data, can be unsuitable. Fuzzy inference offers a way to deal with this uncertainty in a pragmatic way by taking what has been learned from these high precision studies and applying expert rules to datasets that are naturally of lower precision (Adriaenssens et al. 2004; Fisher 1999). Whilst this Beaver Dam Capacity (BDC) model is valuable, it can predict only the maximum number of dams that can be supported; it does not predict the likely number of dams across a given area. However, BDC was found to predict the suitability for damming as those reaches with higher modelled dam-capacity were preferentially selected for damming over those with lower modelled dam-capacity (Macfarlane et al. 2017). Therefore, whilst Beaver Dam Capacity equates to the maximum number dams a section of stream can support, it can also be considered as a metric for estimating the suitability of a given reach for dam construction.

We therefore chose to develop the modelling framework outlined by Macfarlane et al. (2017), as it addresses the need for a contemporary understanding of dam suitability and utilises a fuzzy-rule system that can account for continuous changes in variables, avoiding stringent/unrealistic rule systems. We also present a new Beaver Forage Index (BFI) model which describes the spatial distribution of beaver foraging habitat and uses this information to inform the BDC model.

Using data from field sign surveys across three distinct GB catchments, where beavers are living wild, we gather empirical data which are used to evaluate the efficacy of the BFI for predicting suitable foraging habitat for beaver and the BDC model for predicting the suitability of reaches for dam construction. Furthermore, we evaluate how modelled BDC relates to observed dam density and estimate the number of expected dams at the catchment-scale.

In support of policy development and management implementation, this study aims to

1. Develop models to predict the distribution of beaver foraging habitat and damming activity for European landscapes, using nationally available datasets.
2. Compare model results with observed beaver foraging signs and damming activity to validate model predictions.
3. Use model results to predict the number of dams that are likely to occur at a catchment scale.

Methods

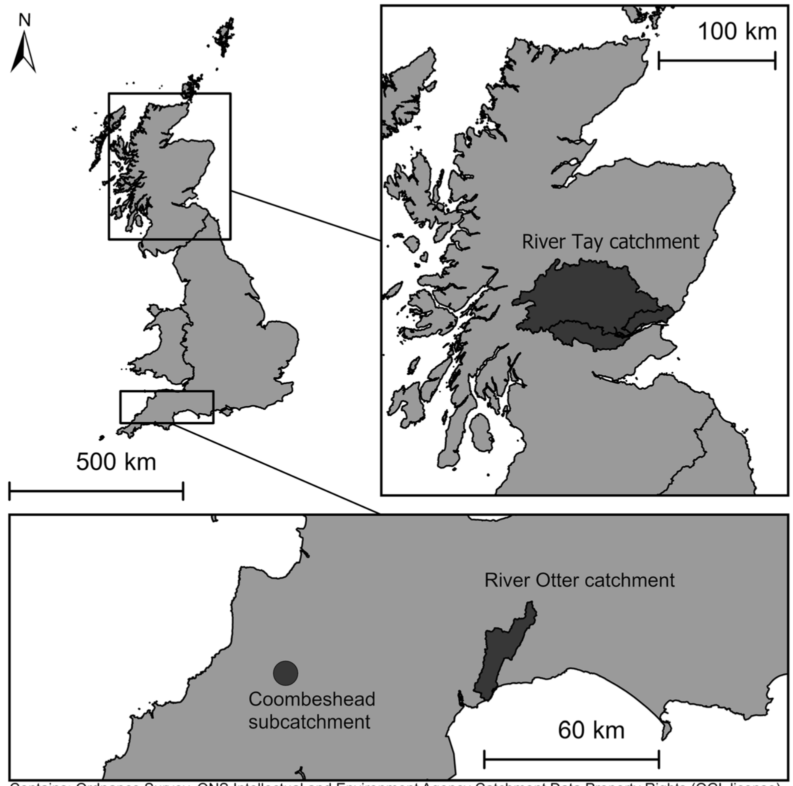
Site descriptions

Three beaver-impacted sites, representing a range of landscape types, were chosen (Fig. 1). The Tay catchment (including the Earn and Forth sub-catchments), Perthshire has a total area of ca. 6507 km^2 and ca. 16,139 km of watercourse up to 7th order. Key landcover types comprise arable farming (13%), grazing (39%), urban (2%), coniferous woodland (10%) and semi-natural habitat (30%) (Rowland et al. 2017). Beavers have been living wild in this catchment since at least since 2007 (Gaywood 2017). A catchment-wide survey (Campbell-Palmer et al. 2018 and in review) in 2017 identified 114 active territories.

The River Otter Catchment, Devon is dominated by intensively managed grassland (51%) and arable (29%) farmland, interspersed by patchy areas of semi-natural (11%) and (sub)urban areas (5%) (Rowland et al. 2017). The total catchment area is ca. 250 km^2 and comprises a total of ca. 595 km of watercourse up to 6th order. Since 2013, when beavers were first publicly reported in the catchment (Crowley et al. 2017), the population has reached approximately 25–40 animals, distributed between eight territories (Brazier et al. 2020).

The third site studied was the Coombeshead subcatchment, within the Tamar catchment in Devon. Free-living beaver family groups have established themselves here and the population has been present since ca. 2015 (Bricknell-Webb 2019

Fig. 1 Site locations in GB



- personal comms). The occupied area comprises 3rd- and 2nd-order streams draining areas of semi-natural woodland (26%), intensively managed grassland (60%), arable land (8%) and heather grassland (5%) (Rowland et al. 2017).

Producing Beaver Forage Index and Beaver Dam Capacity models

A diagram of the model workflow is shown in Fig. 4 with further details provided in the following subsections.

Computational requirements

The BHI and BDC models are reliant upon Python 3.6 (Python Software Foundation 2019) and utilises Geopandas (http://geopandas.org/), Rasterio (https://rasterio.readthedocs.io/en/stable/index.html), arcpy (ESRI 2015) and scikit-fuzzy (Warner 2012) modules; code in SI.8. Statistical analysis was carried out using R (version 3.5.1) (R Core Team 2017); code in SI.9. Processing was undertaken on a personal computer with Windows 10 OS, Intel CORE i7 processor and 16GB RAM. Maps were produced using ArcPro GIS version 2.4.1.

Beaver Forage Index data preparation and execution

Vegetation is important for classifying beaver habitat (Hartman 1996; John et al. 2010; Pinto et al. 2009; St-Pierre et al. 2017). No single dataset contained the detail required to depict all key vegetation types, relevant to beaver foraging. Therefore, a composite dataset was created from OS VectorMap Local data (Ordnance Survey 2018b), The Centre for Ecology and Hydrology (CEH) 2015 land cover map (LCM) (Rowland et al. 2017), Copernicus 2015 20 m tree cover density (TCD) (Copernicus 2017) and the CEH woody linear features framework (WLFF) (Scholefield et al. 2016).

Vegetation datasets were assigned suitability values (zero to five), which are summarised in Table 1. Values were assigned based on a review of relevant literature (Haarberg and Rosell 2006; Jenkins 1979; Nolet et al. 1994; O'Connell et al. 2008), field observation and qualitative comparison with satellite data. Vector data were converted to raster format (resolution of 5 m) to enable array-based calculation between datasets. TCD data were resampled to 5 m (finest common resolution) and aligned with converted vector layers. A full list of suitability values for vegetation datasets can be seen in SI.1–4. An inference system was used to combine these four raster datasets to create a continuous description of the suitability of land cover for beaver foraging at 5 m resolution

Table 1 Beaver Forage Index (BFI) value descriptions and the input data land classes attributed to each BFI value for the following data layers: OS Vector, CEH LCM 2015, Copernicus TCD data and CEH WLFF. For further information on all land class values for these datasets see SI.1–4

BFI value	Value description	OS vector classification	CEH LCM 2015 classification	Copernicus tree cover density range (%)	CEH woody linear features framework (WLFF)
0	No vegetation	Boulders, sand, shingle, building, water	Water, rock, saltmarsh, (sub) urban	0	–
1	Unsuitable	Heathland, unimproved grass, marsh	Acid grassland, calcareous grassland, heather, improved grassland, bog	1–3	–
2	Barely suitable	Reeds, shrub and heathland	Arable and horticulture, neutral grassland	4–10	–
3	Moderately suitable	Coniferous woodland, shrub and marsh, shrub and unimproved	Coniferous woodland	11–50	–
4	Suitable	–	–	51–100	WLFF present
5	Preferred	Broad-leafed woodland, shrub, mixed woodland, orchard	Broadleaf woodland	–	–

(Fig. 5). This inference system prioritises the most reliable data for a given land use type; if this dataset contains no value for a given location, the highest value of coincident datasets is used (see SI.8 for BFI code).

Beaver dam capacity data preparation

The stream network (Ordnance Survey 2018) was split into working reaches to extract discrete information following Macfarlane et al. (2017). The network was split at intersections, features < 200 m long were used as final reaches. Features > 200 m were split into the minimum number of equal parts to ensure that all were < 200 m long. Mean reach length across all sites was 122 m (± 47 SD).

The OS Terrain 5 m Digital Terrain Model (DTM) (Ordnance Survey 2017) was stream-burned (Saunders 1999; Turcotte et al. 2001) by reducing the elevation of raster cells coinciding with the vector stream network by 30 m. Elevations at the beginning and end of each reach were extracted, and the difference is divided by the reach length to calculate approximate gradient. Contributing hydrological area for each reach was determined from the intersecting value of a flow accumulation raster layer (Maidment and Morehouse 2002), multiplied by the raster resolution. Reach stream order was determined using the Strahler method (Strahler 1957). As stream order was derived from a burned DTM, post-processing was required; stream order values > 1st order were reduced by one, and erroneous 1st order values, along stream edges, were removed.

To estimate stream power at low and high flows, Macfarlane et al. (2017) used Q2 (high flow) and Q80 (low flow) flow exceedance values, in their North American study. Given the similarity of the structure of dams constructed by *Castor* species, we maintained this standard. Mean daily flow data were obtained (National River Flow Archive 2018) for all gauges within the hydrometric area of each catchment. Q2 and Q80 flow thresholds were calculated for each gauge, and rating curves for flow and contributing catchment area were developed using a non-linear least squares fit. Total stream power at Q2 and Q80 was then calculated for each reach using Eq. 1.

$$\Omega = \rho \, g \, Q \, S \tag{1}$$

where Ω is stream power (watts/m^2), ρ is water density (1000 kg/m^3), g is acceleration due to gravity (9.8 m/s^2), Q is discharge (m^3/s) and S is slope.

Mean bankfull width was obtained by buffering all reaches to 20 m. Buffers were then clipped by a channel area polygon (Ordnance Survey 2018b). Reach channel area was then divided by reach length to obtain mean width.

Reach BFI values were obtained for two search areas, 10 m (streamside) and 40 m (riparian) from the bank edge. Whilst most beaver foraging takes place within 10 m of a watercourse, feeding can occur > = 40 m from water (Haarberg and Rosell 2006; Iason et al. 2014; McComb et al. 1990). Both search areas extend 100 m up and downstream to account for connectivity of reaches. The mean of the top 50% of BFI values in each search area was extracted to understand the suitability of the best available habitat within a given reach. As beaver can behave as generalists (Nolet and Rosell 1994), they require only limited resources for habitation and dam construction; therefore, this value is more useful for classifying vegetation than the overall mean.

Beaver Dam Capacity model execution

To quantify the number of dams that the habitat within a reach can support, we combined our understanding about the streamside and riparian vegetation suitability. A fuzzy inference system (FIS) (Salski 1992) is used to classify the suitability of surrounding vegetation. The framework for the vegetation FIS is based upon Macfarlane et al. (2017); however, alterations to the rules list (SI.5) and thresholds were incorporated to account for differences in vegetation type, land use and input data in the more intensively managed European landscapes studied herein. Figure 2 shows the FIS design with streamside and riparian BFI values as antecedent variables and dam capacity as the consequent variable.

The output from the vegetation FIS, low-flow stream power (Q80), high flow stream power (Q2) and slope are combined using a second FIS. The rules list is presented in SI.6 and Fig. 3 depicts the model mechanism.

Following the combined FIS, an inference system was used to constrain the model further. Reaches with an average width > 25 m (to differentiate large waterbodies/lakes), a contributing catchment area > 250 km^2 or stream order > 5th are considered to have no dam capacity; 5th order streams are capped at 0.9 dams/km; stream orders ≤ 4th remain unchanged. The full modelling workflow is summarised in Fig. 4. These constraints are in-line with other studies (Gurnell 1998; Rosell et al. 2005; Stevens et al. 2007) that observed dam construction very rarely in 5th order streams and never in > 5th order streams.

Following model execution, simplified dam capacity categories were established to facilitate interpretation. Reaches with a capacity of 0 dams/km were categorised as 'None', those with 0–1 dams/km as 'Rare', 1–4 dams/km as 'Occasional', 5–15 dams/km as 'Frequent"and 16–30 dams/km as 'Pervasive'.

Field sign survey

Field surveys were conducted between October 2017 and January 2018. All areas known to contain beaver were surveyed, covering ca. 1310 km (11%) of the River Tay catchment, ca. 61 km (10%) of the River Otter catchment and 1.8 km (29%) of the Coombeshead sub-catchment. Feeding sign locations, observed dams and known locations of removed/collapsed dams were recorded using a handheld Global Navigation Satellite System (Trimble Geo 7X) and loaded into a GIS (ArcPro 2.4.1). Campbell-Palmer et al. (2018 and in review) provide full detail of field-survey protocols.

All feeding sign and dam locations were 'snapped' to the nearest reach using Python packages: Shapely (version 1.6.4) and GeoPandas (version 0.6.0). All reaches that intersected a feeding sign or dam were classified as active and or dammed.

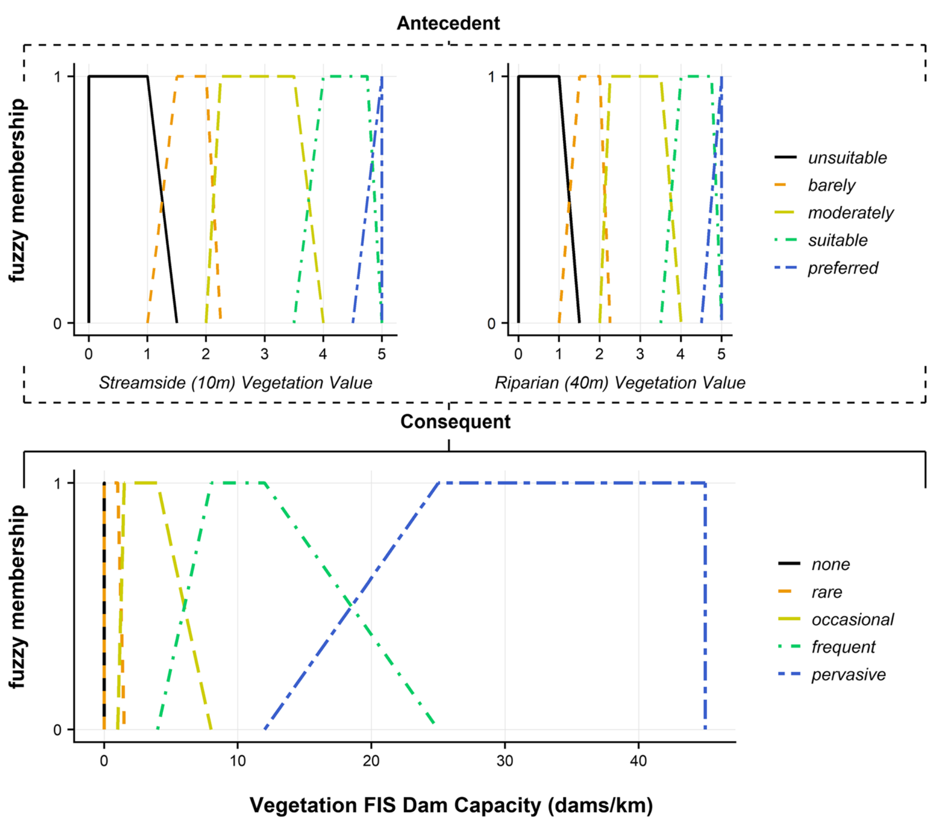


Fig. 2 Vegetation fuzzy inference system: antecedent conditions, streamside (10 m) (top-left) and riparian (40 m) vegetation (top-right) suitability are used to derive the consequent dam capacity (base-centre) supported by vegetation

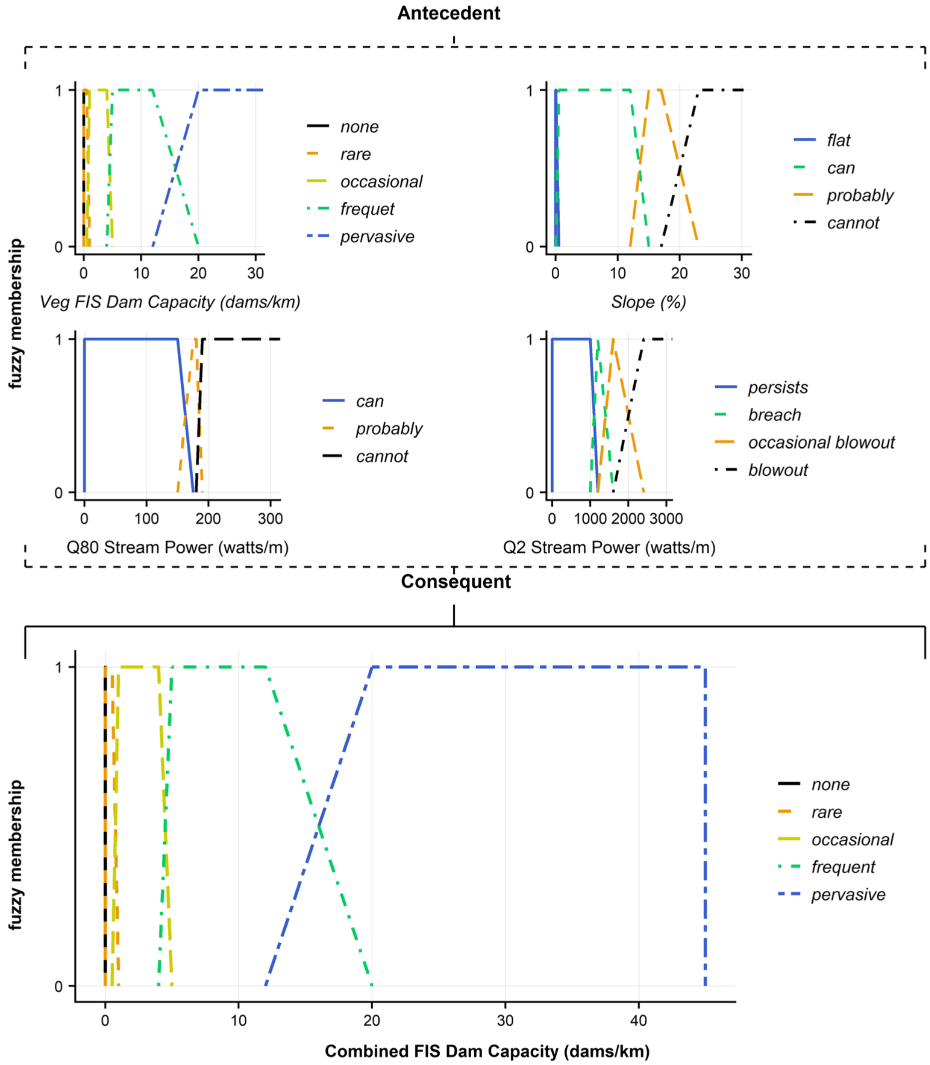


Fig. 3 Combined fuzzy inference system design: vegetation dam capacity (top-left), slope (top-right), Q80 (mid-left) and Q2 (mid-right) stream power are antecedents, consequently providing dam capacity (base-centre)

The number and density of dams per active reach were then calculated (Table 3).

Dams and field signs located within the enclosed site discussed in Law et al. (2016) were excluded from the analysis as it is unclear if the damming observed within enclosures is representative of natural damming behaviour.

Evaluating Beaver Forage Index

The mean of the top 50% of BFI values, within a 40-m buffer area for each reach, were used to evaluate the efficacy of the BFI index in predicting the suitability of habitat for beaver. The resulting continuous values are derived from a range of integers; to reflect this change, we classified these scores into five categories: unsuitable (<= 1), low (<= 2), medium (<= 3), high (<= 4), preferred (<= 5). Subsequently, we calculated the number of active and non-active reaches within each BFI category. A categorical binomial Bayesian model was then undertaken using the 'RStan' package (Stan Development Team 2018) to determine the probability that a reach within a given category may contain signs of beaver activity. An uninformative, uniform prior was used to allow the full range of probability to be objectively explored (Wade 2000). Following the calculation of posterior probability distributions for all BFI categories, the Maximum A Posteriori (MAP) and 95% credible intervals (CI) were derived Fig. 6. Bayes factors (Hooten and Hobbs 2015) were used to quantify the relative likelihood of observing signs of beaver activity between reaches of different categories (Table 1).

Evaluating Beaver Dam Capacity model results

BDC results were evaluated to determine whether or not BDC was an effective predictor of reaches that were suitable for

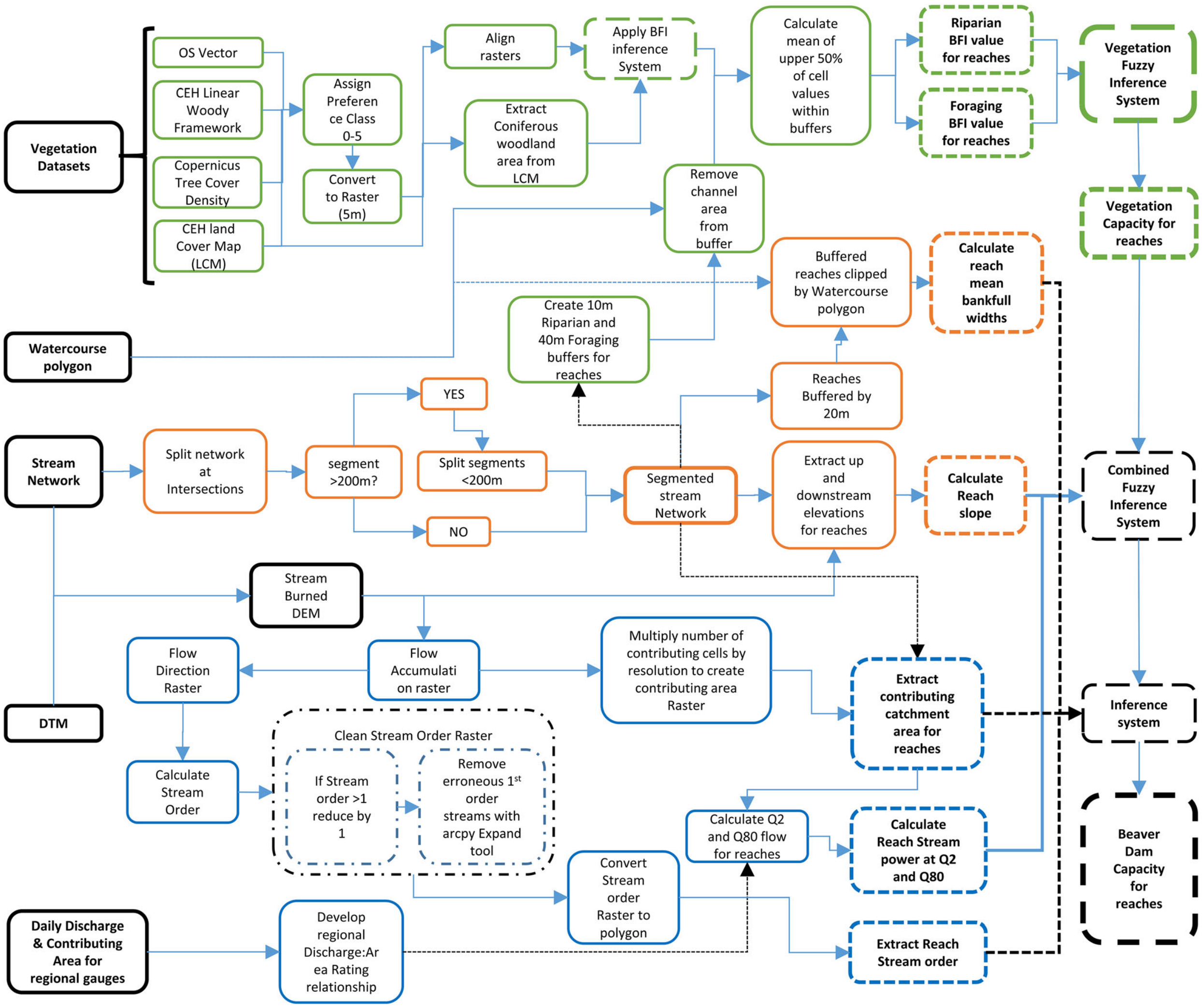


Fig. 4 Beaver Dam Capacity (BDC) model workflow. Black (solid outline)—input data, green—vegetation processing, orange—terrain processing, blue—hydrology/hydraulic processing, black (dashed outline)—(fuzzy) inference systems

dam construction. This was carried out, as with BFI, using a binomial Bayesian framework. Once again, a generative binomial model was applied for each of the 5 BDC categories; the MAP and CI were derived from the posterior distribution (Fig. 9) and Bayes factors were derived (Table 2). This Bayesian approach was used to evaluate the results of the BDC and BFI models because it explicitly describes the probability of an outcome (either activity or dam construction) and the uncertainty associated with that outcome (Ellison 2004), allowing us to evaluate precisely the relative preference of beaver towards reaches from the different categories.

Predicting numbers of dams

The modelled maximum number of dams per reach was compared with observed dam numbers to determine if modelled

Table 2 Bayes factor matrix—describing the relative likelihood of observing signs of beaver activity between different BFI categories. Numbers in italic show the MAP Bayes factor, and 95% credible intervals are given in square brackets

Unsuitable (<= *1*)				
13.54 [10.78, 17.74]	Low (<= *2*)			
17.97 [14.43, 23.38]	*1.32* [1.15, 1.52]	Moderate (<= *3*)		
18.53 [15.35, 24.99]	*1.41* [1.23, 1.64]	*1.06* [0.94, 1.22]	High (<= *4*)	
30.71 [25.36, 40.6]	*2.31* [2.05, 2.62]	*1.71* [1.56, 1.95]	*1.64* [1.45, 1.84]	Preferred (<= *5*)

dam capacity is an effective predictor of observed dam density. Analysis was carried out for active reaches only to minimise the effect of limited range expansion. Of the 2104 active reaches, 58 contained dams. The distribution was therefore zero-inflated and over-dispersed, as confirmed by the 'dispersion test' function from the AER package (Kleiber and Zeileis 2008). A range of models are available for modelling zero-inflated distributions (Martin et al. 2005). Four different zero-inflated models (Hurdle and zero-inflated with both negative binomial and poisson distributions) and two general linear models (poisson and negative binomial distributions) were compared. Performance, fit and over-dispersion of these models were evaluated using Akaike information criterion (Bozdogan 1987), the Vuong test for nested models (Merkle and You 2018) and hanging rootograms (Kleiber and Zeileis 2016). The zero-inflated negative binomial (ZINB) model was selected as it had the best overall performance (Fig. 10a). Dam numbers and 95% confidence intervals (CI) ('boot' package, Canty and Ripley 2017) were then calculated for all catchments with the assumption that all reaches were active (Table 3).

To evaluate the ZINB model's predictive performance, a cross-validation approach was used (Fig. 10b) (Picard and Cook 1984). Data were randomly split into training (70%) and test (30%) subsets 1000 times. The training subset was used to derive a ZINB model. The test dataset was randomly subset at every percentile (100 subsets) to test the model over a range of different scales (ca. 600 m–70 km of channel). The ZINB model was applied to all test data subsets, and the sum of the predicted number of dams for the subset was calculated. A linear regression (with zero-intercept) and prediction intervals were derived for predicted versus observed dam numbers to assist with the assessment of the model performance (see SI.9 for model selection, CI derivation and cross-validation code).

Results

Field survey results

Surveys carried out across the three study sites revealed that a total of 2104 reaches (258 km of stream) contained signs of beaver activity (Table 3). As the largest catchment with the most established beaver population, the Tay catchment contains by far the largest length of active river channel (221 km). Thirty-five kilometres of the River Otter and < 2 km of the Coombeshead subcatchment were found to contain signs of beaver activity (Table 3).

A total of 89 dams were identified in 58 different reaches across all catchments with 41, 35 and 13 in the Tay, Otter and Coombeshead (sub)catchments respectively (Table 3).

Evaluating Beaver Forage Index (BFI) model results

The BFI clearly distinguishes regions of varying landcover; for example, in Tayside, upland areas were markedly devoid of suitable forage; lowland arable agriculture and coniferous woodland provide moderate forage suitability, and riparian deciduous woodland provides the most suitable foraging habitat for beavers (Fig. 5a). Visual inspection of the BFI suggested good levels of coincidence with suitable habitats identified in satellite/aerial data (SI.11). Binomial Bayesian evaluation revealed that, with an increasing BFI value within 40 m of the riverbank, there was a corresponding increase in the probability that a reach would be active (Fig. 6). Preferred reaches, with 40-m BFI scores > 4, were 1.64 (95% CI [1.45, 1.84]) times more likely to be active than those reaches with a score > 3 and < 4. Unsuitable reaches, with a 40-m BFI scores <= 1 were 30.71 (95% CI [25.36, 40.6]) times less likely to be active than preferred reaches. Reaches with scores > 1 and <= 4 (categories: low, medium, high) displayed relatively tightly grouped probabilities of observing signs of beaver activity; medium and high groups were slightly more likely to be active than those in the low category but these groups display clear overlap in credible interval range suggesting these categories have comparable suitability for beaver foraging.

Evaluating Beaver Dam Capacity model results

Broad spatial patterns in the BDC model results can be observed (Fig. 7). For the Tay, the majority of reaches within frequent and pervasive categories are in lowland areas where food and building resources are plentiful, and stream gradients lower (Fig. 7c). Low capacity reaches are common in upland

Table 3 Bayes factor matrix—describing the relative likelihood of beaver dam construction in active reaches of different BDC categories. Numbers in italic show the MAP Bayes factor, and 95% credible intervals are given in square brackets

None				
20.16 [9.91, 1932.14]	Rare			
38.06 [17.31, 3395.36]	*1.48* [0.74, 4.01]	Occasional		
46.14 [23.7, 4517.14]	*1.86* [1.01, 5.25]	*1.16* [0.61, 2.89]	Frequent	
78.5 [44.23, 7574.58]	*3.54* [1.99, 8.43]	*1.96* [1.2, 4.7]	*1.59* [0.94, 3.34]	Pervasive

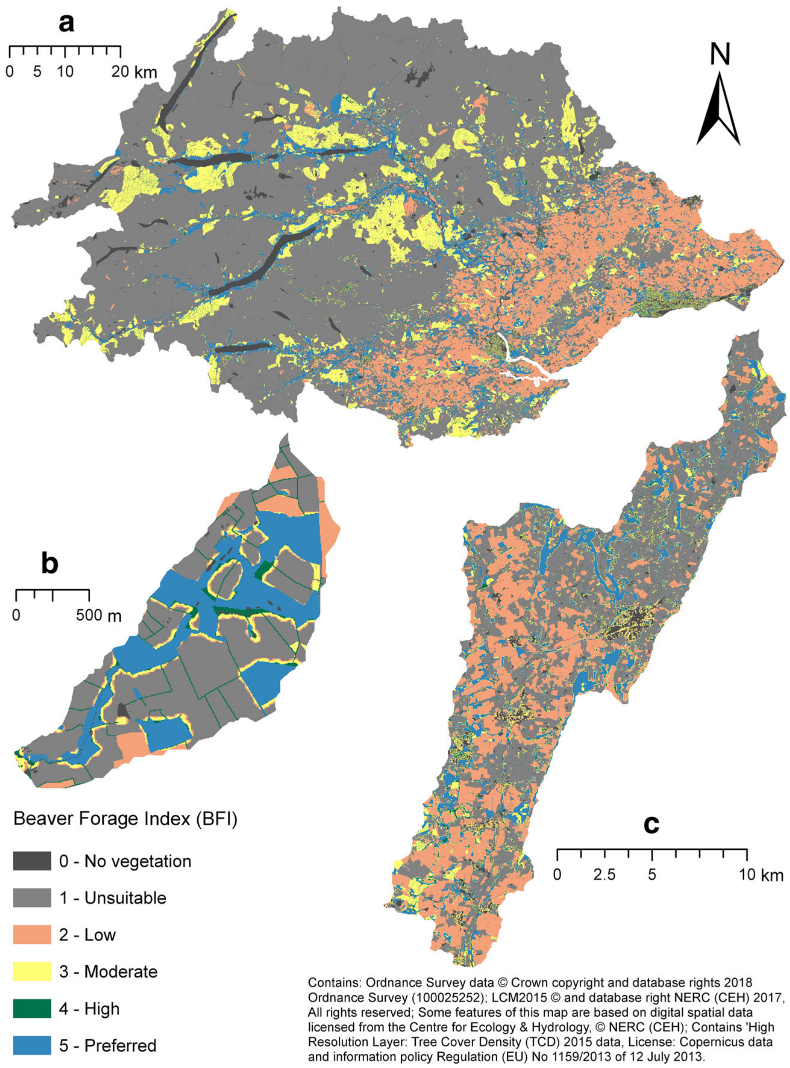


Fig. 5 Beaver Forage Index (BFI) model results for **a** R. Tay catchment, **b** Coombeshead subcatchment and **c** R. Otter catchment. The BFI describes the preference of beaver towards a given land cover type, where areas of greater deciduous woodland cover and or suitable forage types are considered preferable

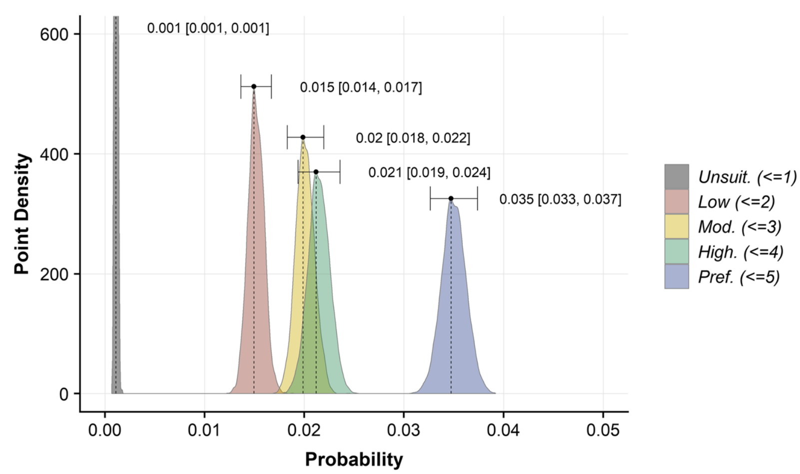


Fig. 6 Posterior probability distribution point density plot for Beaver Forage Index (BFI) categories. Maximum A Posteriori (MAP) and 95% credible intervals (in square brackets) are provided for each category

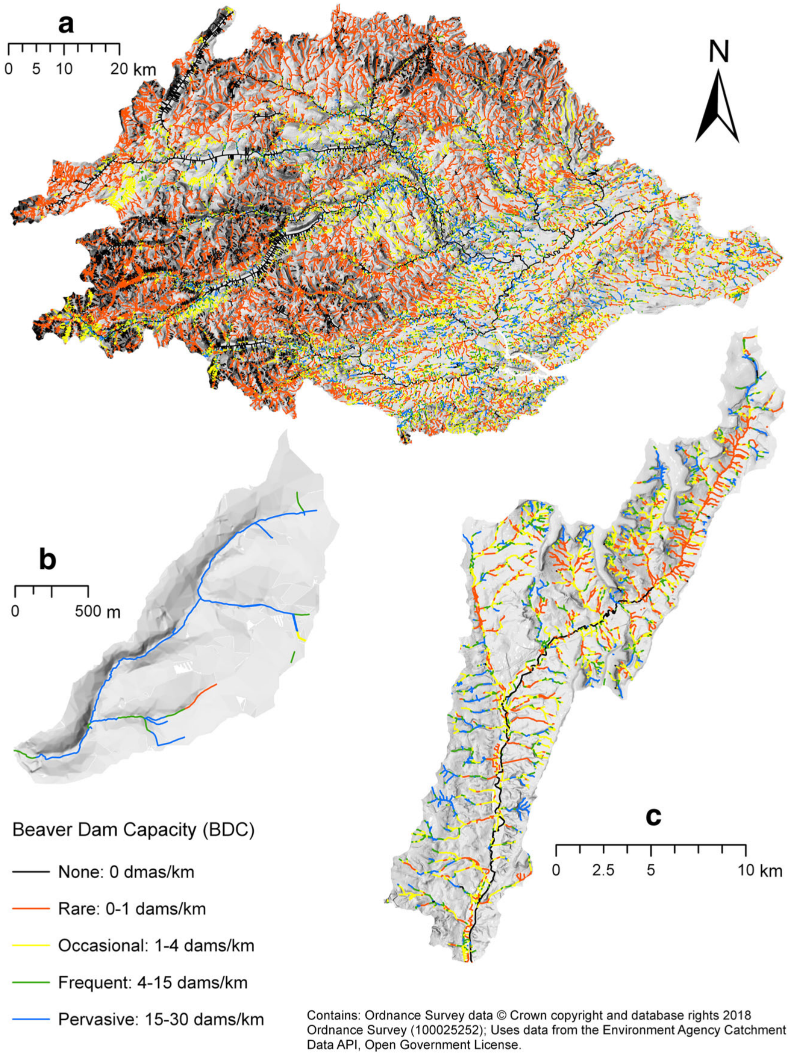


Fig. 7 Beaver Dam Capacity (BDC) model results for **a** R. Tay catchment, **b** Coombeshead subcatchment and **c** R. Otter catchment. BDC describes the density of beaver dams that can be supported within a given reach

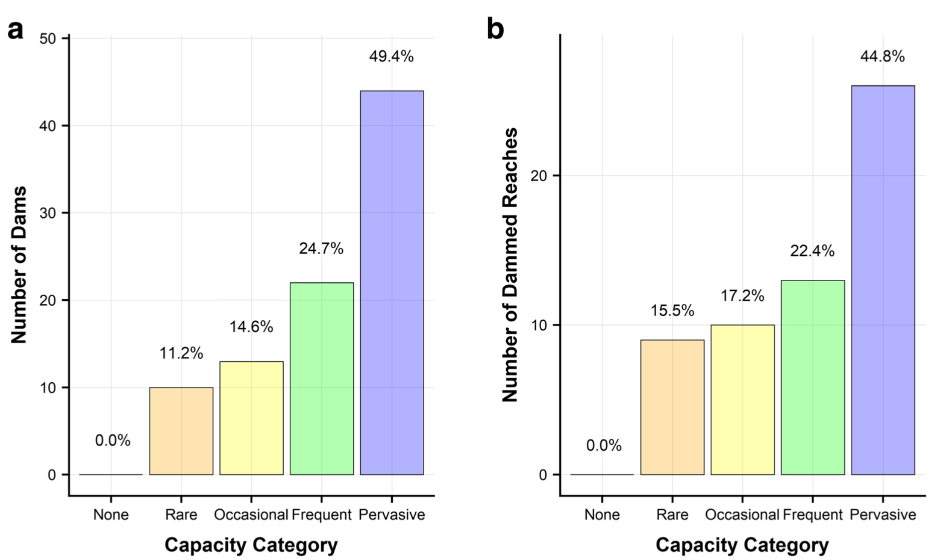


Fig. 8 Bar plots showing the number of dams that were observed during field surveys, across all three sites, within different dam capacity categories. **a** Total number of dams per capacity category. **b** Number of dammed reaches within each dam capacity category

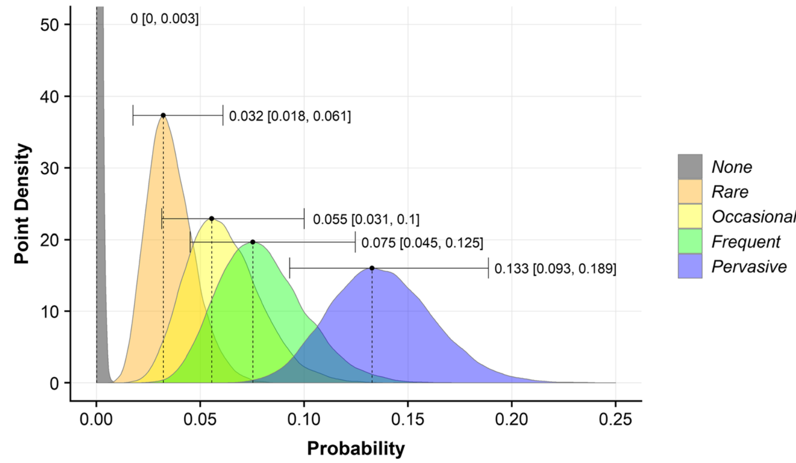


Fig. 9 Posterior probability distribution point density plot for Beaver Dam Capacity (BDC) model categories shows the probability of dam construction when a reach is active for all BDC categories. Maximum A Posteriori (MAP) and 95% credible intervals (in square brackets) are provided for each category

regions where deciduous woodland is lacking, and steeper gradients dominate. In the Otter catchment, areas of higher dam capacity predominate in lower order streams within deciduous woodland (Fig. 7b). Areas of lower capacity were most prevalent within intensively managed grasslands and on larger rivers where stream powers are high.

Much of the Coombeshead subcatchment is classified as pervasive (Fig. 7d). Only reaches with reduced access to woody vegetation had lower capacity. Additional maps illustrating model outputs are provided in SI.11.

Figure 8 shows total number of dams (Fig. 8a) and total number of dammed reaches (Fig. 8b) in each category across all catchments. No dams were observed in reaches where the BDC model predicted no capacity. An increasing number of dammed reaches are observed with higher capacity categories. 74.1% of dams and 67.2% of dammed reaches were observed in pervasive or frequent capacity categories.

Figure 9 shows the posterior probability distribution from the binomial Bayesian analysis of dammed active reaches. With increasing dam capacity, there is a corresponding increase in the probability that a reach will be dammed. Table 2 shows the relative likelihood of dam construction between categories and, for example, shows that active ‘Pervasive’ reaches are 3.54 (95% CI [1.99, 8.43]) times more likely to be dammed than active ‘Rare’ reaches. Notably, the probability of dam construction almost doubles between ‘Frequent’ and ‘Pervasive’ reaches from 0.075 (95% CI [0.045, 0.125]) to 0.133 (95% CI [0.093, 0.189]).

Predicting numbers of dams

Modelled dam capacity and observed dam density are significantly related ($p = 0.013$) in the count portion of the ZINB model and in the presence/absence portion ($p = 0.006$) (Fig. 10a and SI 16). This result indicates that BDC is both an

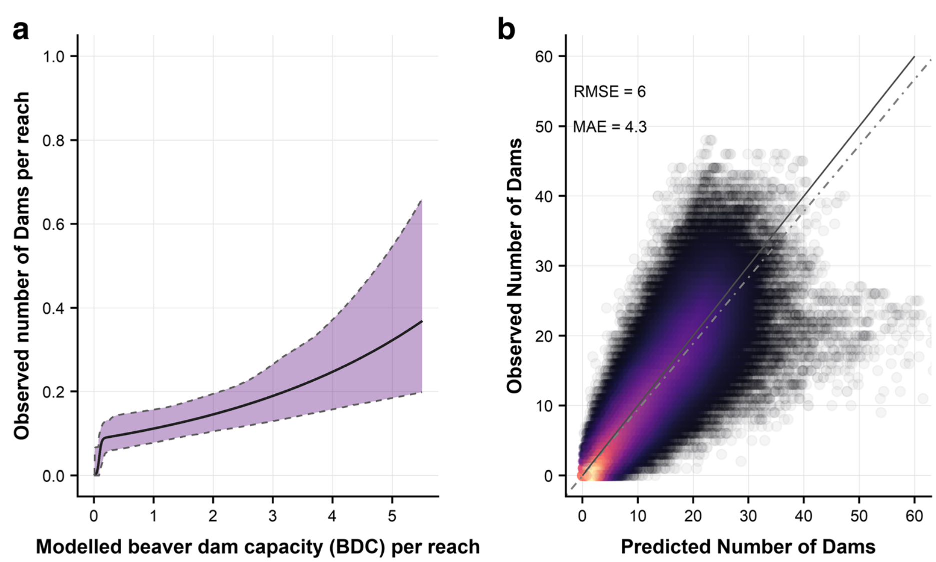


Fig. 10 Zero inflated negative binomial (ZINB) regression was used to evaluate the relationship between modelled Beaver Dam Capacity (BDC) and observed numbers of beaver dams for reaches containing beaver activity. **a** The ZINB model, where the coloured zone indicates the 95% confidence bands. **b** Cross validation was used to evaluate the performance of the ZINB model across different scales (600 m–70 km): dashed line shows a linear regression (with zero intercept) and the dotted line indicates the 1:1 line

effective predictor of dam counts across large spatial scales and for understanding the probability of dam presence or absence for a given reach, aligning with findings from the binomial Bayesian analysis of dam frequency per category in active reaches. Cross-validation showed a strong correlation between the ZINB model prediction and observed dam counts (Fig. 10b). Root mean square error (RMSE) and mean absolute error (MAE) were 6.1 and 4.3 respectively.

Results from the BDC and ZINB models are presented in Table 3. The majority (67.8%) of reaches across the Tay are shown to have no or rare capacity to support dams and only 12.8% are classified as frequent/pervasive. This suggests approximately 51% of the predicted number of dams would be contained within just 12.8% of the river network. Under a scenario where all reaches contain signs of beaver activity, the ZINB model predicts that 6173 (95% CI [3385, 11,597]) dams may be constructed across the whole catchment (ca. 6500 km^2), equivalent to a density of 0.4 (95% CI [0.2, 0.7]) dams/km. The pervasive category accounts for the largest proportion of predicted dams; however, occasional reaches are predicted to support more than frequent reaches due to the greater length of channel within the category (3142 km and 1030 km for occasional and frequent reaches respectively).

Thirty-six percent of the River Otter was classified as having rare or no capacity to support dams. Fifty-nine percent of the predicted number of dams, if all reaches were active, were predicted to occur within frequent and pervasive reaches which make up 31% of the river network. Reaches classed as occasional are expected to support the second highest proportion of dams (ca. 32%), due to the high prevalence of this reach type (34% of the river network). The predicted number of dams that may be built throughout the catchment (ca. 250 km^2), under a total occupancy scenario, is 468 (95% CI [262, 814]) or 0.8 (95% CI [0.4, 1.4]) dams/km. A scenario whereby all reaches within a catchment contain signs of beaver activity, at any one time, is highly unlikely; therefore, these figures should be considered an upper estimate of what may be expected if catchments reach population carrying capacity and no management, such as the removal of beaver or dams, is undertaken.

The Coombeshead subcatchment was dominated by reaches with a high capacity to support dams. The predicted number of dams for this subcatchment was between 6 and 16. Currently, there are 13 dams within this subcatchment.

It is also notable that, at present, 64% and 56% of observed beaver signs (by channel length), in the Tay and Otter catchments respectively, are located within reaches with no capacity to support damming (Table 4).

Discussion and conclusions

In this study, we have developed two models to predict: (i) the spatial distribution of beaver foraging habitat and (ii) the suitability of river reaches for beaver damming. Using empirical survey data, showing the spatial distribution of beaver foraging signs and dam locations, we validated the model predictions across three distinct (sub)catchments. This revealed that models effectively predicted the suitability of both foraging habitat and reaches preferred for dam construction. Model results were then used to predict the likely number of dams that may occur across (sub)catchments, under a scenario in which all reaches contain signs of beaver activity.

Modelling the distribution of beaver foraging habitat and damming activity in European landscapes

Beaver Forage Index (BFI) model

Vorel et al. (2015) describe beaver as a choosy generalist, implying that, in habitats where their preferred woody forage materials (*Salix* spp. and *Populus* spp.) are present, beaver will preferentially feed on these species. However, in locations where these species are not available, or populations have occupied these areas, the behaviour of beaver becomes more generalist (Fustec et al. 2001; Nolet and Rosell 1994; Vorel et al. 2015). Therefore, it is reasonable to assume that any model that effectively incorporates willow or poplar-dominant riparian woodland will, to some extent, reasonably predict primary beaver habitat. However, if more marginal habitats are not included in a model, it is highly likely that, as a population expands and beavers are forced to use generalist strategies to exploit marginal habitat, the model will fail to identify these areas of viable habitat. Such an assertion is in line with the dystopic distribution hypothesis (Fretwell 1972; Fretwell and Lucas 1969) that marginal habitats are important for expanding beaver populations and floating individuals (Nolet et al. 1994). This could explain why Stringer et al. (2018) observed that, whilst most beaver territories occurred in areas with substantive deciduous woodland cover, some did not and were therefore not identified as suitable by their model. In the development of the BFI, we have used similar datasets to Stringer et al. (2018) for defining regions of continuous broadleaved woodland; but, in addition, we have included data which describes other sources of forage such as discontinuous shrub, rough grassland, reeds, arable fields and narrow linear woody features such as hedgerows. The value of adding such datasets is highlighted by Fig. 6 which shows clearly that those reaches within the 'preferred' category have far greater probability of containing signs of beaver activity and those with sub-optimal resources may still support beaver but are less preferred. Furthermore, those intermediate categories ('low', 'medium', 'high') were found to have a similar probability of containing signs of beaver activity. We can state therefore, that the BFI results align with our own empirical observations and those of other authors (Fustec et al. 2001; Nolet and Rosell 1994; Vorel et al.

Table 4 Results for all sites showing the length of channel, modelled dam capacity, predicted number of dams and number of observed dams

AOI	Capacity category	Channel length (km)	Stream network (%)	Length of active channel (km)	Active channel (%)	Observed dams (n)	Observed dams (%)	Predicted n dams across catchment (n-dams [95% CI])	Predicted dams (%)
Tay	None	3088.04	19.13	141.69	64.01	0	0	17.4 [0, 81.92]	0.28
	Rare	7838.85	48.57	27.83	12.57	6	14.63	646.91 [122.42, 2284.27]	10.48
	Occasional	3141.86	19.47	14.87	6.72	8	19.51	2335.09 [1315.73, 4181.78]	37.83
	Frequent	1029.69	6.38	17.16	7.75	8	19.51	1162.44 [765.73, 1865.61]	18.83
	Pervasive	1040.73	6.45	19.8	8.95	19	46.34	2011.12 [1181.63, 3184.27]	32.58
	All	16,139.16	100	221.35	100	41	100	6172.95 [3385.51, 11,597.85]	100
Otter	None	33.71	5.67	19.43	56.18	0	0	0.23 [0, 1.09]	0.05
	Rare	178.34	30.02	5.46	15.78	4	11.43	37.5 [6.64, 95.29]	8.01
	Occasional	199.38	33.56	5.69	16.45	5	14.29	150.68 [84.02, 273.91]	32.2
	Frequent	92.95	15.64	2.76	7.99	14	40	106.85 [69.94, 172.75]	22.83
	Pervasive	89.76	15.11	1.24	3.6	12	34.29	172.72 [101.81, 271.09]	36.91
	All	594.14	100	34.58	100	35	100	467.97 [262.41, 814.13]	100
Coombeshead	None	0.01	0.21	0	0	0	0	0 [0, 0]	0.01
	Rare	0.29	4.35	0	0	0	0	0.05 [0.01, 0.12]	0.45
	Occasional	0.23	3.53	0	0	0	0	0.19 [0.11, 0.33]	1.78
	Frequent	0.99	15.1	0	0	0	0	1.06 [0.72, 1.64]	10.16
	Pervasive	5.04	76.81	1.65	100	13	100	9.14 [5.27, 14.28]	87.6
	All	6.57	100	1.65	100	13	100	10.44 [6.11, 16.38]	100

2015) that, whilst beaver primarily choose habitat with preferred woody forage, they can occupy reaches with less abundant or alternate resources.

Temporal variability in habitat selection is not explicitly considered in this study, but we know that seasonal selection of habitat changes due to the increased availability of grasses, forbs, macrophytes and crops (Campbell-Palmer et al. 2016; Law et al. 2014; Svendsen 1980). Excluding macrophytes, for which there is no nationally available data, we have, as far as possible, included these types of habitat within the BFI to ensure that year-round habitat is accounted for. A consideration of the effects of temporal variation in forage choice could provide a spatial and temporal understanding of how beaver utilise resources in a river system, advancing our understanding of their population dynamics.

Through the felling of trees, beaver can alter the community and structure of riparian woodland. In so doing, they can, in arid or high latitude/altitude landscapes, consume preferred foraging resources faster than they can regenerate, leading to the succession of less preferred species (Campbell et al. 2005; Fryxell 2001; Rosell et al. 2005). In temperate landscapes, it is suggested that resource consumption is likely to be exceeded by regeneration (at least at the landscape-scale) and therefore resources will not be totally depleted (Nolet et al. 1994). Therefore, when using this modelling approach for areas under more extreme climatic conditions, landcover datasets should be regularly updated to capture beaver-induced impacts on vegetation structure and composition.

Beaver Dam Capacity (BDC) model

Macfarlane et al. (2017) were interested in dam capacity to help inform the design of river restoration projects aiming to mimic the behaviour of beaver in support of, for example, salmonid conservation (Bouwes et al. 2016). Such an approach could be of great value with the increasing interest in natural flood management and restoring natural processes (Dadson et al. 2017; Environment_Agency 2017; Iacob et al. 2014; Lane 2017) across Europe. But, from a management perspective, we have found the concept of dam capacity to often be misinterpreted and presumed to represent a likely outcome in the event of beaver occupancy. Our validation approach has allowed us to interpret the BDC results in an alternative manner. The use of a Bayesian validation procedure tells us precisely the probability of dam construction in each capacity category when reaches are active. These probability estimates provide a tangible metric with which to inform management strategies and monitoring programmes. Furthermore, the increase in the likelihood of damming with increasing BDC scores indicates that BDC results do align with empirical observation.

Using model results to predict the number of dams that are likely to occur at the catchment scale

Given that BDC is a strong predictor of observed dam counts, we have used it to estimate the number of dams that are likely to occur at the catchment scale using ZINB regression. We acknowledge the uncertainty associated with these predictions (Fig. 10); however, this level of uncertainty becomes less problematic when applied to larger areas of interest, so we therefore suggest that this approach is used at the subcatchment scale as a minimum (ca. ≥ 5 km^2). Whilst the ZINB model was developed only on reaches where beaver were active, we anticipate that, as populations approach carrying capacity, the relationship between estimated dam capacity and observed dam numbers may change. Therefore, this relationship could be revisited as beaver population densities increase.

Frequent and pervasive reaches, predicted to accommodate the highest number of beaver dams, are predominantly found in areas of riparian woodland. These tend to be associated with land use where the risk of conflict is less, although this can vary between specific sites and ownerships. In the Tay and Otter catchments, predicted dam counts were highest in the pervasive category followed by the occasional category. Occasional reaches are typical of agricultural streams lined by discontinuous woody vegetation. These reaches make up a large proportion of both the Otter (30%) and Tay (20%) catchments, and therefore numerous dams will occur within these reaches but, given the lower probability of dam construction, at a lower density than in the reaches with higher modelled capacity.

Our results show that 64% and 56% of active reaches, in the Tay and Otter catchments respectively, have no capacity to support dams. Therefore, it is reasonable to say that, at present, the majority of beaver populations in these catchments will not construct dams. However, it should also be noted that many human-wildlife conflicts that result from beaver activity result from factors other than dam construction. Such activity includes, but is not limited to, tree felling, burrowing and herbivory on crops (Auster et al. 2019; Campbell-Palmer et al. 2016; Crowley et al. 2017; Gaywood et al. 2015). Whilst aspects of this modelling work may help to build understanding on the distribution of such impacts, it cannot be used to explicitly identify where this activity is more likely.

Conclusion and directions for future research

Herein, we have demonstrated the ability of models to describe the distribution of beaver foraging habitat and where dams are likely to be constructed and how many may occur. Models were validated using the results from a survey of beaver activity signs across the Tay, Otter and Coombeshead (sub)catchments, providing confidence in model results. The predicted number and distribution of beaver dams provide important insight into the current and future impacts of beaver and what the management implications of beaver might be. Model results show that that dams are more likely to occur in low order streams ($<= 4$th order) with plentiful woody riparian vegetation and less likely to occur in larger rivers with limited riparian woodland. However, agricultural landscapes with patchy riparian woodland may still provide marginal habitat which can support beavers and their dams. The Tay, Otter and Coombeshead (sub)catchments could support a dam density of 0.4 (95% CI [0.2, 0.7]) dams/km, 0.8 (95% CI [0.4, 1.4]) dams/km and 1.6 (95% CI [0.9, 2.5) dams/km respectively, and, at present, more than half of all reaches containing signs of beaver activity, across the three (sub)catchments, are unlikely to be dammed by beaver. The modelling procedures, outlined in this study, provide new and robust insight into beaver foraging habitat suitability, the distribution of beaver dams and the density of dams that could be expected within European landscapes.

These findings support the development of national policy concerning the reintroduction and recolonisation of beaver across native extents as well as informing local and regional management strategies.

In anticipation of the continued expansion of beaver across Europe, impacts on ecosystem and hydrological function require quantification at catchment-scales. Whilst there is a strong and developing understanding of the localised impacts of beaver (e.g. Catalan et al. 2017; Law et al. 2016; Puttock et al. 2017, 2018), few studies (e.g. Bouwes et al. 2016; Johnston and Naiman 1990; Martin et al. 2015) have monitored their landscape-scale effect. Future work on localised beaver impacts may wish to consider upscaling their findings, using a BDC modelling approach, to estimate the landscape-scale effect beaver might have. Further modelling efforts should aim to determine where beaver activity (including damming, tree felling and burrowing) may result in conflicts to allow appropriate mitigation to be put in place, but also to identify where it should be encouraged to maximise benefits.

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Data availability statement Geospatial datasets, generated during the current study, are not publicly available due to the requirement of source data licences and the privacy of landowners. On reasonable request, the data may be obtained from the corresponding author, dependent on the provision of the required data licences. Observed and modelled dam densities, integral to validation and prediction, are provided in SI9.

The source datasets analysed during the current study are made available from the following locations:

OS Mastermap Water Network Layer: https://www.ordnancesurvey.co.uk/business-and-government/products/os-mastermap-water-network.html

OS Terrain 5: https://www.ordnancesurvey.co.uk/business-and-government/products/os-terrain-5.html

National River Flow Archive: https://nrfa.ceh.ac.uk/data

OS VectorMap Local: https://www.ordnancesurvey.co.uk/business-and-government/products/vectormap-local.html

CEH Land Cover Map: https://doi.org/10.5285/bb15e200-9349-403c-bda9-b430093807c7

Copernicus TCD: https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density/status-maps/2015

CEH Linear Woody Framework: https://www.ceh.ac.uk/services/woody-linear-features-framework

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Chapter 5. Monitoring, modelling and managing beaver populations at the catchment scale.

This paper presents findings from a 5-year survey of Eurasian beaver *(Castor fiber)* field signs in the River Otter catchment, SW England, which were used to estimate territory counts over the study period. In combination with a spatially explicit method for estimating territory capacity along a river network, we used this empirical understanding to predict future beaver population change, under the assumption of logistic population growth. Model predictions were then used to test the impact of a range of theoretical territory removal management scenarios to simulate the potential impact of population management on future dynamics.

Natural England have recently released a public consultation to help inform future beaver management and releases in England. The Scottish government have also recently allowed the translocation of animals beyond the Tay catchment. Therefore, there is a pressing need to better understand how beaver populations will develop in Great Britain to inform conservation and management. The methods presented are reproducible (accompanied by an R package, {beavertools}) and could also be applied in regions outside of GB.

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RESEARCH ARTICLE

Monitoring, modelling and managing beaver (*Castor fiber*) populations in the River Otter catchment, Great Britain

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Abstract

1. Eurasian beaver (*Castor fiber*) were nearly hunted to extinction but have recovered to occupy much of their former range. Beaver were extirpated from Great Britain c. 400 years ago but have recently been reintroduced. The River Otter catchment, Devon was the site of the first licensed wild release of beavers in England. With further releases being considered, there is a need to better understand population dynamics of this native, keystone species to inform conservation and management.
2. Field signs were surveyed from 2015 to 2021. A semi-automated territory detection method was adopted to estimate territory counts. A spatially explicit model was developed to estimate the ecological territory capacity of the catchment. Future territory expansion was modelled using logistic growth curves; initial growth rate was estimated from observed territory counts and the estimated territory capacity range was used to define the limiting value of the growth curve. Beaver territory removal was simulated, across a range of management intensities and start times, to determine potential impacts of translocation or lethal control upon population dynamics.
3. Territory numbers increased from four to 18, inclusive of four additionally released individuals, during study period. In the absence of population management, the territory capacity of the catchment was estimated to range between 120 and 183; this may be reached between 2028 and 2057. Simulated territory removal, where territories were removed at a fixed rate from the sum of the estimated total population and the population increase for that year, demonstrated large uncertainties in predicted population responses. Simulations with territory removals >3/year all predicted potential population collapse. This finding emphasizes the need for caution when considering population management strategies; translocation of animals out of the catchment or culling should be considered only when populations are established and all alternatives have been considered.

4. These results provide critical information for the expected rate and magnitude of beaver population change in the River Otter catchment. The methods provide a reproducible and generalizable approach for understanding beaver population change, which can inform policy on the reintroduction of beavers and the potential timing and intensity of future beaver population management.

KEYWORDS
beaver, *Castor fiber*, logistic growth, management, population dynamics

1 | INTRODUCTION

Eurasian beavers (*Castor fiber*) were extirpated from Great Britain (GB) and much of Europe c. 400 years ago (Kitchener & Conroy, 1997). Some isolated populations remained in mainland Europe (Nolet & Rosell, 1998) and, following widespread conservation and natural recovery, beavers have returned to much of their prior extent, with population size estimated at a minimum of 1.5 million (Halley et al., 2021). Beavers are a European Protected Species and are now protected, across much of Europe, under the EU Habitats Directive.

Beavers are well known for their engineering abilities: building dams and lodges, digging burrows and canals and felling trees. These impacts can transform riparian landscapes into complex wetlands (Brazier et al., 2021; Larsen et al., 2021). Beaver disturbance provides many benefits for a range of taxa, in turn increasing biodiversity (Law et al., 2019; Stringer & Gaywood, 2016). Enhanced water storage, sediment accumulation and floodplain connectivity has also been shown to attenuate high-flow events (Puttock et al., 2017, 2021; Westbrook et al., 2020), increase base flows (Majerova et al., 2015; Woo & Waddington, 1990) and reduce downstream nutrient transport (Puttock et al., 2018). However, this disturbance can result in conflict where beaver impacts intersect anthropogenic activity (Campbell-Palmer et al., 2016). For example, dam construction can result in localized flooding of farmland or infrastructure and burrows may increase the risk of bank collapse (Schwab & Schmidbauer, 2003). It is therefore vital to understand beaver population dynamics so that management initiatives can maximize benefits whilst minimizing negative impacts on anthropogenic land use or landowners who may bear much of the cost of beaver reintroduction, whilst not always accruing all of the benefits (Auster et al., 2020, 2021b).

Monitoring beavers and their behaviour using biologging methods can be challenging; they are hard to track with radio transmitters due to their physiology, semi-aquatic nature, subterranean dwelling and social grooming (which may result in the loss of tracking devices): these approaches also raise welfare concerns (Campbell-Palmer & Rosell, 2015). Though several important and insightful studies (e.g. Arjo et al., 2008; Graf, Mayer, et al., 2016) have shown the value of such methods, the costs and challenges of deploying these techniques at scale are non-trivial. However, beavers leave conspicuous signs throughout the areas they inhabit, such as woody foraging signs, dams and lodges. These signs have been used effectively to monitor the distribution and expansion of beaver populations across large areas (Campbell-Palmer et al., 2021; Fustec et al., 2001; John & Kostkan, 2009; Mayer et al., 2017). As central place foragers (Haarberg & Rosell, 2006; Mahoney & Stella, 2020), beaver feeding signs can provide a valuable indication of the central localities of territories or home ranges with higher densities of feeding often found near dwellings (Fryxell & Doucet, 1991; John & Kostkan, 2009; Mortensen et al., 2021).

There are four described models for beaver population growth (Hartman, 1994, 2003; Petrosyan et al., 2016, 2019). The first is the *irruptive* growth model (Hartman, 2003), characterized by rapid population expansion followed by sudden population decline, until a dynamic equilibrium is reached when the population is limited by the resource recovery rate (Petrosyan et al., 2016). This growth model is typical of northern regions where the climate is harsh (Hartman, 1994, 2003; Petrosyan et al., 2016). Where forage resource recovery is greater but habitat quality is poor, *single* and *multi-step* population growth may occur where beavers increase carrying capacity over time by improving habitat through their engineering (Petrosyan et al., 2016). In temperate environments, where forage resources are plentiful and regrowth is greater than beaver foraging rates, the main regulating factor on the population is territoriality. Under this scenario, it is established that population growth follows the *logistic* model (Barták et al., 2013; Brommer et al., 2017; Kingsland, 1982; Korablev et al., 2011; Petrosyan et al., 2013, 2016). In this situation, the population is not limited by resource recovery and therefore the rate of population growth is determined by the population size and available habitat. The Gompertz growth function has also been used to model beaver population growth and, though mathematically distinct from the logistic function, similar assumptions of population density-controlled growth rates are assumed (Johnson-Bice et al., 2020). All of these growth models describe a general trend in population change; oscillatory fluctuations are to be expected along the trajectory of change (Petrosyan et al., 2016).

This study seeks to understand beaver population change in the River Otter catchment, England, since their reintroduction, using field sign surveys. We then present a spatially explicit approach for estimating territory capacity along a river network which allows us to adopt the logistic population growth model to estimate how beaver populations may change in the future and how any potential

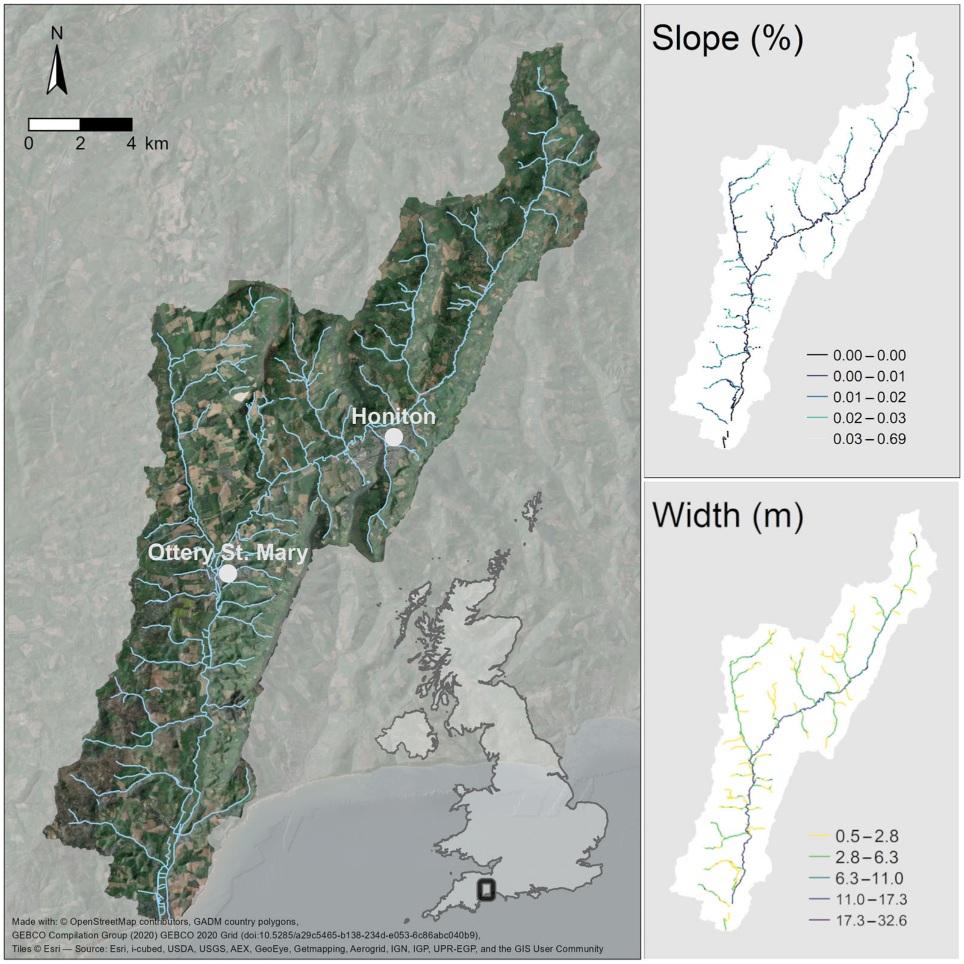

FIGURE 1 The River Otter catchment and its river network. The River Otter catchment has an area of 237 km^2 and is located in Devon, south-west of England. The right-hand panels show the stream gradient (slope) and channel width

translocation or lethal control management may affect population dynamics.

The aims of this study are as follows:

1. Quantify the number of territories present in the River Otter catchment annually between 2015 and 2021;
2. Predict the maximum number of territories that can be supported (ecological territory capacity) in the River Otter catchment;
3. Model future population growth to understand the rate of population change and the impact of management (translocation/lethal control of beaver territories).

2 | MATERIALS AND METHODS

2.1 | Location

The River Otter catchment is located in the south-west of England (Figure 1). The catchment area is approximately 237 km^2 with 592 km of channel. The land use comprises grassland (51%), arable farmland (29%), semi-natural (11%), and (sub)urban (5%) areas (Rowland et al., 2017). The riparian zone mainly comprises agricultural land and riparian woodland/scrub that is dominated by Willow (*Salix* spp.) and Alder (*Alnus* sp.). Hazel (*Betulaceae* sp.), Blackthorn (*Prunus* sp.) and Elder (*Sambucus* sp.) are also locally abundant. The River Otter rises in the Blackdown hills, approximately 275 m above sea level, and flows for c. 40 km before reaching the estuary. The river flows through Honiton and Ottery St. Mary, at which point the river channel is approximately 10- to 15-m wide. Most streams in the catchment have a riffle pool morphology with pools being up to 2 m deep, downstream of Ottery St Mary.

In 2013, the presence of wild-living beavers, on the River Otter in Devon, was made public; however, the earliest known observation occurred in 2008 (Brazier et al., 2020; Crowley et al., 2017). In 2015, five animals, which comprised kits and breeding adults, were captured (and re-released) providing strong evidence of successful breeding and a high likelihood of dispersing individuals within the system (Brazier et al., 2020; Campbell-Palmer et al., 2021). As part of a 5-year trial to monitor the impacts of the beavers, four additional animals were

TABLE 1 Woody feeding sign effort category classifications and descriptions

Effort category	Description
Low	Fewer than 20 *cut stems* with <7 cm diameter; <10 hands area of *bark stripping*
Medium	More than 20 *cut stems* or any individual stem >7 cm diameter; >10 hands area of *bark stripping*
High	Stem diameter >20 cm—either felled or deeply incised (≥10 cm)

Note: Effort classes were used as weights for kernel density estimation. The use of hand measurements for bark stripping provided a simple approximation for area of impact to increase survey efficiency. All impacted tree species were classified using this technique. The most frequently impacted tree species were Willow (*Salix* spp.), Hazel (*Betulaceae* sp.), Blackthorn (*Prunus* sp.), and Elder (*Sambucus* sp.). Other species were less frequently foraged—further information on this can be found in Brazier et al. (2020).

successfully released, comprising a male and female, in 2016 and 2019 (Brazier et al., 2020). Beavers are now permitted to remain in this catchment and expand into neighbouring catchments.

2.2 | Field survey

Field surveys were undertaken during the winter season (December–February) annually from 2015–2016 to 2020–2021 using a standardized design as in Campbell-Palmer et al. (2021). A trained beaver-signs surveyor walked all sections of the catchment where access was granted and were known to contain beaver activity. Spot checks were carried out on bridges and public access points to check for their presence in the wider catchment.

The surveyor walked along one side of the river, recording visible signs on both banks using a Trimble Geo7x handheld GNSS device. The key signs that were recorded (and referred to in this paper) were woody feeding signs, dams and dwellings. Feeding signs were recorded for each tree (i.e. a tree with multiple feeding signs was recorded once). Only recently felled/impacted trees were counted; therefore, a tree would only be recounted in a subsequent year if it had been impacted again. Fresh signs were identified by their visibly lighter colour which darkens over time (Campbell-Palmer et al.,). Feeding signs were assigned an effort classification to describe the amount of time and energy expended at that location, which increases with larger tree diameters (Fryxell & Doucet, 1991). These categories are described in Table 1. Foraging effort will also be determined by tree species, and beaver preference for that species (Fryxell, 1992; Gallant et al., 2004). This variability in effort is challenging to estimate with confidence. We consider it unlikely that it could have had a large role in the River Otter catchment as forage selection is generally homogeneous and dominated (>70%) by Willow (Brazier et al., 2020). Only dams and dwellings with evidence of recent activity, such as freshly laid sticks, were recorded.

Two data frames were created from the field sign data: one of all recent woody feeding signs for each year and another for all beaver dams and dwellings, referred to herein as confirmatory signs. We considered such field signs to be confirmatory because dams and lodges are typically only built within the home range of a family group (Fryxell & Doucet, 1991; John & Kostkan, 2009).

Woody feeding sign distributions are presented in Figure 3. Dam and dwelling locations are provided in Supporting Information S1.

No licensing was required to carry out this field work. However, as the majority of the riparian zone within the catchment is privately owned, permission to access the land was required before carrying out field sign surveys.

2.3 | Semi-automated territory detection

All analysis was carried out using R (version: 4.1.0) (R Core Team, 2020) and code to reproduce the analysis is given in Graham (2021). Key R package dependencies include tidyverse (v1.3.1) (Wickham et al., 2019), ggspatial (v1.1.5) (Dunnington, 2021), sf (v1.0.4) (Pebesma, 2018), raster (v3.5.2) (Hijmans, 2021), spatialEco (v1.3.7) (Evans, 2021), osmdata (v0.1.6) (Padgham et al., 2017), gridExtra (v2.3) (Auguie, 2017), exactextractr (v0.7.0) (Baston, 2020) and investr (v1.4.0) (Greenwell & Kabban, 2014).

Various methods exist to determine territory locations and extents. One of the most frequently used techniques is the mapping of beaver lodges and winter caches (Brommer et al., 2017; Hay, 1958); however, as neither of these field signs are reliably built in all beaver territories in the River Otter catchment, possibly due to climate, hydrology, and/or bank substrate, additional information was required to estimate the location of territories. Other authors have used beaver field sign locations and their spatial clustering/partitioning to improve territory locations estimates (Fustec et al., 2001; John & Kostkan, 2009). Herein, we adopted a similar approach by using beaver foraging signs to create a kernel density raster for each survey season using spatialEco (Evans, 2021). Weights were applied to the points based on their effort category class to give greater prominence to areas of high feeding effort (Fryxell & Doucet, 1991). Low, medium, and high foraging classes had weights of 1, $1e^{+03}$, and $1e^{+06}$, respectively; a low threshold value of $1e^{-10}$ was used to remove areas of extremely low density. These specific weights and low threshold limits were chosen based on local knowledge of beaver territory locations to increase the chance of distinguishing coincident regions of high-density foraging. This method should be considered a tool to aid the interpretation of population dynamics rather than something that is quantitatively objective, and therefore its development is critically linked with expert understanding.

The foraging density rasters (for each year) were then used to generate two polygon regions, the first of which included values greater than the low threshold ($1e^{-10}$) to define activity regions and the second that defined all regions of feeding density >95th percentile. These areas were considered to describe the central places of beaver activity as beavers feed in higher densities closer to their dwelling. If an activity region intersected a central place region, the activity region was classified as a possible territory. If an activity region intersected either a dam or dwelling, it was considered a confirmed territory.

Following this automated step, it was then necessary for the surveyors to review these predictions. Where known territories existed but were not effectively distinguished in the automated processing or possible territories were known to be active, but no dams or dwellings were found, the classes of these regions were reclassified as active territories. If two adjacent territories were not distinguished, an additional territory was added to the count for that year. This was required in one location for survey years 2018–2019, 2019–2020 and 2020–2021.

For this study, we therefore define a beaver territory as an area of continuous beaver activity that comprises a region of foraging with a density ≥95th percentile and contains evidence of resident behaviour such as a dwelling or dam. These territories may be home to one or more individuals.

During the 2020–2021 survey, a new active territory was located by surveyors. The landowner was unwilling for this territory to be surveyed and it is therefore excluded from the mapped data presented below. For the statistical analysis, an additional territory was added to the final territory count for that year to inform predicted population change estimates.

2.4 | Modelling ecological territory capacity

This approach was built upon the modelling outputs from Graham et al. (2020) which provide a river network split into <200-m-long reaches. Each reach contains modelled predictions for:

i. Beaver Forage Index (BFI) for the riparian area within 40 m of the river bank. BFI describes the preference of beaver towards surrounding vegetation cover (Graham et al., 2020). The value is derived from a raster dataset with a spatial resolution of 10 m and is derived from Nationally available, remotely sensed data describing vegetation and land-use cover. Classes are assigned a value from 0 (unsuitable) to 5 (preferred), depending on beaver preference for that specific class (e.g. 0 for urban areas, 3 for Coniferous woodland and 5 for broadleaf woodland).
ii. Beaver Dam Capacity (BDC) (Macfarlane et al., 2017; Stoll & Westbrook, 2020) which describes the density of dams that could be supported by the reach and also the preference of beavers towards damming the reach. The BDC value can range between 0 and 30 dams/km. The BDC model considers a range of input variables including (i) hydromorphic descriptors such as estimated discharge at high and low recurrence intervals, stream power, stream gradient and stream width; (ii) vegetation suitability (derived from the BFI) within 10 and 40 m of the bank.

For every reach within the river network, an attempt was made to generate a theoretical territory: a target reach length was randomly drawn from a uniform distribution between 1337 and 1923 m which equates to one standard deviation around mean territory lengths reported by Campbell et al. (2005), Graf, Mayer, et al. (2016), John and Kostkan (2009), Mayer et al. (2017) and Vorel et al. (2008). The stream reach was then buffered by half the target length value. The length of the river network that intersected this buffer, with a stream order greater than or equal to the original reach, was measured. An iterative adjustment was then carried out for each territory section; where the territory length does not fall within ±10% of the target territory length, the buffer is increased/decreased by 50% of the previous buffer size depending on whether it is less/more than the target length (±10%). This process is repeated up to three times or until the length falls within the target range. If the desired length is not achieved after three attempts, no territory is generated for the reach; a step required to reduce computational time. For the River Otter catchment, this results in the territories being formed for c. 60% of reaches ($n \sim 3750$); however, these territory areas intersect the full river network and therefore every part of the river system was considered subsequently.

Following the creation of potential reaches, a preliminary filtering step takes place. All reaches with a BDC <1 dam/km, in territories where the core reach has a stream order <5, were first removed because it is expected that, to establish territories in small streams, dams are required due to the absence of deep water to conceal lodge entrances or cache woody material (Hartman, 1996). The minimum and mean BFI values for observed territory areas were calculated by intersecting river reaches (containing attributed BFI values) with observed territory areas giving values of 1.3 and 3.0 for the minimum and mean, respectively. Whilst it cannot be shown that this range of vegetation quality is representative of territories when catchments are at capacity, it provides a plausible range that likely captures the habitat quality required to maintain a stable territory. These values were used to test two scenarios; low and high minimum viable forage quality of territories. All potential territories with an average BFI less than the specified minimum value, either 1.3 or 3.0, were removed for the low and high threshold scenarios, respectively. For remaining territories, an iterative process was carried out where all intersecting territories were located and the one with the highest mean BFI value was retained. This step was carried out multiple times, with each successive step using the retained territories from the previous. The result is a selection of territories that do not intersect but offer the highest average BFI.

There were two key sources of variability in this method: the potential territory generation and the required minimum habitat quality. To capture this variability, a simulation was carried out; 100 potential territory scenarios were generated and, for each scenario, the two BFI thresholds were tested to provide a minimum and maximum estimate of territory capacity for a given potential territory scenario. This method therefore gives us a strong understanding of the potential range and uncertainty in our territory capacity predictions; the distribution of territory capacity predictions for both the low and high BFI thresholds is presented in Supporting Information S5.

Using the river network to frame this modelling is a simplification of potential beaver range; beavers also use still waterbodies disconnected from the river network. Some viable habitat patches were therefore not considered which could result in the slight underestimate of territory capacity. In addition, the BFI and BDC data assigned to this network consider a single moment in time; beaver are known to modify ecosystems by both expanding suitable habitat (Peinetti et al., 2009) and degrading it (Little et al., 2012) which could therefore have varied impacts for habitat availability and potential carrying capacity. Further, the duration that a given territory may remain viable for will be spatially and temporally variable. Some territories with abundant resources may remain viable in perpetuity, where the tree regrowth rate exceeds the forage rate. However, other marginal territories may remain viable only for a limited time. A likely result of this is that catchment carrying capacity will fluctuate with time and beaver population density. Our approach may not account for this long-term variability.

2.5 | Predicting future population dynamics

In order to model population growth, we assumed that growth conforms to the logistic curve, as shown by (Barták et al., 2013; Brommer et al., 2017; Korablev et al., 2011; Petrosyan et al., 2013, 2016). In order to approximate this curve, we had to estimate two key parameters:

i. The initial growth rate of the population;
ii. The territory capacity of the catchment which we can consider to be the asymptote or limiting value of the logistic curve.

To calculate the initial rate of population growth, a general linear model (GLM) with a Poisson error distribution and log link was fit to the observed territory count data using R's glm function (R Core Team, 2020). A log link was used as we expect the rate of expansion to be nonlinear in accordance with the logistic growth theory (Kingsland, 1982). The derivation of this model includes count data which are a combination of natural population growth and introduced animals (four in total over the 5 years). This model therefore describes initial population growth inclusive of managed introductions. We suggest that, were adjacent catchments to contain beavers, these introductions would be comparable to the natural migration of those animals into the catchment .

We established a range of values to define the asymptote (K) of the population growth curve from the territory capacity modelling (Section 2.4). Across this range (increments of $n = 1$), we calculated at what point the predictions, from the Poisson GLM of the fitted data, reach half that of the limiting value ($K/2$). This provides an estimate for the inflection point of the logistic curve; when 50% of available territories are occupied, the population becomes self-limiting and the absolute growth rate (AGR) starts declining (Paine et al., 2012). Then, we calculated the time taken to reach this value and multiplied by 2, giving us the approximate time to reach the asymptote. This value was joined to the observed territory count data and a nonlinear least squares model was fitted in R with the nls function using the SSlogis self-start model (R Core Team, 2020) to determine the logistic function. This model was fit across the full territory capacity range and 95% confidence intervals (CI) were derived using the investr package (Greenwell & Kabban, 2014). To incorporate the uncertainty related to territory capacity predictions, all 63 models across the territory capacity range were averaged and the most extreme confidence limits were retained.

2.6 | Simulating territory removal management

The most direct and impactful way to reduce beaver population size is by removing animals from the catchment either by translocation or culling (Parker & Rosell, 2014). Whilst such management approaches are considered as 'last-resort' options and were never implemented during the 5-year River Otter trial (Brazier, et al., 2020), they have been utilized elsewhere (Campbell-Palmer et al., 2021; Parker & Rosell, 2014) and are thus important to understand in terms of their impact on populations. To test the effect of removing beaver territories on population dynamics, a range of management scenarios were applied with two variables: the year that territory removal begins (2022, 2026 and 2030) and the number of territories removed annually (between 2 and 8). From the start time of simulated management, territories were removed iteratively from the predicted territory counts providing a projection of population change under a range of theoretical management scenarios. This simulation assumes that entire territories are removed which in practice may be challenging but this simplified scenario still provides helpful insight into beaver population control. A larger matrix of simulations is provided in Supporting Information S6.

3 | RESULTS

3.1 | Quantifying numbers of territories

3.1.1 | Field survey

The total number of feeding signs increased from 398, in the winter of 2015–2016, to 871 in 2020–2021 (Figures 2 and 3). High-impact feeding signs (felled/incised trees with stem diameter >20 cm) increased in number from 6, in 2015–2016, to 41 in 2020–2021. Changes in the trends of recorded feeding signs are presented in Figure 2, which shows increases in the number of observed woody foraging signs across effort classes and an increase in the estimated number of territories.

The distribution of feeding signs expanded rapidly over the survey period; initially, the majority of foraging activity was located in the lower reaches of the River Otter but feeding signs were soon found along smaller streams and ditches as habitat on the main rivers became occupied (Figure 3).

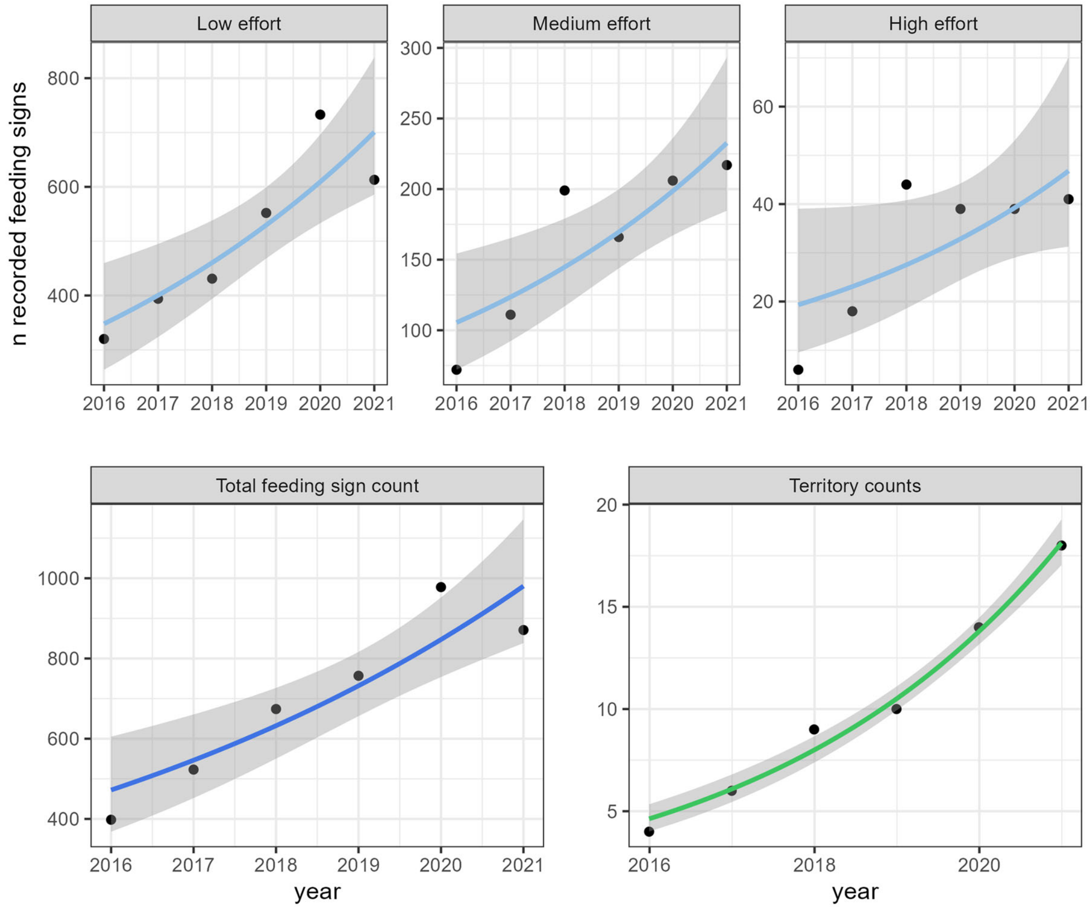

FIGURE 2 Change in the number of recorded feeding signs for all feeding effort classes (top); the total number of feeding signs (bottom left) and the number of territories (bottom right). For all plots, the trend is described by a Poisson general linear model (with log link) and shaded standard errors

3.1.2 | Semi-automated territory detection

Kernel density mapping, shown in Figure 4, revealed how the intensity of foraging has increased substantially over the survey period. The frequency of 'hotspots' increased over time, indicating that the number of central foraging places has increased. As the density of signs increases, the gaps between areas of activity decrease.

The estimated number of territories in the River Otter catchment increased from four in 2015–2016, to 18 in 2020–2021 (Figures 2, 5, and 7).

3.2 | Modelling the ecological territory capacity

Ecological carrying capacity was estimated to be between 120 and 183 territories. For illustration, we present two examples from the simulation in Figure 6 which includes a scenario for the higher (Figure 6a) and lower (Figure 6b) BFI thresholds. The territory counts generated in these examples do not conform exactly to the maximum and minimum determined from the overall simulation because each scenario was generated at random.

3.3 | Predicting future population growth

Modelling future population dynamics using logistic curves (Figure 7) showed that beaver populations are expected to reach ecological carrying capacity in the River Otter catchment between 2030 and 2057: 95% CI [2028, ∞]. Therefore, from the time of their release, it will take approximately 21–50 years to reach capacity. These modelled data can also be used to evaluate the population dynamics in more depth, for example, by inspecting the changing rates of population expansion and rates of territory formation (Hartman, 1994); for an assessment of these factors, see Supporting Information S7.

Theoretical territory removal scenarios, presented in Figure 8, show management approaches can have a very wide range of impacts depending on the intensity of territory removal and the timing of such

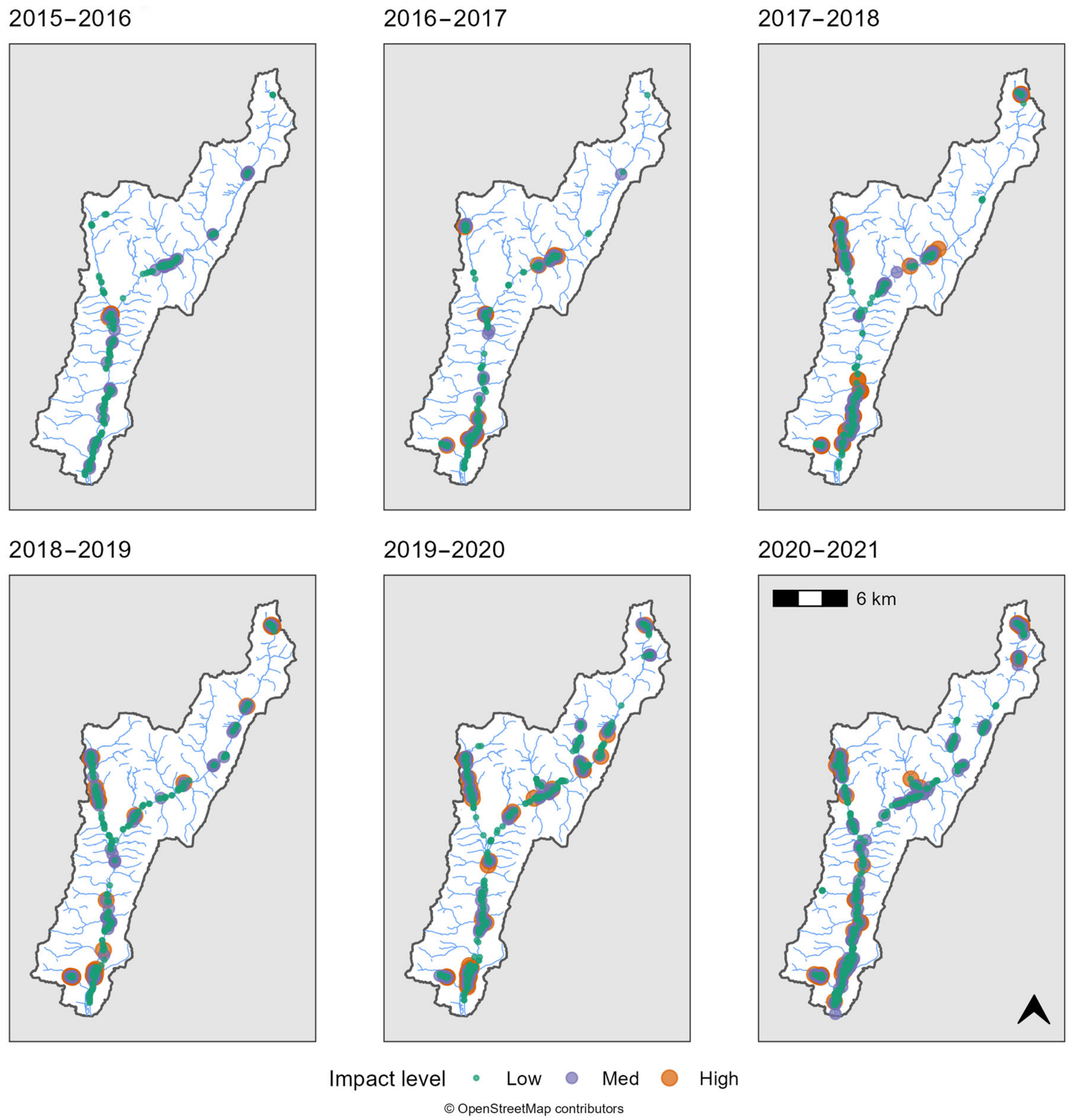

FIGURE 3 Plot of feeding signs recorded in the River Otter catchment each survey year. Impact levels approximate the time/energy expenditure for each sign. A description of feeding sign classifications is given in Table 1

interventions (Supporting Information S6 presents a more extensive scenario matrix). The uncertainty associated with these predictions is also substantial. For example, Figure 8 shows that in most scenarios, there is a high possibility that the population will decline and become unviable; if three territories were to be removed annually beginning in 2022, this could lead to either the loss of the population or meeting predicted capacity. Indeed, only five of the scenarios presented in Figure 8 avoid the risk of population collapse. These scenarios also highlight the potentially rapid decline of the population if concerted population control efforts are enacted in the shorter term, for example, where >3 territories/year are removed.

4 | DISCUSSION

4.1 | Quantifying numbers of territories

In this study, we have estimated the number of beaver territories present within the River Otter catchment between 2015 and 2021. In combination with a method for estimating ecological territory carrying capacity, we have made projections for population growth, up to its capacity, and simulated the impact of a range of territory removal management scenarios on population dynamics.

This work demonstrates the value of carrying out low-cost field sign surveys to monitor beaver populations. We present a methodology that builds upon other similar surveys to reveal important landscape-

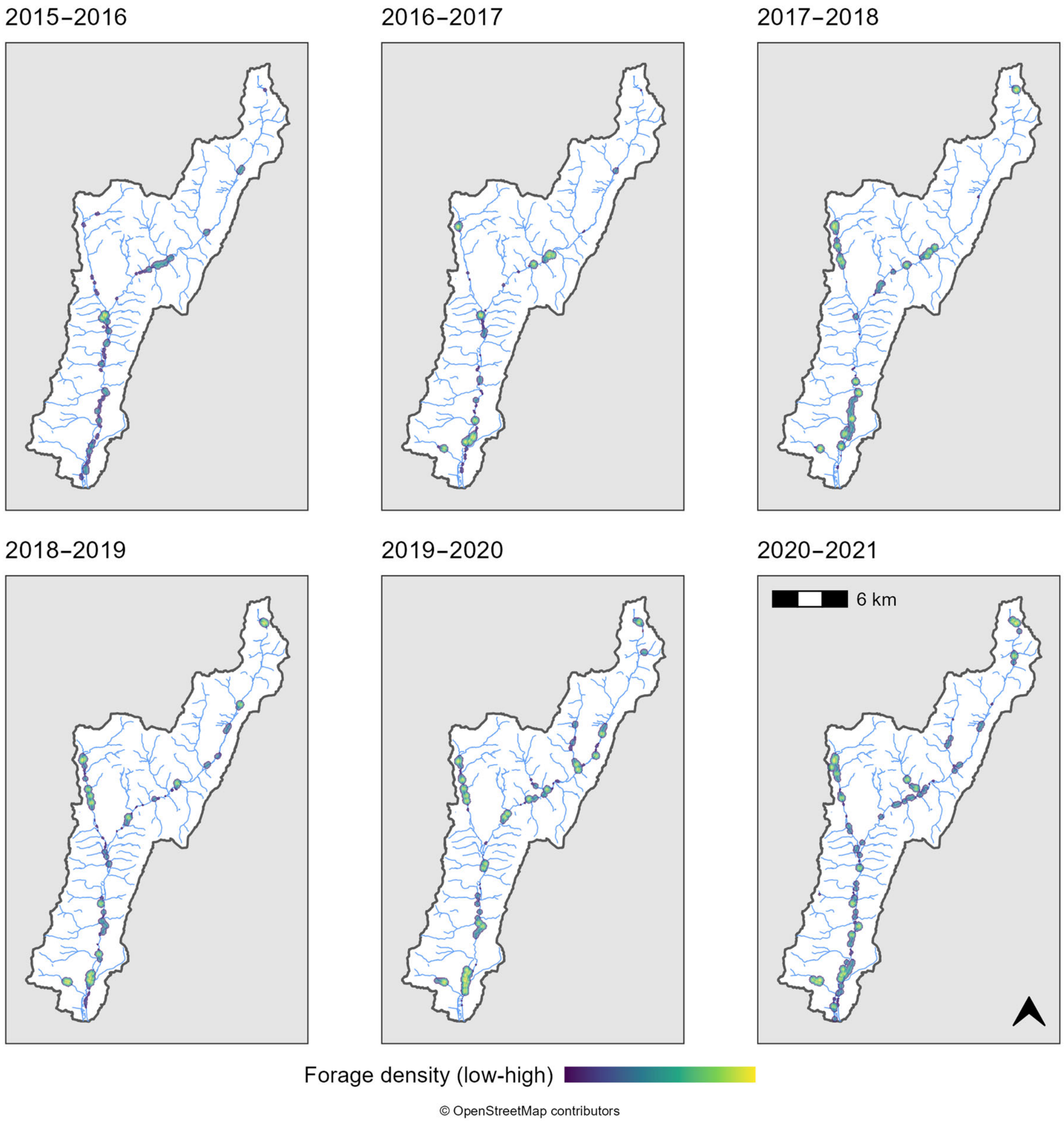

FIGURE 4 Kernel density of foraging signs for each survey year. Regions are inflated by using a kernel bandwidth of 250 m, rather than the 200 m used for the analysis, for data visualization purposes. This is required to better represent areas of activity but is inappropriate for analysis as it risks the merging of coincident territories during the automated territory detection step. For the 200 m kernel bandwidth image, please see Supporting Information S2. The colour scale presented is the log10 transformation of the feeding density weighted by feeding effort class—exact values are less important than relative difference which is considered here with a simplified linguistic scale

scale understanding of beaver population dynamics (Campbell-Palmer et al., 2021; Fustec et al., 2001; John & Kostkan, 2009). The approach may provide less information and lower levels of inference than bio-logging (Arjo et al., 2008; Graf, Hochreiter, et al., 2016; Graf, Mayer, et al., 2016); however, the costs related to bio-logging may be prohibitive. Arjo et al. (2008) and Graf, Hochreiter, et al. (2016) used transmitters costing c. €160 each. These costs do not include trapping/tracking time or licensing and there are also implications for animal welfare to consider (Campbell-Palmer & Rosell, 2015). Therefore, we suggest that the approach detailed herein, which can provide spatial information across whole catchment scales, demonstrates considerable value due to its scalability and relatively low cost, which required c. 10–15 person days of survey for each year. Surveys are likely to become more difficult and time consuming with increasing catchment size and remoteness, where good road/vehicle access to a river system increases efficiency (Campbell-Palmer et al., 2021). Such approaches will be required as wild beaver populations continue to expand across GB and Europe (Campbell-Palmer et al., 2021; Halley et al., 2021)

Critical to the success of these field sign surveys is their standardization; in this study, methods were identically replicated each year affording direct comparison of feeding density and therefore confi-

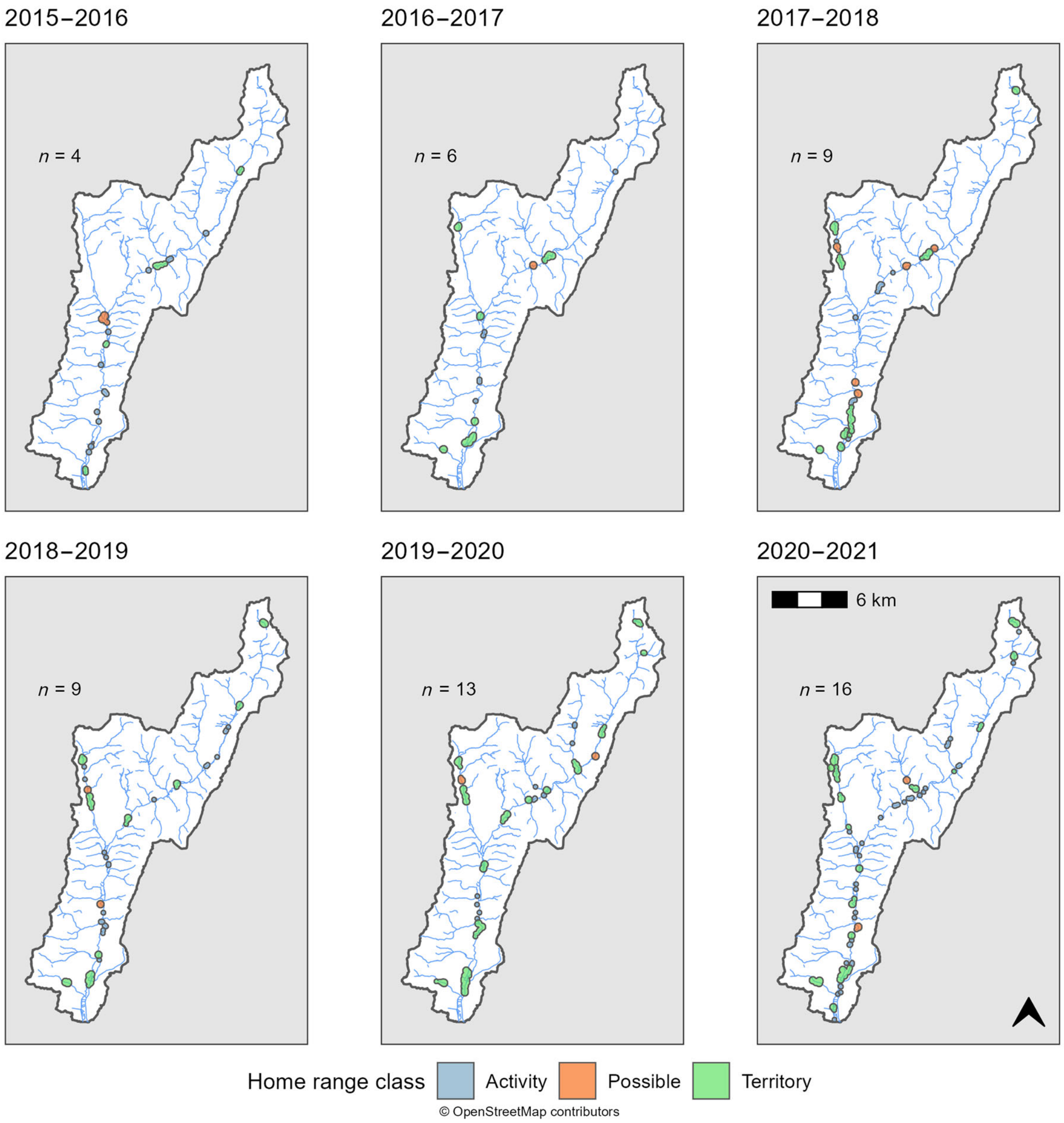

FIGURE 5 Territory areas and classifications for each survey year—derived from the semi-automated territory detection. Regions are inflated by buffering territory/activity areas by 100 m for data visualization purposes. The image without the additional buffer is provided in Supporting Information S3. The number of activity regions classified as territories is given in each panel as *n*

dence in the interpretation of derived kernel density maps (Figure 4) and semi-automated territory estimation (Figure 5). We propose this method as a standardized way to monitor beaver population change which has potential to increase understanding of beaver population distributions and habitat selection if adopted more broadly. Where population sizes and ranges increase considerably, it may not be possible to record individual tree-level impacts. In this case, the methods may be adapted to consider beaver impacts at the reach scale (Campbell-Palmer et al., 2021). The flexibility in the kernel density methods and subsequent semi-automated territory detection allow for adjustments to model parameterization that can accommodate variations in survey methods; however, a consistent method is required across each epoch of the survey to robustly evaluate change between time periods.

There are, of course, some limitations that should be discussed with the use of woody feeding sign surveys. As generalists, beavers feed on a variety of vegetation types. In British and Northern European populations, it is typical for beaver to graze on some herbaceous vegetation during the summer months; however, it is often challenging to identify this feeding behaviour. Access to river banks during the summer, when vegetation is typically at peak biomass, is also difficult. We therefore carried out surveys during winter, when feeding is predominantly on woody material. The presence of woody habitat will therefore strongly impact the distribution of feeding signs and, in turn, inference of territory locations. This is an important but not

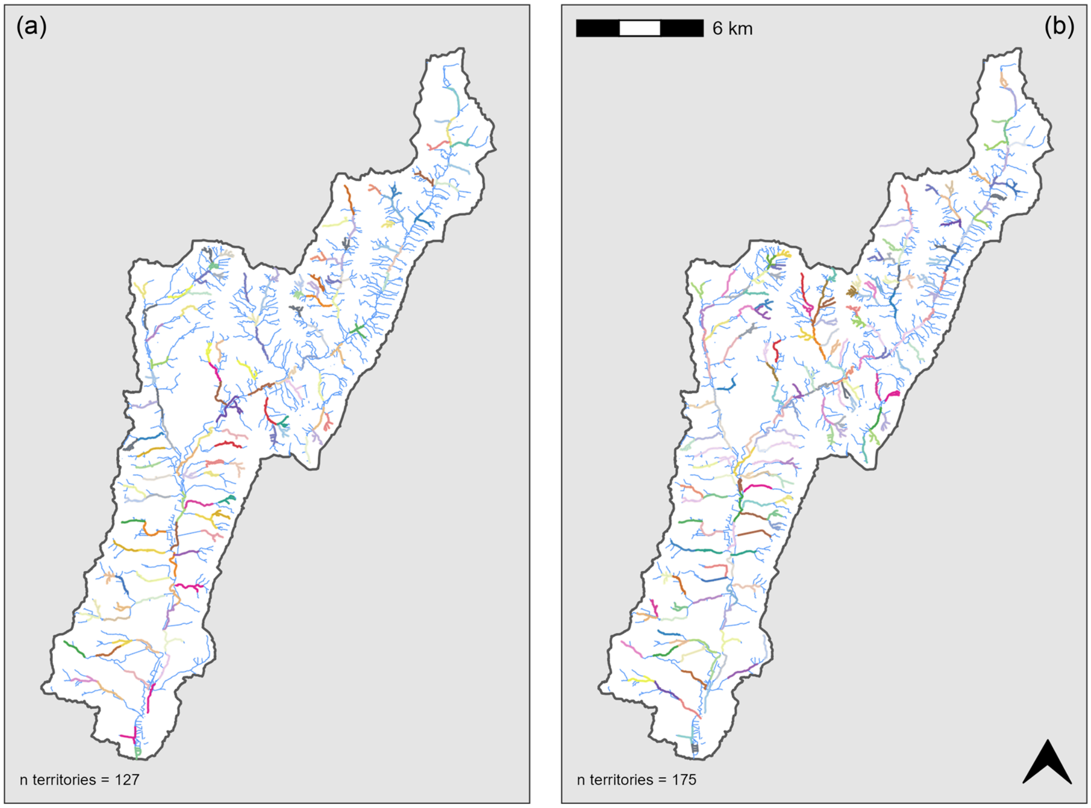

FIGURE 6 Example scenarios from the territory capacity simulation. Coloured polygon regions denote unique territory areas; their colours are randomly assigned to differentiate between coincident regions. Panel a is derived using the higher minimum Beaver Forage Index (BFI) threshold of 3.0; panel b uses a minimum BFI threshold of 1.3. We can interpret these limits as the upper and lower estimates of the minimum forage quality required to sustain a territory

prohibitive issue because it is widely accepted that woody habitat is extremely important for beavers and they will preferentially seek out these locations (Graham et al., 2020; Macfarlane et al., 2017; Vorel et al., 2015; Zwolicki et al., 2019). As beaver populations grow, the density of woody feeding signs increases dramatically, as demonstrated in Figure 4; therefore, it becomes more challenging to differentiate between neighbouring territories as they begin to border each other (Campbell et al., 2005; Graf, Mayer, et al., 2016). This is why we adopted a semi-automated approach which allowed for expert oversight/intervention to evaluate the accuracy of automated predictions. In this study, we did not consider territorial signs such as scent mounds because only very few were located. As populations increase in size and territory marking becomes more common (Rosell & Nolet, 1997), scent mounds could be used to further improve the distinction between neighbouring territories, as demonstrated by Campbell et al. (2005).

Not considered in this study are the potential impacts of the population's genetic composition and future disease/environmental events. Campbell-Palmer et al. (2020) show that the River Otter's beaver population is closely related which could have repercussions for its long-term viability and indeed its resilience to varying environmental factors. Scenario based modelling which considers such genetic and environmental risk factors is an important next step in predicting future beaver population dynamics.

4.2 | Predicting ecological territory capacity

There are numerous examples of models, both statistical (Barták et al., 2013; Hartman, 1994; Korablev et al., 2011; Šimůnková & Vorel, 2015) and mechanistic (Petrosyan et al., 2013, 2016, 2019), which describe beaver population dynamics. However, these examples rely on long-term datasets where populations have already reached or are nearing capacity. For example, Petrosyan et al. (2016, 2013) demonstrate the value of mechanistic modelling approaches for beaver in Russia, providing a framework to derive powerful understanding of population dynamics. In particular, these models capture the short-term oscillatory nature of population change. However, such a model could not be applied in this (and indeed most) instance(s) where many input variables are unknown and long-term calibration data are absent. Consequently, we have presented a simplified statistical approach to predict average change in the beaver population. With further

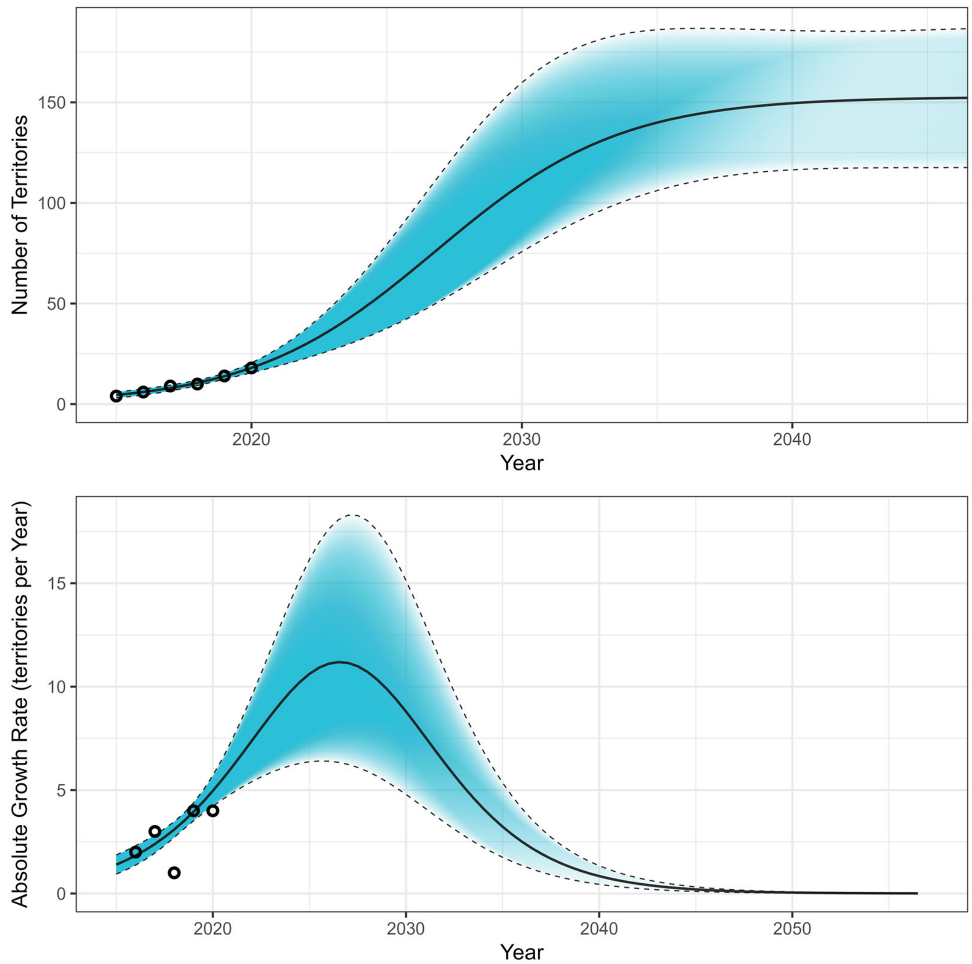

FIGURE 7 Top panel shows the beaver population growth model for the River Otter catchment. The bottom panel shows the absolute growth rate over time. Circular points indicate observed territory counts derived from field surveys, solid lines represent the mean, and dashed lines represent the 95% confidence intervals. These models are a composite of the 63 models with varying asymptote values derived from the ecological territory carrying capacity range (120–183). Darker shading indicates greater agreement across the models

work and continued monitoring of the population, we would hope to incorporate the level of complexity demonstrated by Petrosyan et al. (2016, 2013) to reduce uncertainty in model predictions. However, our approach was necessary in order to inform decision-making and management of a rapidly expanding species now, as opposed to decades later when the empirical data are long term.

4.3 | Modelling future population growth

Though the projections of the population models presented herein extend well beyond our current empirical observations, the projected densities compare favourably with other studies (Barták et al., 2013; Korablev et al., 2011; Šimůnková & Vorel, 2015). A comparison of observed and modelled estimates of beaver territory density is presented in Table 2. Most notably, Hartman (2003) recorded territory densities of up to 0.6 km^2 as a maximum in Sweden; this value intersects the predictions of this study with the maximum territory density estimates of 0.50–0.77 km^2 (Supporting Information S7). Barták et al. (2013) conducted a detailed survey of beaver populations and found the largest density to exist in northern Czech Republic. Here, the densities were between 0.2 and 0.35 territories/km; again intersecting our own predictions for the River Otter of between 0.2 and 0.31 territories/km.

4.4 | Social versus ecological carrying capacity

It should be noted that alongside the ecological carrying capacity that has been modelled herein, there will also be a social carrying capacity which might be considered as a socially acceptable/tolerable, or even optimal (from a human perspective) number of beaver territories

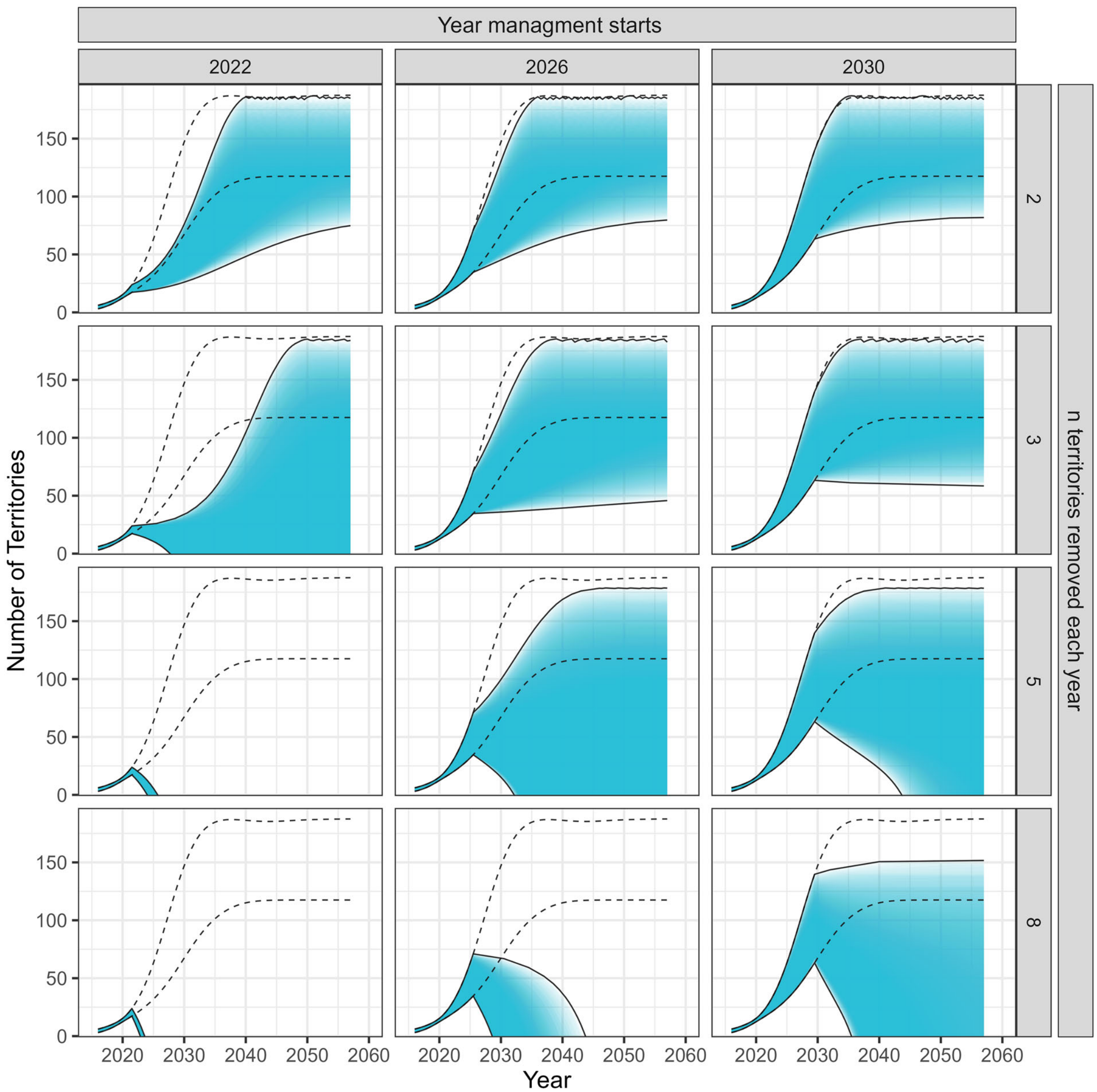

FIGURE 8 Facet plot depicting the impact of a range of theoretical management scenarios upon territory dynamics in the River Otter catchment. These examples show the impact of territory removal (i.e. by culling or translocation) when started on different years and for a range of management intensities. Seven of the 12 scenarios could result in population collapse. A larger matrix of management scenarios is presented in Supporting Information S6. Solid lines represent the upper and lower 95% confidence intervals of the model; dashed lines represent the original model without consideration of territory removal. These models are each a composite of the 63 models with varying asymptote values derived from the ecological territory carrying capacity range (120–183). Darker shading indicates greater agreement across the models. A corresponding figure presenting the impact of territory removal on absolute growth rates is provided in Supporting Information S8

within any given catchment. This is likely to be far lower than the projected ecological carrying capacity as it will reflect the impact of beaver management approaches in areas where beavers might cause conflict. It is extremely hard to predict at what point this social carrying capacity will be reached and how it is likely to vary spatially in response to conservation, species protection, and the specifics of land management within different catchments. It is critical to note that the most desirable beaver management strategy, and one that requires least management effort in the long term, is promoting increased and renewed coexistence (Auster et al., 2021a, 2021b) and thus, reducing conflict (Frank, 2016). Renewed coexistence between beavers and humans is preferable because it is frequently observed that, where whole territories are removed through translocation or lethal control, the habitat is rapidly reoccupied by this territorial species necessitating repeated management (Campbell-Palmer et al., 2016). However, in intensively managed anthropogenically altered environments, active population

TABLE 2 Maximum territory density for the River Otter, based on modelled territory capacity estimates compared with either maximum observed (*) or modelled (**) territory density derived from other work

Density description	River Otter	Hartman (1994)*	Korablev et al. (2011)*	Barták et al. (2013)*	Parker and Rosell (2014)*	Šimůnková and Vorel (2015)*	Petrosyan et al. (2016)**
By channel length (terr./km)	0.2–0.31	–	0.14	0.2–0.35	0.26	0.55	–
By catchment area (terr./km^2)	0.5–0.77	0.6	0.12	–	–	–	0.99–1.15

Note: These various studies were carried out with different methods and are from a range of geographic regions with varying habitat and management/hunting practices and therefore are not directly comparable but provide context to predictions for the River Otter catchment.

management is inevitable at some stage. Therefore, we have modelled a number of territory removal scenarios where a given number of animals are removed from the catchment each year beginning on a range of future dates (Figure 8). Here, we see that the removal of whole territories can have wide ranging effects on projected outcomes, depending on the intensity and timing of the removal. Most notable is the prediction that for 7 of the 12 territory removal scenarios, there is the potential for population collapse. Although there is strong evidence to show that beavers can recover from over hunting (Parker & Rosell, 2014), our findings demonstrate how much care should be taken when considering the translocation or culling of beavers in establishing populations. Indeed, any population management must also align with IUCN guidelines which argue for the protection of species such as beavers under the Habitats Directive.

In reality, no management scheme is fixed in time and therefore the examples presented are theoretical, but this further emphasizes the need to understand the number of territories within a catchment enabling the continued adjustment of management strategies. With an understanding of the territory capacity, we can make reasonable predictions as to the projected rate of population growth and therefore the potential impacts of population management in the long term and with consideration of the viability of reintroduced populations of a European Protected Species, such as the beaver.

5 | CONCLUSIONS

This study demonstrates the value of using standardized woody feeding sign surveys for monitoring beaver population dynamics. These surveys can be used to describe the current distribution of beaver activity and enable the estimation of total territory numbers. Over multiple years, these data can then inform our understanding of population change. In combination with estimates for ecological territory carrying capacity, we can also predict future population expansion under varying territory removal management scenarios using the logistic growth model. This understanding provides important information for beaver management; the timing and intensity of any translocation or lethal control can have wide ranging and uncertain impacts on population density or viability. Therefore, population management should be carried out very cautiously, especially whilst population densities are low and co-existence strategies, which are likely to be most effective, have not yet been exhausted.

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AUTHOR CONTRIBUTIONS

Hugh Graham, Alan Puttock, Roisin Campbell-Palmer, Richard Brazier, Karen Anderson and Mark Elliott developed the experimental design. Jake Chant, Mark Elliott, Roisin Campbell-Palmer and Hugh Graham carried out beaver sign surveys. Hugh Graham and Alan Puttock undertook data processing and analysis. Hugh Graham led the writing of the manuscript. Richard Brazier secured the funding for the research. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

At the time of writing, Mark Elliott and Jake Chant were employed by Devon Wildlife Trust and were involved with the management and delivery of the River Otter Beaver Trial. Roisin Campbell-Palmer was employed by Devon Wildlife Trust to carry out beaver population health monitoring as a private consultant. Richard Brazier, Alan Puttock and Hugh Graham were voluntary members of the River Otter Beaver Trial Science and Evidence Forum.

DATA AVAILABILITY STATEMENT

All data and code to support the reproduction of this work are available from https://doi.org/10.5281/zenodo.6818269 (Graham, 2021). Due to licensing restrictions, the Beaver Forage and Dam Capacity data are assigned to an open rivers dataset (OS Open River Network) rather than the more detailed OS Mater Map which was used for the manuscript. Due to the reduced network detail, territory capacity estimates differ from those stated in this manuscript. If you wish to access the Master Map data for this work, please contact the lead author and the data can be provided subject to licensing constraints.

PEER REVIEW

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SUPPORTING INFORMATION

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

Supplementary Information

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Chapter 6. Synthesis and Conclusions

In this chapter, sections 6.1-6.4 synthesise the key findings presented in the data chapters (2-5), summarising the management implications and discussing future research needs arising from each chapter. In section 6.5, the combined understanding from these chapters is discussed in relation to the overall management implications of beavers in a changed British landscape. Section 6.6. details the research impact of this work with final concluding remarks presented in section 6.7.

6.1 Chapter 2 - beaver pond complexes enhance floodplain processes, attenuating peak flows.

In Chapter 2 we showed that, following the construction of a beaver pond complex, there was a significant peak flow attenuation effect during storm events and that this effect increased with increasing storm magnitude. Hydrological event response geometry changed substantially after the pond complex was built; with an increase in the lag times (time from peak rainfall to peak flow) and a decline in the rising limb gradient. These changes were not observed in the neighbouring control catchment. That we observed increasing attenuation with increasing event magnitude is significant because it strongly indicates that storm water storage continues to increase even when the pond is full. We suggest that, in locations, such as the study site with its low gradient valley profile, stormwater storage is likely to accrue as transient floodplain storage due to an increase in the active floodplain area.

These findings are important in the context of the wider literature and debate surrounding natural flood management because the efficacy of beaver wetlands in attenuating flood flows has been challenged (though not formally published). The argument for such suggestions is that beaver ponds are relatively small and are almost always full, especially during the wet season. As a consequence, there is typically little to no freeboard in an actively maintained beaver pond (Larsen et al., 2021); therefore the ponds do not function like human-made offline storage ponds (Lockwood et al., 2022) . This assertion neglects to consider that the fundamental mechanisms controlling flow attenuation at beaver wetlands are not the ponds themselves but the wider wetland which substantially increases the surface area of active floodplain, during a flow event (Westbrook et al., 2006). It is widely accepted that floodplain activation is a key method of flood alleviation (Ellis et al., 2021; Lane, 2017; Norbury et al., 2021) and we suggest that it is the reduction of the flow threshold required to activate the floodplain which is the key driver of flow attenuation. The data analysis presented in this chapter is firmly supported by what is fast becoming a substantial body of literature demonstrating the significant effect of beaver wetlands on flood flows (Grygoruk and Nowak, 2014; Nyssen et al., 2011; Puttock et al., 2021, 2017; Westbrook et al., 2020, 2006; Woo and Waddington, 1990).

The use of Natural Flood Management (NFM) and working with natural processes to address the challenges of flooding has gained considerable interest, particularly in the UK (Ngai et al., 2021). The key difference between designed NFM work and beaver wetlands is the greater level of control that is maintained with a human-engineered project; the location and stakeholders involved are pre-arranged and the outcomes of the project are also more predictable. However, this work comes with maintenance costs (Ellis et al., 2021). Conversely, beavers are likely to build wetlands in a less predictable manner but will maintain structures for longer and possibly at a greater density than their man-made counterparts. Crucially though, there is no need to debate or compare the relative value of NFM vs. beaver wetlands because the two approaches are wholly compatible and even complementary. Beavers are now well known to adopt woody fence-like structures known as beaver dam analogues as *starter dams* which are less likely to breach in degraded/incised systems (Bouwes et al., 2016; Pollock et al., 2014, 2007). Indeed there has been extensive research to establish where these structures should be constructed to align with natural beaver behaviour (Macfarlane et al., 2017). NFM may therefore help to enhance habitats locally to support the reestablishment of beaver territories where degraded morphology makes this a challenging.

Where beavers build dams in locations, such as Budleigh brook (chapter 2 study site), that enable the activation of floodplain processes, their impacts should be tolerated and perhaps even further enhanced with NFM because of the likely benefits for both biodiversity and flood resilience (Brazier et al., 2020b). Whilst this will not always be possible, we should strive for a management system which supports landowners to accommodate the return of beavers and river systems that function more naturally, delivering pronounced ecosystem service benefits (Brazier et al., 2020b; Larsen et al., 2021).

6.1.1 Chapter 2 - Future Research

With the ability to model where damming will likely occur (Dittbrenner et al., 2018; Graham et al., 2020; Macfarlane et al., 2017), we can combine this understanding with continued empirical hydrological monitoring to begin investigating the catchment impact of beaver upon flow regimes using a range of hydrological modelling approaches. With a growing database of beaver-impacted sites with continuous hydrological monitoring, the next step is to build hydraulic and hydrological models that can be trained on these empirical data. With these derived models, it will be possible to estimate impacts to flows at and above the highest measured flow events and for locations not yet occupied by beavers. This is important because, as demonstrated in Chapter 2, the statistical models that describe the peak-flow ~ rainfall relationship do not provide sufficient confidence for extreme peak flows, >97th percentile. Once this is achieved for multiple sites, it will then be necessary to model statistically how environmental factors such as channel slope, cross-valley gradient, land cover, and hydrological regime influence the rainfall runoff relationship. Then, dam building scenarios may be generated, and the attenuation effect of each dam estimated from environmental factors. These dams, and their relative influence on flow, could be included within rainfall runoff models to estimate the cumulative effect of all dams on hydrological function. This research would present crucial information in terms of the potential contribution of beaver wetlands to natural flood management strategies; potentially influencing our current dependence on hard engineering interventions to mitigate flooding impacts.

There are clearly some important and interesting parallels between NFM and beaver wetlands in their ability to modulate hydrological regimes. What is required in the future is some level of standardisation in the reporting and measurement of flow alterations through, for example, the reporting of consistent metrics across projects and by adopting methods that can be interpreted across a variety of scales and landscapes so that their findings can be discussed in relation to future projects. We have presented both novel approaches and more traditional analyses that may help to facilitate comparison across both NFM projects and beaver wetlands. However, there is a requirement for researchers to communicate and consolidate around the best practices in this field.

6.2 Chapter 3 - Beaver foraging increases canopy structure heterogeneity.

Chapter 3 demonstrates that beavers have a statistically significant effect on riparian woodland canopy structure. By felling trees, beavers open the canopy in a way that is patchy and non-uniform. The riparian canopy, in areas without beaver foraging, was comparatively more stable and underwent less change. Whilst declines in canopy elevation were pronounced in beaver impacted areas, there were also subtle but notable increases, indicating that canopy height change was not only characterised by tree felling. This canopy growth was in line with other studies which report enhanced primary productivity in beaver wetlands (Fairfax and Small, 2018; Jones et al., 2009; Peinetti et al., 2009) and may have resulted from increased water availability due to wetland creation, reduced crown competition and/or increased light penetration.

This study also presents robust methods for change detection using drone-based SfM in complex vegetated landscapes. We demonstrate the importance of adopting robust, spatially explicit error propagation when calculating the difference between elevation models from different epochs. The implication of this finding is that such cost-effective monitoring techniques may be used more widely across vegetated systems to detect change. However, careful thought is required when designing these types of surveys to ensure that appropriate error propagation and survey methods are adopted so that the levels of precision and accuracy, required to detect a given environmental response, can be delivered.

6.2.1 Chapter 3 - Future Research

The impact of beaver on vegetation will be spatially variable. In Chapter 3, we investigated the structural impacts of beaver in a semi-natural riparian woodland over a one-year period. It is important that, with expanding beaver populations across Great Britain, the spatial variation in beaver impacts on woodlands with a variety of species compositions are investigated. Therefore there is a need to continue this line of enquiry across a range of riparian environments over longer time periods to establish a strong empirical basis for managing beavers in riparian woodland.

There is now a considerable body of literature that describes the preference of beavers towards different tree species and their impact on riparian vegetation community composition (Donkor and Fryxell, 1999; Goryainova et al., 2014; Nolet et al., 1994; Peinetti et al., 2009). By combining this knowledge base with continued surveys of structural and functional change in riparian woodland, affected by beaver, it is possible to begin exploring the landscape scale impact of beaver foraging. To do so would also require data describing the structure and species composition of riparian woodland at a relevant scale. Recently, there have been significant advances in the availability of Light Detection and Ranging (LiDAR) data describing the physical structure of riparian vegetation in GB (e.g. Environment Agency, 2022). This, in combination with optical and radar remote sensing data, can facilitate the generation of a dataset describing the spatial classification of riparian tree species (Breidenbach et al., 2021) in addition to structural properties such as canopy height and density. Lastly, with the information gained from chapter 4 of this thesis, we can combine all these data/knowledge sources to untangle the landscape scale effect of beavers on riparian vegetation.

Such an analysis could prove vital for researchers concerned with the importance of woody riparian habitats for river channel shading and the potential knock-on impacts for stream temperatures, which are rising globally (van Vliet et al., 2013). River shading has been proposed as a crucial means of buffering high temperatures during drought periods (Dugdale et al., 2020; Feld et al., 2018), therefore, in regions with low vegetation cover, isolated trees may be disproportionately valuable. A landscape scale understanding of these habitats and their interaction with beaver foraging could form a crucial management tool in the future if beaver populations continue to expand.

From a technical perspective, chapter 3 outlines some novel applications for SfM change detection in vegetated systems. Further research in this domain would be extremely valuable. Drone, sensor and SfM technology is rapidly evolving field with improved software and hardware becoming available at an increasingly affordable price point. Therefore, it is right that the methods explored in this chapter be applied with more up to date sensor/drone hardware and the latest software to update our understanding of the most appropriate change detection methods across a diversity of vegetated landscapes. However, worthy of discussion is the requirement for such fine scale understanding of vegetation structure change in beaver landscapes, a tree census or photographic documentation may provide a suitable level of understanding from the perspective of beaver management/monitoring – this will of course depend on the desired scale and precision of the analysis but should be considered carefully by future researchers.

6.3 Chapter 4 - Modelling beaver habitat and dam capacity.

The paper presented in Chapter 4 demonstrates the ability to predict, with known confidence, the distribution and suitability of beaver forage habitat, the density of dams that could be supported and the likely number of dams that may occur across whole catchments. Building on a modelling framework originally designed for North American landscapes, we were able to develop an approach that generalises across spatially disparate regions with variable land uses and climatic conditions. This was achievable due to the use of fuzzy inference which enables a pragmatic, mathematically based way to evaluate complex systems that are characterised by substantial uncertainty.

The importance of this research is twofold: It provides an immediately useful tool for policy makers and managers to inform decision making but also enables the prediction of potential impacts and their distribution in the future. The ability to forecast in this way, with a strong understanding of uncertainty, will help to inform management strategies to maximise beaver benefits and plan for potential conflicts in heavily modified anthropogenic environments. Further, this model forms a missing link between site-scale understanding of structural and functional impacts and the landscape scale effect of beaver on natural processes.

This paper sits alongside what is now a large body of work that aims to predict the distribution of beaver habitat and their impacts (Barnes and Mallik, 1997; Curtis and Jensen, 2004; Dittbrenner et al., 2018; Hartman, 1996; Macfarlane et al., 2017; McComb et al., 1990; Pinto et al., 2009; Stoll and Westbrook, 2020; Stringer et al., 2018; Suzuki and McComb, 1998; Swinnen et al., 2019, 2017). Despite the large availability of such methods, there is still a challenge that relates to the generalisability of these methods across different ecosystems (Baldwin, 2013; Barnes and Mallik, 1997). Macfarlane et al. (2017) proposed one of the best solutions to this challenge, hence why we adopted these methods as a starting point for our own work in GB. However, core to this modelling approach are the expert-based rules that control the fuzzy-inference system; we must consider the possibility that our expert knowledge is imperfect and therefore we must also consider how we might build the infrastructure required to update our prior knowledge in this domain. I propose a solution below.

6.3.1 Chapter 4 - Future Research

Datasets now exist across GB (Brazier et al., 2020a; Campbell-Palmer et al., 2020; Graham et al., 2022), Europe (Fustec et al., 2003, 2001; Hartman, 1996; Hartman and Tornlov, 2006; Swinnen et al., 2017; Vorel et al., 2015), Russia (Danilov, 1995; Danilov and Fyodorov, 2015; Goryainova et al., 2014; Petrosyan et al., 2019, 2016) and North America (Hafen et al., 2020; Macfarlane et al., 2017) that describe the geographic location of beaver dams and other signs, such as feeding or lodges. Indeed, there are also likely to be many more datasets collected by local or national agencies that are not in the public domain. The compilation of these data to form a publicly available and open-source database across geographic regions would be invaluable for several reasons. Firstly, it offers the opportunity to update our priors regarding how beavers behave across different habitats and climatic zones – all expert knowledge is biased to our local experiences and there is still so much to learn from researchers and mangers across the full extent of the beaver's range. The availability of a much larger volume of data also opens up the opportunity to reduce the reliance on expert opinion to define rules-based systems in favour of modern machine learning approaches (Peters et al., 2014). With the availability of a global beaver dam impacts database it will become possible to deploy a greater range of models to predict beaver habitat and impacts that are less reliant on expert opinion and more reliant on data. The availability of such data also facilitates the standardisation of methods and modelling approaches across both North American and Eurasian landscapes which will help to consolidate the understanding gained from the different species in different landscapes.

Indeed, with the availability of global remote sensing and hydrological datasets, there is an opportunity to estimate beaver habitat and dam capacity at the continental scale, this research could begin to unravel how much we have really lost through the long-term persecution of this species (Halley et al., 2020) and help to reinforce the importance of supporting the expansion of this species at scale both in Europe and North America.

The BFI and BDC models, presented in Chapter 4, already provide valuable management tools. However, there is an opportunity to enhance the framework by considering where human-beaver conflicts might occur and where this conflict might be most costly. Importantly, potential economic estimates of the costs should be considered to establish an impartial metric on which to prioritise the need for management. For example, the cost of repairing a damaged or flooded road might greatly outweigh the inundation of a field and therefore such locations could be prioritised for regular inspection to avoid costly damage and conflict. This model could be used to build an inventory of priority/high risk locations and identify "easy win" sites that offer opportunities for beaver reintroduction in areas with a low risk of conflict.

6.4 Chapter 5 Beaver Population change during the ROBT and predicted future population growth.

The number of beaver territories in the River Otter catchment has increased from an estimated four to eighteen between 2015 and 2021. Territory counts were obtained using a standardised field sign survey method, which adopts a pragmatic and simple means of mapping the distribution of beaver impacts at the catchment scale. This empirical field sign data was used alongside a semi-automated approach to make robust estimates of territory numbers over time. This generalisable technique serves as a useful method which could help to monitor beaver population density and distribution into the future. We modelled the maximum number of beaver territories that could be supported within the catchment; this was estimated between 120 and 183. Using the observed rate of population growth and the estimated territory carrying capacity range, we adopted the logistic growth model to predict future population change under a range of lethal control/translocation management scenarios. We show that removing beaver territories can lead to very uncertain impacts on the population, in some cases even leading to population collapse. It is acknowledged that a socially-acceptable carrying capacity will be reached sooner than the estimated carrying capacity and therefore population management will be required at some stage to regulate numbers. However, great care should be taken to ensure the viability of the population is not compromised. Regular field sign surveys should be used to support decision makers to ensure that any management is proportionate, conservative and in line with IUCN guidelines (IUCN and SSC, 2013; Larsen et al., 2021).

The findings of this study are important from the perspective of beaver population management; it enables forward planning, the allocation of resources and could help to inform future translocation, for example. Further, the methods are transferable and offer a low-cost approach for understanding how wild beaver populations may utilise river systems as populations expand.

The simulation of beaver population dynamics presented herein is the most detailed carried out in GB. Unlike previous work (South et al., 2000) that models population movement at a coarse gridded cell level across larger spatial extents, the approach we have taken enables a much finer grain of insight which has further shown that the predicted requirements for successful beaver establishment in British river systems may have been over estimated. The importance of small, patchy habitat has become clear and the assumption that beaver require extensive and continuous riparian woodland to survive has been disproven, given their evident success both in the River Otter, the wider Tay catchment in Scotland (Brazier et al., 2020b; Campbell-Palmer et al., 2020; Graham et al., 2022) and indeed across mainland Europe (Halley et al., 2020)

6.4.1 Chapter 5 -Future Research

In this study we only investigated the within-catchment movement of beavers, unlike South et al. (2000) who modelled the movement of beavers within and between catchments across Scotland, albeit at a coarser spatial scale. In order to scale our work between catchments it is necessary to combine what we have learned regarding the within-catchment population dynamics of beaver with evidence of beaver dispersal beyond the boundaries of a catchment. I have found no published empirical evidence that discusses the propensity or ability of beavers to disperse between catchments and, due to the license restrictions of the River Otter Beaver Trial (which required any dispersed animals to be returned to the catchment) there was no opportunity to gather this data, during this project. However, now that the animals, within the River Otter catchment, are allowed to disperse naturally (following the conclusion of the trial period), it is imperative that sightings are recorded and dispersal rates are estimated. One this is achieved; it will be possible to join successive catchment level models with a ‘leakage’ coefficient which describes the rate at which beavers disperse from the catchment in response to the availability of habitat and population pressure within the source catchment. This work would help to facilitate a national strategy for the reestablishment of beavers more widely.

6.5 Overall Management Implications: beavers in a changed landscape

Due to centuries of landuse intensification, watercourse modification through dredging and realignment, and the construction of human-made dams and weirs, our rivers now have a severely degraded morphology. This degraded form has serious impacts for hydro-ecological function (Brown et al., 2018). Where streams are confined and disconnected from their floodplains, bed incision increases, the disconnection worsens, and the diversity of instream and riparian habitat is reduced (Brown et al., 2018; Steiger et al., 2005). River systems can support hugely diverse ecological communities; one of the key reasons for this is the frequent disturbance that is associated with rivers (Naiman et al., 1993). Regular over-bank flows, erosion, woody debris dams and in-channel vegetation all contribute to the formation of structurally heterogeneous river systems that can be multi-threaded and comprise numerous instream habitats that support a wide diversity of species (Naiman et al., 1993; Ward, 1998). Such rivers are all but lost in Britain, but beaver offer some hope in being able to restore many of these processes in the areas they inhabit (Brown et al., 2018).

It should be noted that such improved, ecologically-rich river systems are not a habitat requirement of beavers. They are a generalist species (Nolet et al., 1994; Vorel et al., 2015) with the ability to successfully dwell within and thrive in landscapes heavily influenced by anthropogenic activity. There are, for example, urban cities both in Europe (Romanowski and Winczek, 2019) and North America (Bailey et al., 2019) that are home to beaver populations and they are known to inhabit intensively farmed landscapes where access to preferred forage is limited (Campbell-Palmer et al., 2016; Graham et al., 2020; Macdonald et al., 1995). The same was evidenced during the River Otter Beaver Trial (Brazier et al., 2020a) and in this thesis, that beaver have expanded throughout the River Otter, a landscape typical of rural Britain, with predominant anthropogenic landuse. Therefore, the success of a beaver reintroduction is unlikely to be limited by the availability of suitable habitat but is likely to be more dependent on the success of coexistence between beavers and people (Auster et al., 2021).

If the benefits of beaver are to be fully realised, they require space to build dams and expand wetland areas. There will be management challenges associated with this and it may not always be possible. A successful management system would seek to support those landowners to tolerate beavers on their land and allow them to restore these lost riverine processes.

The work presented in this thesis supports these efforts; firstly by demonstrating some of the structural benefits beavers present for our ecosystems, building on the already substantial evidence base that their behaviour is, on balance, hugely positive for ecosystem function (Brazier et al., 2020b; Gurnell, 1998; Larsen et al., 2021; Law et al., 2019). Additionally, a range of methods, modelled data and software tools are presented which can, and in some cases have already, support the design and planning of beaver management strategies. Being able to predict where beavers may have an impact, along with a better understanding of the rate that populations will expand, empowers governing bodies and managers to develop effective, evidence-based management strategies that can be supported by a range of stakeholders.

6.6 Research Impact

Preliminary findings and data from this PhD thesis contributed to the ROBT Science and Evidence Report (Brazier et al., 2020a). The ROBT has had a substantial impact on beaver policy in England. Beavers have been granted permission to remain in the River Otter catchment and expand naturally beyond the catchment boundary. Further, beavers have now been granted legal protection, listed in Schedule 2 of the Conservation of Habitats and Species Regulations 2017 (Bird-Halton, 2022).

The modelling work presented in Chapter 4 has been adopted by Natural England, the Environment Agency, Nature Scot, Natural Resources Wales and, The Wildlife Trusts to inform their beaver management strategies. As part of this collaboration, I expanded this modelling work to the national scale (Appendix 10).

6.7 Conclusion

This thesis has contributed to the understanding of beaver impacts on the structure and function of hydro-ecological systems. Further, it demonstrates a set of modelling tools that help to bridge the gap between local scale understanding of structural change and predicting functional change at the catchment scale.

This study, alongside a sizeable and growing scientific knowledge base, has clearly demonstrated that beavers have the potential to restore lost natural processes. Their activity has undeniable benefits for hydrological, geomorphic and ecological processes but their impacts can often impact anthropogenic landuse. The development of an effective management scheme that supports landowners to share the landscape, and allow beavers access to larger floodplain areas, is essential.

With beavers expanding across Britain, we should anticipate challenges. Beaver management must evolve with the types of problems faced and the communities that are involved. The benefits of returning beavers to British rivers are significant, not only in terms of their ability to restore lost ecosystem structure and function, but also because beavers effect change on such a rapid timescale. Their impacts are therefore immediate and visible; so too are the benefits for local ecosystems. Beavers can help reframe the way we view and manage our river systems by forcing us to acknowledge the value of disturbance, space and “messiness” in restoring and maintaining natural hydro-ecological function.

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Appendix 1. Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands

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Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands

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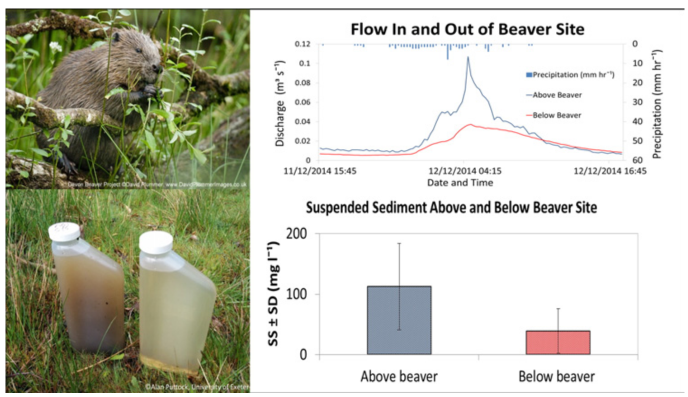
HIGHLIGHTS

- Beavers in wooded site, on first order tributary draining from agricultural land.
- Beaver activity has resulted in major changes to ecosystem structure at the site.
- Beaver activity increased water storage within site and attenuated flow.
- Reduced sediment, N and P, but more DOC in water leaving site.
- Important implications for nature based solutions to catchment management issues.

GRAPHICAL ABSTRACT



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ABSTRACT

Beavers are the archetypal keystone species, which can profoundly alter ecosystem structure and function through their ecosystem engineering activity, most notably the building of dams. This can have a major impact upon water resource management, flow regimes and water quality. Previous research has predominantly focused on the activities of North American beaver (*Castor canadensis*) located in very different environments, to the intensive lowland agricultural landscapes of the United Kingdom and elsewhere in Europe.

Two Eurasian beavers (*Castor fiber*) were introduced to a wooded site, situated on a first order tributary, draining from intensively managed grassland. The site was monitored to understand impacts upon water storage, flow regimes and water quality. Results indicated that beaver activity, primarily via the creation of 13 dams, has increased water storage within the site (holding ca. 1000 m^3 in beaver ponds) and beavers were likely to have had a significant flow attenuation impact, as determined from peak discharges (mean 30 $\pm$ 19% reduction), total discharges (mean 34 $\pm$ 9% reduction) and peak rainfall to peak discharge lag times (mean 29 $\pm$ 21% increase) during storm events. Event monitoring of water entering and leaving the site showed lower concentrations of suspended sediment, nitrogen and phosphate leaving the site (e.g. for suspended sediment; average entering site: 112 $\pm$ 72 mg l^{-1}, average leaving site: 39 $\pm$ 37 mg l^{-1}). Combined with attenuated flows, this resulted in lower diffuse pollutant loads in water downstream. Conversely, dissolved organic carbon concentrations and loads downstream were higher. These observed changes are argued to be directly attributable to beaver activity at the site which has created a diverse wetland environment, reducing downstream hydrological connectivity.

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Results have important implications for beaver reintroduction programs which may provide nature based solutions to the catchment-scale water resource management issues that are faced in agricultural landscapes.

1. Introduction

Beavers are widely referred to as ecosystem engineers (Hartman and Tornlov, 2006; Wright et al., 2002) as they modify river systems and surrounding riparian areas to create suitable habitat for themselves which subsequently benefits a wide range of other species. Beavers are also termed keystone species, having a disproportionately large impact upon fluvial ecosystems, relative to their abundance (McKinstry et al., 2001). The biggest hydrological impact of beavers results from their dam building ability and the consequent impoundment of large volumes of water in ponds (Butler and Malanson, 2005; Hood and Bayley, 2008). Dam and pond features can alter hydrological regimes, both locally and downstream (Burchsted and Daniels, 2014; Polvi and Wohl, 2012) whilst beavers also create bank side burrows, lodges, tunnels and canals to facilitate access to foraging areas (Gurnell, 1998). All of the aforementioned activities increase the structural heterogeneity of their environment (Rolauffs et al., 2001) having not only hydrological and geomorphological impacts, but creating a diverse range of habitats with significant (positive) biodiversity implications (Rosell et al., 2005).

Eurasian beavers (*Castor fiber*) were previously common across Europe including the UK. However, populations were greatly reduced by human activities, particularly over-hunting (Collen and Gibson, 2000), being effectively absent from the United Kingdom by the 16th Century (Conroy and Kitchener, 1996). Stimulated by the EC Habitats Directive, reintroduction programs have seen the re-establishment of Eurasian beaver colonies across northwest Europe (de Visscher et al., 2014), including Scotland (Jones and Campbell-Palmer, 2014). However, in England, there is currently only one known wild population, subject to a rigorous five year monitoring program (Natural England, 2015).

In addition to reported biodiversity benefits (Correll et al., 2000), it has been suggested that beavers could play a key role in the provision of environmental ecosystem services (EES) and as a nature based solution for the management of our river catchments (Brazier et al., 2016). Beaver dams can reduce channel flow velocity (Burchsted and Daniels, 2014) and attenuate storm event hydrographs (Nyssen et al., 2011) with positive impacts on flood risk alleviation (Collen and Gibson, 2000). During drier periods, increased water storage capacity (Hammerson, 1994) can help to maintain base flows, alleviating the risk of droughts downstream (Leidholt-Bruner et al., 1992). The altered flow regimes and water storage capacity also modify nutrient and chemical cycling in freshwater systems. Pond-dam complexes often act as sediment traps, storing fine sediments and nutrients which alter in-pond nutrient cycling (Klotz, 2007) supporting a positive effect on downstream water quality (Naiman et al., 1986).

Knowledge of how beavers impact on the environment and the role they may play in the provision of ecosystem services is vital to inform policy regarding both the reintroduction of *C. fiber* in the United Kingdom and the wider management of these animals in intensively-managed agricultural catchments worldwide (Burchsted and Daniels, 2014). However, much of the available research into the impacts of beavers focuses on the North American beaver (*C. Canadensis*) rather than the Eurasian beaver (*C. fiber*). Whilst there are behavioural similarities between the two species (Rosell et al., 2005), differences, particularly in the European landscape; with intensive agriculture and dense networks of infrastructure mean that their impacts cannot be presumed directly comparable with North American studies (Gurnell, 1998).

Therefore, to quantify the impacts of reintroducing the Eurasian beaver upon water storage, water quality and flow regimes this study addresses the following hypotheses:

H1. Beaver constructed features including dams, canals and burrows/lodges, significantly increase water storage within the landscape.

H2. Beaver dams significantly alter flow regimes resulting in attenuated storm flows.

H3. Beaver ponds act as sinks for diffuse pollutants, significantly improving water quality downstream.

2. Methods

2.1. Study site

Research was undertaken at the Devon Beaver Project controlled reintroduction site in Devon, South West England (DWT, 2013). The site is situated on a small first order stream in the headwaters of the River Tamar catchment, which is the only flow input to the site. Drainage ditches around the perimeter hydrologically isolate the site, ensuring that flow in can confidently be compared with flow out (also via one channel only). The site experiences a temperate climate with a mean annual temperature of 14 °C and mean annual rainfall of 918 mm (Met Office, 2015). In March 2011, a pair of Eurasian beavers was introduced to a 3 ha enclosure, dominated by mature willow and birch woodland, in addition to gorse scrub. Upstream, the site has a 20 ha contributing area dominated by grazed grassland. As illustrated in Fig. 1, beaver activity at the site has created a complex wetland environment, dominated by ponds, dams and an extensive canal network (DWT, 2013).

2.2. Experimental design, data collection and data analysis

2.2.1. Site structure and water storage

To quantify the spatial extent of surface water across this complex site, a combination of walkover, conventional ground-based surveys and unmanned aerial vehicle (UAV) surveys were undertaken. The walkover survey was undertaken prior to beaver reintroduction in 2010 as this was the best approach to survey the very densely vegetated site. The ground-based surveys utilised a Leica Total Station (TCR1205) to map the surface area of each pond and the average depth of each pond at the same time every year (March) from 2013, when seasonal reductions in vegetation cover allowed deployment of such hardware. Whilst being a highly complex site displaying a rapid and ongoing change, these data permitted an estimate of annual changes in both surface areas and pond volumes (area multiplied by mean of surveyed depth at 5–10 positons within the pond) to be made from 2013 to 2016. The UAV surveys were undertaken during the winters of 2014 and 2016 (See Puttock et al., 2015 for further details), to provide high-resolution ortho-mosaic images of the site (see Fig. 2). Winter flights were undertaken to minimise occlusion of the terrain and underlying pond structure by the deciduous vegetation canopy. Each pond (Fig. 2) was equipped with a dipwell at its deepest point to monitor water level from October 2014 onwards. Prior to these manual measurements of pond depths and bathymetry were made in parallel with annual total station surveys. Dipwells were instrumented with HOBO U20L pressure sensors (Onset, Bourne USA) with a 0–4 m range and 0.1% measurement accuracy (i.e. 4 mm measurement increments), recording data on a 15 min time step. Water level was calculated relative to atmospheric pressure recorded on site using HOBOware Pro 10.8 (Onset Bourne USA).

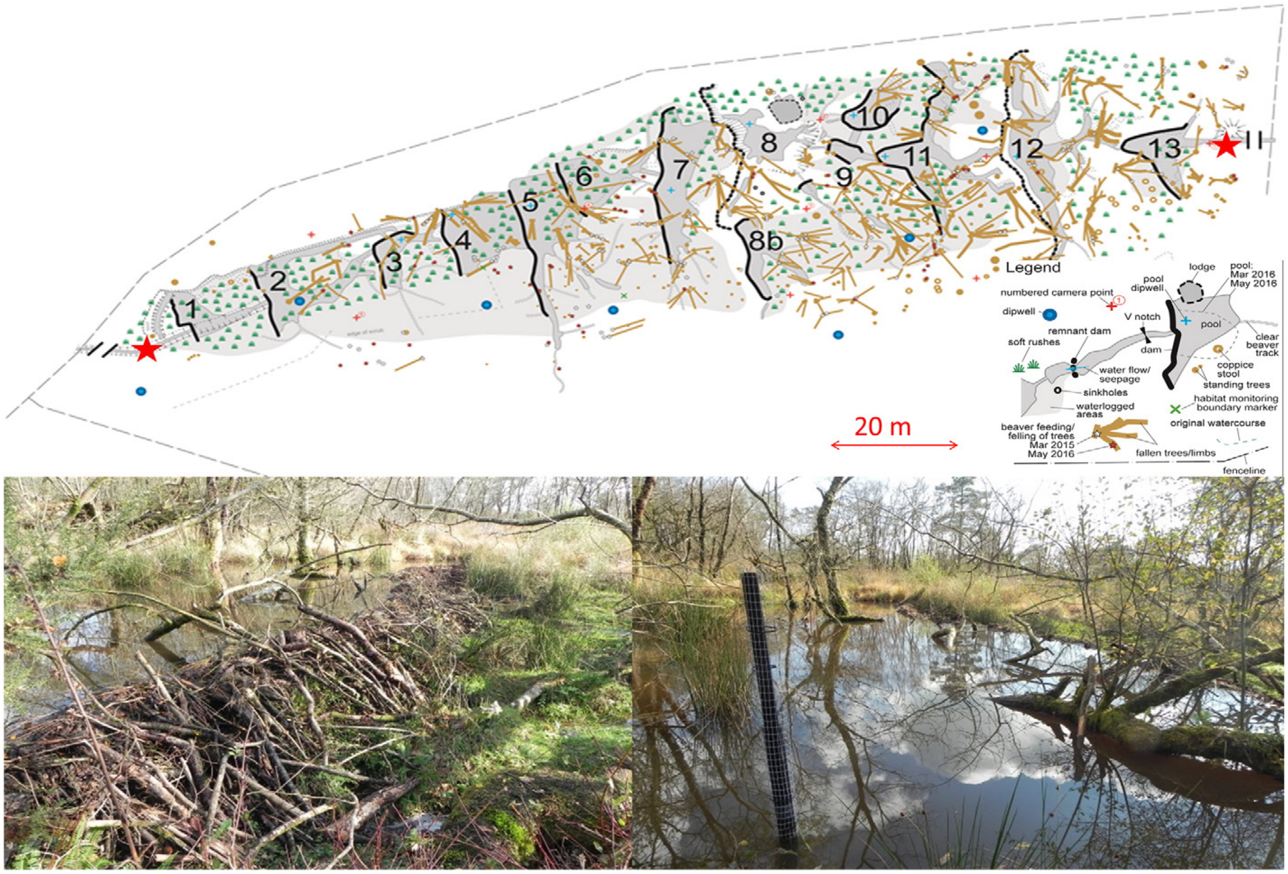

Fig. 1. Top: 2016 site schematic, reproduced with permission from SW Archaeology. Bottom: photos illustrating beaver created pond and dam structures. Bottom right pond illustrates a dipwell used to quantify change in water level over time. Images reproduced with permission from Devon Wildlife Trust. Red stars indicate location of Above Beaver (above pond 13) and Below Beaver (below pond 1) monitoring stations.

2.2.2. Flow

To understand the impact of beavers upon hydrological function (H1 and H2) flow in and out of the site was monitored to create a continuous record of discharge from October 2014 to January 2016. The Above Beaver (AB) and Below Beaver (BB) monitoring stations (Fig. 1) were equipped with a rated v-notch weir (60° angle) and stilling well. A depth to discharge relationship was calculated using the ISO (1980) and USBR (1197) recommended Kindsvater-Shen equation (Eq.1).

$$Q = 4.28\, C_e \tan\left(\frac{\theta}{2}\right)(H + k)^{5/2} \tag{1}$$

V-notch weir, depth to discharge calculation. Q = discharge ($L\ s^{-1}$); H = head on weir (cm); θ = angle in degrees; C_e and k are functions of θ (Kulin and Compton, 1975).

At each v-notch the stilling well was instrumented with an in-situ submersible pressure transducer (IMSL–GO100, Impress, United Kingdom). Rainfall was monitored using a tipping bucket rain gauge with 0.2 mm bucket size (RG1, Adcon Telemetry, Austria). All the above equipment connected to a 3G telemetry network (Adcon Telemetry, Austria), providing a live data feed of rainfall and water level/flow on a 15 min time step. Rainfall was recorded as a total for that 15 min time step whilst level was a mean value that could be converted to discharge (Eq. 1) to give an instantaneous discharge and multiplied by time (both for events and entire monitoring period) to calculate total discharge.

To characterise the flow regime at each site, event separation was undertaken on the rainfall and discharge data collected. This method was a modified version of that developed by Luscombe (2014) and as developed previously by Deasy et al. (2009); Glendell (2013). Briefly, the start of an event was identified as rainfall lasting longer than 15 min, with breaks <60 min. Baseflow was determined by discharge at the start of the event and the end point of the event was classified as the time at which baseflow returned to the pre-event level. The following event parameters were determined and are analysed herein: EP = Event Precipitation; Q_t = Total Event discharge; Q_p = maximum recorded event discharge; Q_{Lag} = time between peak rainfall and peak discharge. When considering the potential impacts of beaver activity upon storm flow and consequent flood risk downstream (H2), the largest events are of most interest. Therefore, the above hydrological analysis was repeated on a sub-set of the 20% largest events as determined by total event discharge entering the site.

2.2.3. Water quality

To determine water quality entering and leaving the site; an ISCO 3700 autosampler (Teledyne Isco, Lincoln, USA) was connected to each v-notch weir, allowing for flow-proportional sampling of water quality (each sample triggered by a 30 mm change in stage), with up to 24 samples during each storm hydrograph. A sampling campaign to determine the water quality of the catchment during rainstorm events was undertaken between 2014 and 2015, resulting in the collection of 226 water samples (across 11 events Above Beaver and 11 events

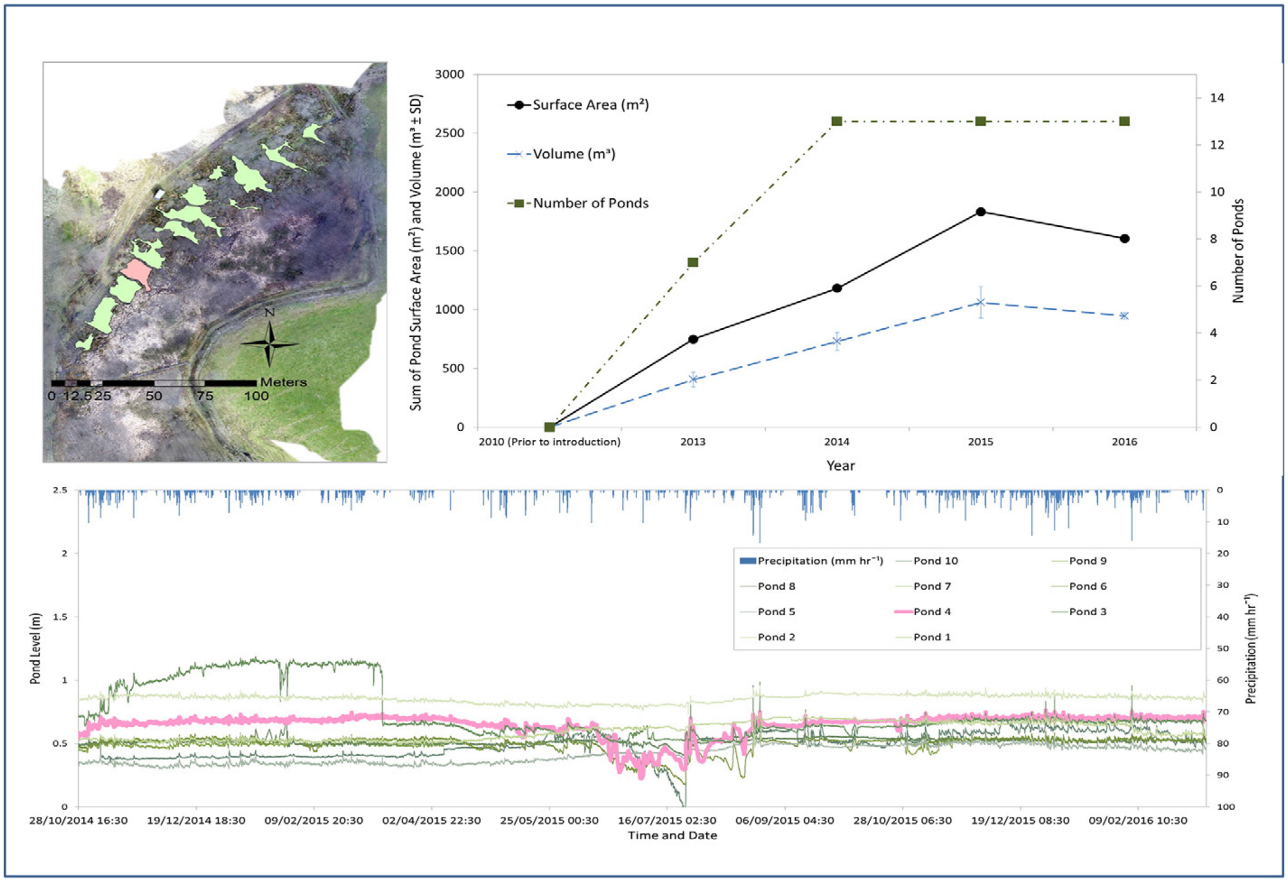

Fig. 2. Top left: UAV orthomosaic of site from 2016 with ponds digitised to illustrate surface water storage, pond coloured pink corresponds with Pond 4 level time series. Top right: graph illustrating change in (1) number of ponds since beaver introduction (green squares); (2) surface area of water in ponds (black circles) and (3) estimated volume of water storage (blue crosses). Bottom: Time series of level in ponds with Pond 4 highlighted and corresponding rainfall time series.

Below Beaver). Samples were retrieved within 24 h and transported back to the laboratory where they were stored in the dark at <4 °C prior to analysis.

Water quality samples were analysed for total oxidised nitrogen (TON), ortho-phosphate (PO_4), dissolved organic carbon (DOC) and pH within 48 h of sample collection (see Glendell (2013)) for relevant storage tests supporting such protocols). Total oxidised nitrogen and dissolved ortho-phosphate concentration were measured colourimetrically via a continuous flow auto-analyser 3 (Bran + Luebbe, Norderstedt, Germany) using Seal Analytical methods G-103-93 for PO_4 (SD 0.015 mg l^{-1}, detection limit 3 μg l^{-1}) and G-109-94 for TON (SD 0.007 mg l^{-1}, detection limit 6 μg l^{-1}). Following filtration, DOC concentration was analysed using a UV spectrometer with a 0–1000 mg l^{-1} range and detection limit (ProPS Trios Gmbh, Rastede, Germany) with a 10 or 20 mm path length at a spectral range of 190–360 nm (Grand-Clement et al., 2014). pH was measured relative to buffer solution standards of pH values 4 and 7 using an Accumet AB15/15 + pH meter (Fisher Scientific, UK) measured at a resolution of 0.01 pH. Total suspended sediment (SS) concentration was determined gravimetrically, by the mass of sediment per sample volume following evaporation. Following collection, each water sample was allowed to settle for 1 week. Without disturbing the sediment, most of the water sample was then decanted and measured. The remaining water and sediment was agitated, measured, poured into a pre-dried and weighed evaporating dish and placed in an oven (80 °C) until dried (Glendell, 2013). Instantaneous loads of relevant water quality variables were extrapolated for the event period sampled, using the Webb and Walling method (Clark et al., 2007; Glendell and Brazier, 2014; Walling and Webb, 1985) presented in Eq. (2).

$$F = K * Qr * \left(\sum_{i=1}^{n} Ci * Qi\right) / \left(\sum_{i=1}^{n} Qi\right) \tag{2}$$

where: F = is the total solute load for sampling period (g); K = time period over which the load occurred (seconds); Qr = mean discharge from a continuous record (m^3); Qi = instantaneous discharge ($m^3\ s^{-1}$); Ci = instantaneous concentration (mg l^{-1}); n = number of samples.

2.2.4. Statistical analysis

To determine if differences in water storage between survey years were significant (H1) a Mann-Kendall non-parametric test was used to determine whether there was significant ($p < 0.05$) change over time. Correlations between dipwell level and rainfall/season were tested using the non-parametric Spearman's rank correlation coefficient. For the event hydrological characteristics (H2) and measured water quality determinands (H3), exploratory analysis illustrated that data were not normally distributed and were therefore log transformed for normality. To establish whether observed variance between sites was statistically significant, an independent two-tailed heteroscedastic *t*-test was used. The tests assumed unequal variance between samples and was carried out at the 95, 99 and 99.9% confidence levels

($p < 0.05$, $p < 0.01$, $p < 0.001$). Correlations between water quality variables were undertaken on non-normalised data using the non-parametric Spearman's rank correlation. All tests were undertaken using SPSS v23 (SPSS Inc., IBM, USA). Unless otherwise mentioned, all errors are standard deviations.

3. Results

3.1. Site structure and water storage

To address H1, results of site surveys were analysed to determine the change in water storage within the site. In 2010, the walkover survey of this site measured no ponded surface water, reporting only a small first-order stream of ca. 183 m length and 93 m^2 surface area. A pair of beavers was introduced to the site in 2011; since when, a significant change in ecosystem structure, most notably a three-order of magnitude increase in ponded surface water storage, has been recorded (Fig. 2). The site has changed from a woodland site, with no permanent surface water storage, to a site dominated by 13 dam-pond structures, with dam lengths extending to 30 m (Fig. 1), covering a surface area of over 1500 m^2 (recorded maximum of 1832 m^2 in 2015 survey). Within the ponds, approximately 1000 m^3 of water is stored at any one time (maximum of 1062 $\pm$ 23 m^3 observed in March 2015).

Site surveys showed that beaver activity has continuously modified the site throughout the study period. Results presented in Fig. 2 show the number of ponds increased from 7, in 2013, to 13 in 2014 and have since remained stable. The corresponding surface area of water increased from 750 m^2 in 2013 to 1181 m^2 in 2014, followed by a further increase to 1832 m^2 in 2015, before showing a slight reduction to 1605 m^2 in 2016; showing a significant increase over the monitoring period ($p < 0.05$, N = 5). Estimated volumes of water stored in ponds, showed a significant upward trend overall ($p < 0.05$, N = 5). More specifically, water volume showed an upward trend between 2013 (405 $\pm$ 61.12 m^3) and 2014 (731 $\pm$ 72.25 m^3) and again an increase to 2015 (1062 $\pm$ 133 m^3), but a decrease between 2015 and 2016 (945.85 $\pm$ 26.97 m^3). Water storage in ponds, measured since 2014 via dipwell levels (Fig. 2) overall showed no significant inter-annual variability ($p > 0.05$, N = 47,887). However, there was intra-annual variability, which was partly driven by rainfall, varying seasonally. Dipwell levels showed a significant correlation with rainfall ($p < 0.01$, $R = 0.116$, N = 47,887), whilst mean levels were higher during the wet season of the hydrological year (1st October–1st April) compared to the dry season ($p < 0.001$, N = 47,887). Whilst not tested quantitatively, intra-annual variability was also observed to be related to beaver dam building or breaching activity, which could both enhance and draw-down water stored in individual ponds.

3.2. Flow

To understand the hydrological response to rainfall at the site and the impact of beaver activity (H2), rainfall and accompanying discharge data for the Above Beaver and Below Beaver monitoring stations, for the entire monitoring period, are presented in Fig. 3. Discharge at both monitoring sites showed a positive correlation with rainfall ($p < 0.01$, Above Beaver $R = 0.218$; Below Beaver $R = 0.181$, N = 59). The hydrological response to rainfall events varied in magnitude at the Above and Below Beaver monitoring stations. Relationships between Above Beaver and Below Beaver rainfall and flow data for a range of summary metrics (total event discharge, peak event discharge and peak rainfall to peak discharge lag time) are illustrated in Fig. 4. As can be seen from the example events in Fig. 3 and relationships for all events in Fig. 4 (peak observed event discharge ($m^3\ s^{-1}$, $p < 0.001$ $R^2 = 0.81$); total storm event discharge (m^3, $p < 0.001$ $R^2 = 0.70$); peak rainfall to peak lag time (minutes, $p < 0.05$, $R^2 = 0.18$), the Below Beaver site shows a more attenuated response to rainfall events than the Above Beaver site, despite the distance between these monitoring locations being <200 m. When comparing population means across the events monitored, Below Beaver events were smaller, showing 34 $\pm$ 9% lower total event discharges during rainfall (AB = 1718 $\pm$ 1641 m^3; BB = 1137 $\pm$ 1059 m^3, $p < 0.05$, N = 59) and 30 $\pm$ 19% lower in terms of peak discharges (AB = 0.04 $\pm$

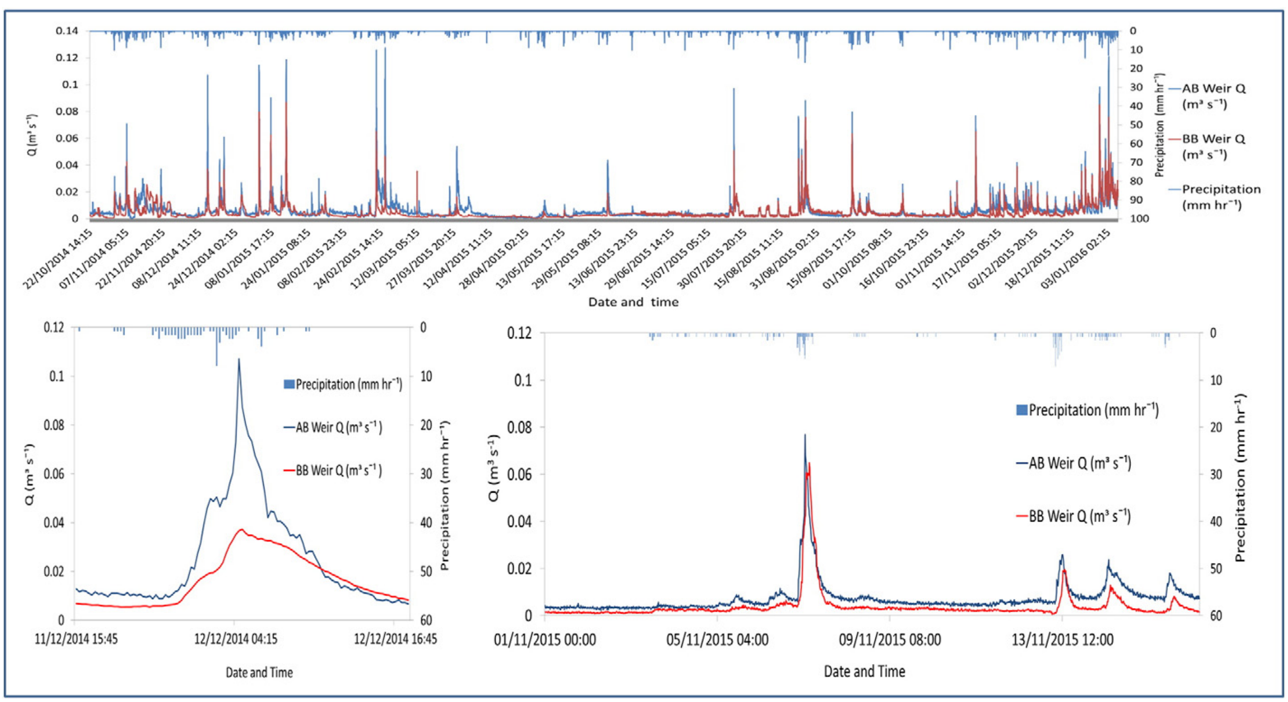

Fig. 3. Top: discharge ($m^3\ s^{-1}$) and rainfall (mm h^{-1}) time series for monitoring period. Bottom left: zoom in on example storm event hydrograph from December 2014. Bottom right: zoom in on example hydrograph from November 2015. For all graphs, blue line is Above Beaver monitoring station (AB) and red line is Below Beaver (BB) monitoring station.

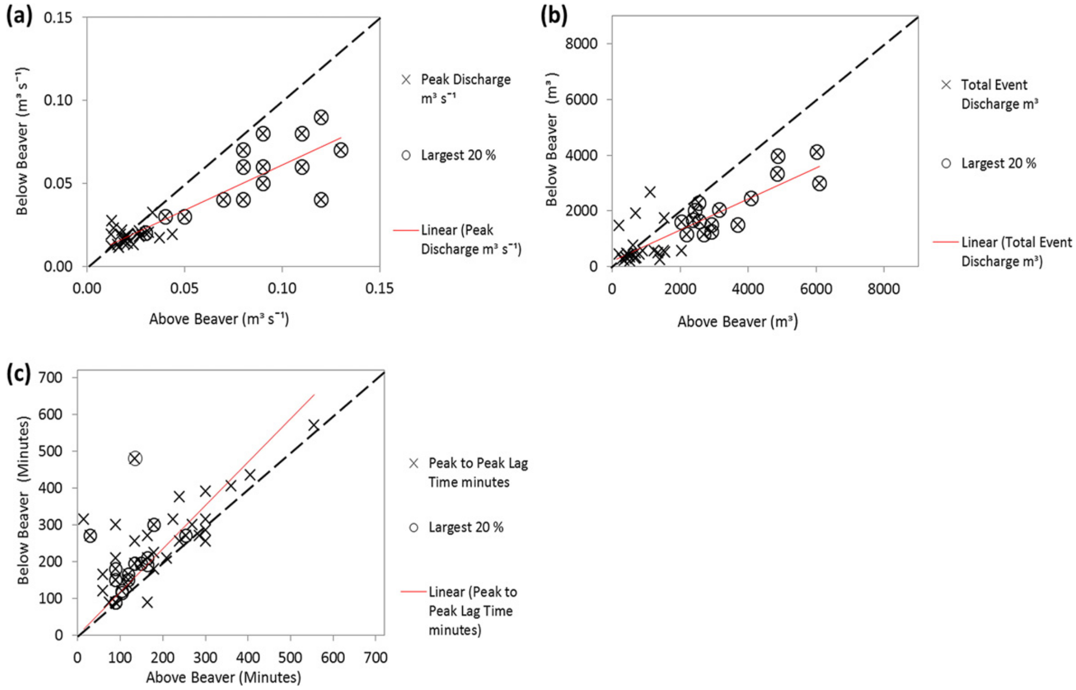

Fig. 4. For each rainfall event (N = 59) extracted from a continuous time-series of flow, relationships between hydrological response Above Beaver (x-axis) and Below Beaver (y-axis). Top left (a): peak observed event discharge ($m^3\ s^{-1}$, $p < 0.001$, $R^2 = 0.81$); Top right (b): total storm event discharge (m^3, $p < 0.001$, $R^2 = 0.70$); Bottom left: (c) peak rainfall to peak lag time (minutes, $p < 0.05$, $R^2 = 0\ 0.18$). For all graphs black dashed line through zero, represents a hypothetical 1:1 relationship between the two monitoring stations, whilst the solid red trend line represents the observed relationship. Black circles highlight results for the top 20% largest events (as determined by total storm discharge entering the site Above Beaver).

0.03 $m^3\ s^{-1}$; BB = 0.03 ± 0.02 $m^3\ s^{-1}$, $p < 0.001$, N = 59). Below Beaver, the hydrological response to rainfall was also more temporally attenuated with 29 ± 21% longer peak rainfall to peak flow lag times (AB = 127 ± 51 mins; BB = 198 ± 100 mins, $p < 0.001$, N = 59) and 32% longer average event durations (AB = 631 ± 335 mins; BB = 783 ± 326 mins, $p > 0.001$, N = 59). Based on a mass balance equation for the site, 22% more water entered the site Above Beaver (235,633 ± 24 m^3) over the monitoring period than left the site Below Beaver (183,617 ± 18 m^3).

Table 1 presents summary results for the top 20% of monitored storm events (N = 16) as classified by total event discharge entering the site, these are also highlighted in the overall dataset presented in Fig. 4 (in black circles). Whilst the top 20% of events contained higher peak and total discharges and shorter lag times compared to the entire dataset, the percentage differences observed were not significantly different ($p > 0.05$) to the complete dataset). During these largest events significant differences were still observed between the Above Beaver and Below Beaver sites. Flows were on average 37 ± 15% lower in terms of total event discharge (AB = 3472 ± 1333; BB = 2158 ± 962 m^3, $p < 0.001$, N = 16), 35 ± 14% lower in terms of peak discharge (AB = 0.08 ± 0.03; BB = 0.05 ± 0.02 $m^3\ s^{-1}$, $p < 0.001$, N = 16), and 28 ± 25% longer in terms of peak rainfall to peak flow lag times (AB = 127 ± 51; BB = 198 ± 100 mins, $p < 0.05$, N = 16) than the Above Beaver flows.

Table 1
Summary statistics for the largest 20% of events observed. ER = event rain; peak Q = peak discharge; total Q = total discharge. % difference is percentage difference between Above Beaver and Below Beaver with direction of change in brackets (±) for each metric.

Event		Above Beaver			Below Beaver			% difference		
Date	ER (mm)	Peak Q ($m^3\ s^{-1}$)	Total Q (m^3)	Lag time (min)	Peak Q ($m^3\ s^{-1}$)	Total Q (m^3)	Lag (min)	Peak Q ($m^3\ s^{-1}$)	Total Q (m^3)	Lag (min)
03/01/2016	37.8	0.09	6028.52	105	0.08	4110.78	115	11.11 (−)	31.81 (−)	8.70 (+)
22/02/2015	24.2	0.13	6094.1	120	0.07	2986.10	165	46.15 (−)	51.00 (−)	27.27 (+)
13/01/2015	33.2	0.12	4886.14	180	0.09	3968.06	300	25.00 (−)	18.79 (−)	40.00 (+)
01/01/2016	29.2	0.12	4859.59	135	0.04	3318.51	195	66.67 (−)	31.71 (−)	30.77 (+)
07/01/2015	30.8	0.09	4095.41	135	0.06	2455.51	480	33.33 (−)	40.04 (−)	71.88 (+)
25/08/2015	32.6	0.09	3696.48	90	0.05	1481.79	180	44.44 (−)	59.91 (−)	50.00 (+)
03/01/2015	23.8	0.11	3143.16	165	0.08	2024.49	210	27.27 (−)	35.59 (−)	21.43 (+)
29/03/2015	11.8	0.05	2933.54	255	0.02	1241.64	270	60.00 (−)	57.67 (−)	5.56 (+)
11/12/2014	24.0	0.11	2923.18	105	0.04	1492.61	120	63.64 (−)	48.94 (−)	12.50 (+)
19/11/2015	19.8	0.03	2705.2	150	0.02	1157.18	195	33.33 (−)	57.22 (−)	23.08 (+)
23/11/2015	18.4	0.04	2562.53	30	0.03	1626.15	270	25.00 (−)	36.54 (−)	88.89 (+)
29/11/2015	13.2	0.03	2431.96	120	0.02	2013.18	150	33.33 (−)	17.22 (−)	20.00 (+)
06/11/2014	23.0	0.07	2376.82	165	0.04	1656.27	190	42.86 (−)	30.32 (−)	13.16 (+)
22/08/2015	30.0	0.08	2200.77	90	0.04	1138.74	90	50.00 (−)	48.26 (−)	0.00 (+)
14/09/2015	27.2	0.08	2556.56	90	0.06	2267.29	90	25.00 (−)	11.31 (−)	0.00 (+)
07/11/2015	15.6	0.08	2050.29	90	0.07	1596.71	150	12.50 (−)	22.12 (−)	40.00 (+)
Mean	24.7	0.08	3471.52	126.56	0.05	2158.44	198.13	37.48 (−)	37.40 (−)	28.33 (+)
Standard dev	7.5	0.03	1332.82	50.78	0.02	962.34	97.59	16.92	15.36	25.10

3.3. Water quality

To address H3, measured concentrations for water quality determinands are summarised in Fig. 5 and detailed in Table 2. Analysis showed that; mean concentrations were higher and significantly different at the Above Beaver site, compared to the Below Beaver monitoring station for: SS (AB: 112.42 ± 71.47 mg l^{-1}, BB: 39.15 ± 36.88 mg l^{-1}, N = 226, $p < 0.001$); TON (AB: 3.35 ± 0.44 mg l^{-1}, BB: 2.19 ± 0.42 mg l^{-1}, N = 97, $p < 0.001$) and PO_4 (AB: 0.10 ± 0.08 mg l^{-1}, BB: 0.02 ± 0.01 mg l^{-1}, N = 123, $p < 0.001$). In contrast, DOC concentrations were significantly lower ($p < 0.001$, N = 226) at Above Beaver, compared to Below Beaver (AB: 5.11 ± 4.65 mg l^{-1}, BB: 11.87 ± 5.96 mg

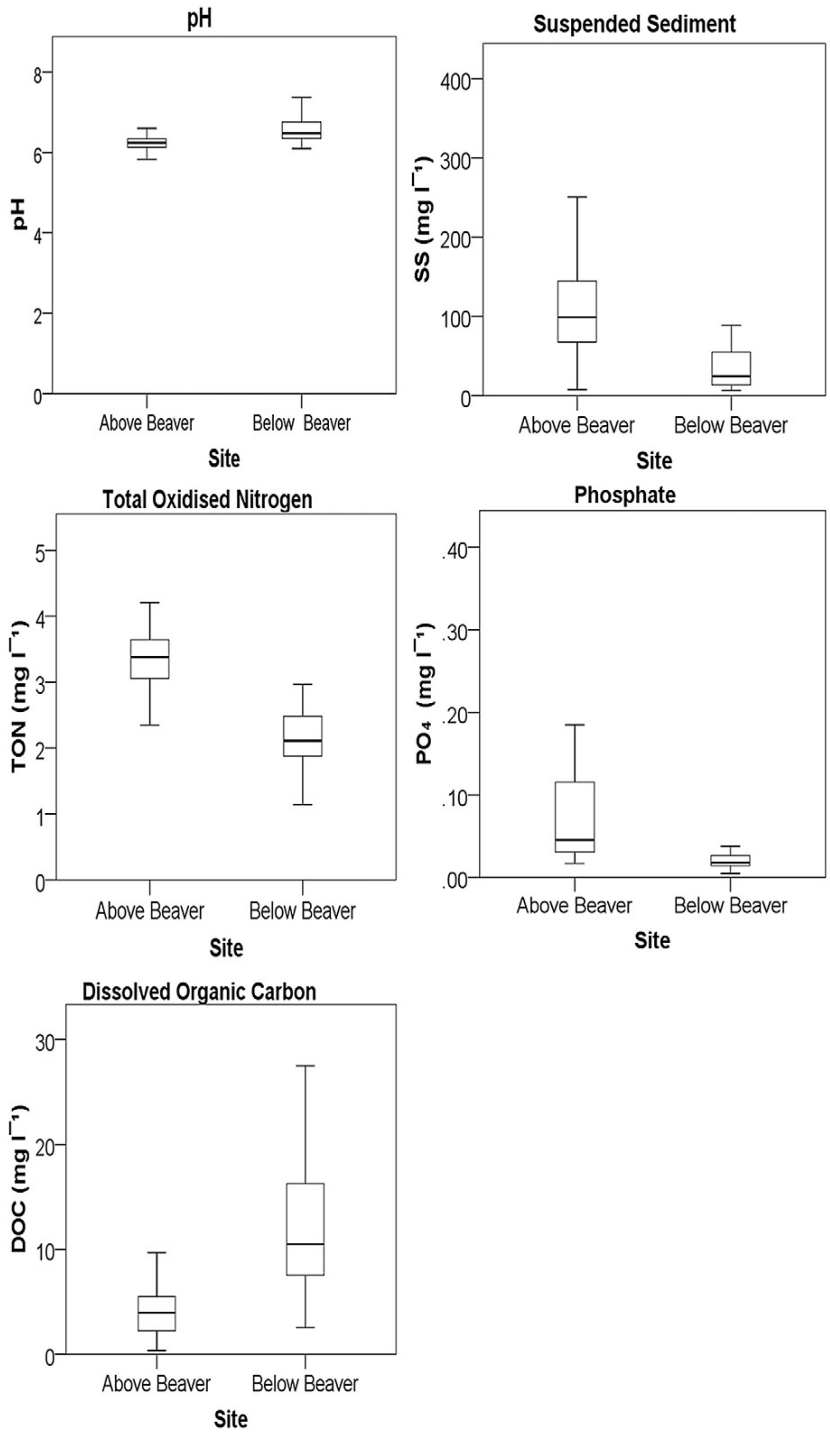

Fig. 5. Box and whisker plots summarising concentrations of measured water quality. Top left = pH ($p < 0.01$, N = 226); Top right = suspended sediment (mg l^{-1}, $p < 0.001$, N = 226); middle left = total oxidised nitrogen (mg l^{-1}, $p < 0.001$, N = 123); Bottom left = phosphate (mg l^{-1}, $p < 0.001$, N = 123) and bottom right = dissolved organic carbon (mg l^{-1}, $p < 0.001$, N = 123). Centre line on bar = median; upper limit of bar = upper quartile; lower limit on bar = lower quartile; whiskers = minimum and maximum values; circles and stars = data outliers.

Table 2
Water quality concentrations, instantaneous loads (calculated by multiplying concentration by discharge) and summary data for monitored water quality events: Above Beaver (AB), Below Beaver (BB). SS = suspended sediment, TON = total oxidised nitrogen, PO_4 = phosphate, DOC = dissolved organic carbon. NA = result not available to laboratory or sample collection issue. Sample Q = instantaneous discharge when sample was collected.

Event Start Date	Site	N	Sample Q (m3 s^{-1})	WQ concentrations (±SD)					WQ instantaneous loads (±SD)			
				pH	DOC (mg l^{-1})	TON (mg l^{-1})	$P0_4$ (mg l^{-1})	SS (mg l^{-1})	DOC (g min^{-1})	TON (g min^{-1})	P04 (g min^{-1})	SS (g min^{-1})
24/10/2014	Above Beaver	24	0.004 ± 0.001	6.23 ± 0.05	3.29 ± 1.27	NA	NA	158.38 ± 49.18	0.83 ± 0.38	NA	NA	38.24 ± 12.31
	Below Beaver	6	0.004 ± 0.001	6.32 ± 0.11	19.13 ± 1.32	NA	NA	57.44 ± 3.63	4.52 ± 1.10	NA	NA	13.48 ± 2.81
09/11/2014	Above Beaver	2	0.018 ± 0.000	6.31 ± 0.05	3.39 ± 0.37	NA	NA	129.26 ± 5.07	3.60 ± 0.40	NA	NA	137.35 ± 5.39
	Below Beaver	6	0.013 ± 0.009	6.45 ± 0.06	19.84 ± 2.10	NA	NA	57.57 ± 5.86	15.34 ± 10.88	NA	NA	42.28 ± 27.29
29/11/2014	Above Beaver	7	0.004 ± 0.002	6.22 ± 0.24	4.12 ± 1.67	NA	NA	144.50 ± 99.63	1.01 ± 0.73	NA	NA	28.03 ± 16.16
	Below Beaver	5	0.003 ± 0.001	6.38 ± 0.06	11.25 ± 0.58	NA	NA	19.31 ± 5.63	1.97 ± 0.76	NA	NA	3.39 ± 1.80
10/01/2015	Above Beaver	11	0.028 ± 0.025	6.21 ± 0.05	4.84 ± 1.10	NA	NA	129.70 ± 42.31	8.05 ± 6.61	NA	NA	189.88 ± 121.59
	Below Beaver	10	0.026 ± 0.021	6.29 ± 0.03	10.05 ± 0.33	NA	NA	42.94 ± 10.17	39.64 ± 12.15	NA	NA	179.77 ± 90.29
12/02/2015	Above Beaver	24	0.007 ± 0.003	6.15 ± 0.04	1.46 ± 0.91	NA	NA	99.09 ± 43.85	0.67 ± 0.47	NA	NA	42.21 ± 29.43
	Below Beaver	8	0.004 ± 0.001	6.21 ± 0.03	7.49 ± 0.22	NA	NA	41.00 ± 8.59	1.88 ± 0.66	NA	NA	10.78 ± 5.65
22/02/2015	Above Beaver	24	0.033 ± 0.028	6.32 ± 0.06	9.60 ± 5.31	3.20 ± 0.62	0.045 ± 0.02	58.06 ± 17.23	15.89 ± 7.32	3.31 ± 1.30	0.064 ± 0.051	111.07 ± 87.17
	Below Beaver	21	0.011 ± 0.011	6.81 ± 0.03	15.66 ± 1.01	1.33 ± 0.19	0.02 ± 0.01	34.17 ± 12.01	3.89 ± 0.01	0.33 ± 0.01	0.005 ± 0.000	8.48 ± 2.17
04/05/2015	Above Beaver	5	0.005 ± 0.001	6.07 ± 0.04	5.83 ± 0.68	3.50 ± 0.18	0.11 ± 0.02	170.23 ± 69.42	1.81 ± 0.51	1.07 ± 0.23	0.032 ± 0.009	50.47 ± 19.98
	Below Beaver	4	0.002 ± 0.001	6.68 ± 0.08	4.35 ± 0.99	1.96 ± 0.36	0.02 ± 0.01	12.38 ± 3.73	0.60 ± 0.41	0.23 ± 0.13	0.003 ± 0.003	1.42 ± 0.78
12/06/2015	Above Beaver	4	0.003 ± 0.001	6.45 ± 0.05	2.24 ± 1.27	3.48 ± 0.18	0.04 ± 0.00	84.50 ± 11.45	0.42 ± 0.21	0.68 ± 0.11	0.008 ± 0.001	16.63 ± 3.64
	Below Beaver	2	0.004 ± 0.000	6.32 ± 0.09	27.19 ± 0.31	1.81 ± 0.18	0.03 ± 0.00	27.77 ± 3.57	6.42 ± 0.32	0.43 ± 0.06	0.008 ± 0.001	6.58 ± 1.06
03/12/2015	Above Beaver	9	0.011 ± 0.006	5.99 ± 0.28	3.41 ± 0.62	3.47 ± 0.17	0.039 ± 0.02	83.90 ± 21.92	2.32 ± 1.46	2.30 ± 1.26	0.027 ± 0.020	59.80 ± 40.56
	Below Beaver	4	0.005 ± 0.001	6.55 ± 0.01	10.78 ± 0.03	2.01 ± 0.07	0.02 ± 0.00	13.43 ± 2.60	3.26 ± 0.59	0.61 ± 0.13	0.006 ± 0.001	4.13 ± 1.53
11/12/2015	Above Beaver	6	0.010 ± 0.002	6.38 ± 0.06	1.55 ± 0.31	4.01 ± 0.15	0.93 ± 0.01	71.18 ± 10.85	0.93 ± 0.29	2.38 ± 0.41	0.026 ± 0.006	41.99 ± 8.09
	Below Beaver	7	0.005 ± 0.003	6.51 ± 0.22	15.53 ± 1.04	2.18 ± 0.27	0.018 ± 0.00	12.71 ± 2.23	4.94 ± 2.81	0.68 ± 0.35	0.006 ± 0.004	4.32 ± 3.31
01/01/2016	Above Beaver	17	0.025 ± 0.017	6.16 ± 0.08	4.36 ± 2.58	2.97 ± 0.35	0.03 ± 0.02	45.91 ± 33.14	5.62 ± 4.13	3.91 ± 2.51	0.055 ± 0.075	83.42 ± 110.05
	Below Beaver	20	0.024 ± 0.011	7.01 ± 0.18	9.72 ± 1.38	2.57 ± 0.24	0.02 ± 0.01	18.64 ± 5.82	13.82 ± 6.83	3.68 ± 1.81	0.034 ± 0.025	26.26 ± 15.19
Mean	Above Beaver	133	0.013 ± 0.010	6.25 ± 0.20	5.11 ± 4.65	3.35 ± 0.44	0.10 ± 0.08	112.42 ± 71.47	3.41 ± 5.77	2.74 ± 1.99	0.03 ± 0.04	54.38 ± 74.38
	Below Beaver	93	0.009 ± 0.007	6.56 ± 0.29	11.87 ± 5.96	2.19 ± 0.42	0.02 ± 0.01	39.15 ± 36.88	7.02 ± 10.08	1.57 ± 1.94	0.02 ± 0.02	20.47 ± 42.26

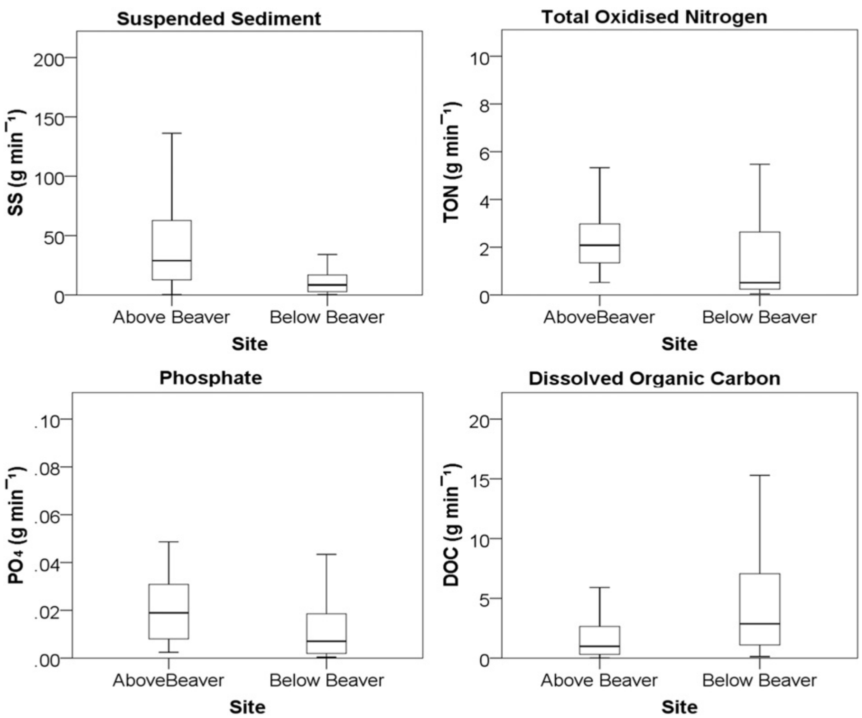

Fig. 6. Box and whisker plots summarising measured water quality instantaneous loads. Top left = suspended sediment (g min^{-1} $p < 0.001$, N = 226); top right = total oxidised nitrogen (g min^{-1} $p < 0.01$, N = 123); bottom right = phosphate (g min^{-1} $p < 0.05$, N = 123); bottom left = dissolved organic carbon (g min^{-1} $p < 0.001$, N = 226). Centre line on bar = median; upper limit of bar = upper quartile; lower limit on bar = lower quartile; whiskers = minimum and maximum values; circles and stars = data outliers.

l^{-1}). The pH of water samples at Above Beaver was slightly more acidic than at Below Beaver (AB: 6.25 ± 0.20, BB: 6.56 ± 0.29) and this difference was consistent enough across the sampling period to be statistically significant ($p < 0.01$, N = 226).

For each sample, concentrations of water quality determinands concentrations were multiplied with discharge at the time of collection to calculate instantaneous loads (Table 2). As summarised in Fig. 6 instantaneous loads were significantly higher at Above Beaver than at Below Beaver for; SS ($p < 0.001$, N = 226); TON ($p < 0.01$, N = 123); PO_4 ($p < 0.05$, N = 123). However, DOC instantaneous loads were observed to be significantly higher at Below Beaver ($p < 0.001$, N = 226). Fig. 7, presents scatter plots of the relationship between discharge and instantaneous nutrient loads. Whilst discharge and instantaneous load are auto correlated and therefore cannot be statistically analysed compared, Fig. 7 illustrates that the linear best fit lines between instantaneous loads and discharge (with the exception of DOC) were steeper at Above Beaver than Below Beaver, indicating that for a given discharge, loads are greater entering the site than leaving. Chemical water quality parameters also showed significant correlations with suspended sediment concentrations ($p < 0.01$) with total oxidised nitrogen (R = 0.628, N = 123) and phosphate (R = 0.811, N = 123) concentrations showing a positive correlation and dissolved organic carbon concentrations showing a negative correlation ($R = -0.278$, N = 226).

Total yields were also calculated for monitored events, to determine the difference between the total amounts of each water quality determinand entering at Above Beaver versus that leaving at Below Beaver. Summary results from each event are presented in Table 3. Calculated event yields all demonstrated that more SS ($p < 0.01$, N = 11), TON ($p < 0.05$, N = 6) and PO_4 ($p < 0.05$, N = 6) entered the site than left following rainfall events. DOC yields were more complex, overall showing a greater mean yield leaving Below Beaver. However, this difference was not significant ($p > 0.05$, N = 11). Whilst most events showed much more DOC leaving the site than entering, the opposite was true for a limited number (3 as shown in Table 3.), so whilst concentrations of DOC were higher below beaver ($p < 0.001$) the total amount and rate of water leaving the site during an event was lower.

4. Discussion

4.1. Site structure and water storage

Beavers engineer ecosystems to create an environment which provides security from predators, alongside easy access to and transportation of food/building materials (Zav'yalov et al., 2010). As beavers are more mobile and confident in water than they are on land (Kitchener, 2001), they have a preference for habitats with large areas of deep, slow flowing water (Collen and Gibson, 2000). Therefore, beavers will not always dam and their construction activity is typically restricted to lower order streams (Naiman et al., 1986), where water depths may not be sufficient for beaver movement and security. When dam building does occur, it increases the area of lentic habitats in systems that are typically dominated by lotic habitats (Hering et al., 2001). The increase in ponded areas above dams can also result in the creation of a stepped profile channel rather than the previous continuous gradient (Giriat et al., 2016). Whilst the structural changes will reduce downstream connectivity, they conversely increase lateral connectivity, forcing water sideways into neighbouring riparian land, inundating floodplains and creating diverse wetland environments (Macfarlane et al., 2015).

Prior to beaver introduction at the study site, a small, first order tributary with a width of ca 0.5 m was surveyed. As illustrated in Figs. 1 and 2, beaver activity has completely transformed the structure of the site, most notably through the construction of thirteen dams, blocking the movement of water, pushing it out laterally and creating ponds behind them. Results presented in Section 3.1. showed a significant increase in both the surface area and volume of water stored within the site that can be unequivocally linked to beaver activity. Therefore, H1; that

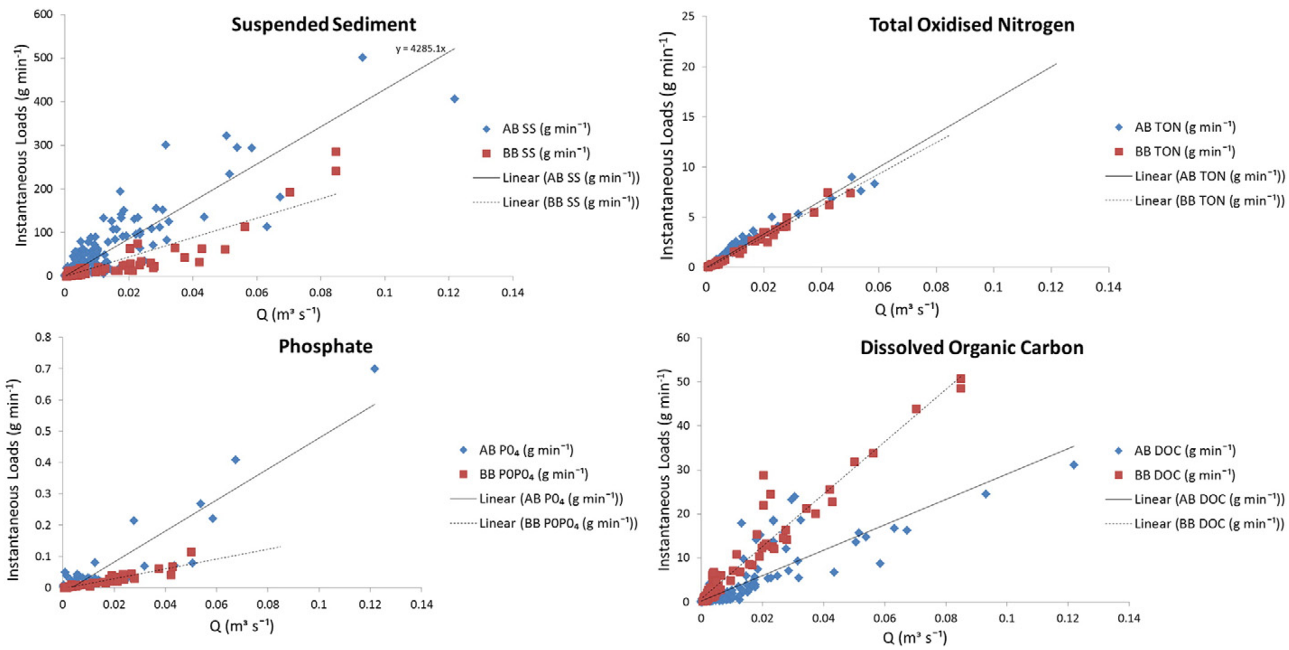

Fig. 7. Lines of best fit between instantaneous loads of measured water quality determinands and discharge ($m^3\ s^{-1}$) at the time of sampling to demonstrate the different gradients at Above Beaver, compared to Below Beaver. Autocorrelation between discharge (Q) and load means that results are not statistically significant; however, they do illustrate the differing relationships observed at the Above Beaver and Below Beaver monitoring sites. Top left = suspended sediment (g min^{-1}, N = 226); top right = total oxidised nitrogen (g min^{-1}, N = 123); bottom right = total phosphate (g min^{-1}, N = 123); bottom left = dissolved organic carbon (g min^{-1}, N = 226). For all graphs: blue diamond's = Above Beaver and red squares = Below Beaver. Solid line = linear line of best fit for Above Beaver and dotted line = linear line of best fit for Below Beaver.

beaver activity significantly increases water storage within the landscape, can be accepted with confidence.

Results, from this study reinforce the view that in small channels, beavers engineer freshwater systems and neighbouring riparian zones to create more suitable conditions (Collen and Gibson, 2000) and that beavers can alter their landscape rapidly over short periods of time. Beavers continually maintain the dam structures of inhabited beaver ponds. Stimulated by the sound of running water (Campbell-Palmer et al., 2015), they will fill gaps and carry out repairs when and where required, often every night, whilst also expanding into new resource gathering areas. Combined with fluctuating water levels driven by rainfall (or lack of rainfall), water storage within beaver impacted environments will be highly variable, but is clearly enhanced when compared with the pre-Beaver landscape.

4.2. Flow

This study quantified flow entering and leaving the beaver impacted site between October 2014 and January 2016. Results from above and below the beaver impacted site during storm events indicated that beaver activity had an attenuating impact upon flow, leading to: longer peak rainfall to peak discharge lag times, lower peak discharge and lower total event discharges. Results also showed more water in total entering the site than leaving, indicating that (1) water storage within the site is significant and (2) that the lateral redistribution and storage of water within the site led to significant infiltration, transmission and evapotranspiration losses (though these were not measured). Thus, these findings, at the headwater catchment scale, support previous findings from work at reach (Green and Westbrook, 2009; Nyssen et al.,

Table 3
Total yield of water quality determinands for monitored water quality events: Above Beaver (AB), Below Beaver (BB) and % difference between AB and BB in addition to direction of change between AB and BB in brackets (+/−). SS = suspended sediment, TON = total oxidised nitrogen, PO_4 = phosphate, DOC = dissolved organic carbon. NA = result not available to laboratory or sample collection issue.

Event N	Event start date	SS (kg)			TON (kg)			P (kg)			DOC (kg)		
		AB	BB	%	AB	BB	%	AB	BB	% less	AB	BB	%
7	24/10/2014	223.74	68.38	69 (−)	NA	NA	NA	NA	NA	NA	4.84	28.42	83 (+)
8	09/11/2014	27.51	9.04	67 (−)	NA	NA	NA	NA	NA	NA	0.72	3.31	78 (+)
9	29/11/2014	67.08	8.02	88 (−)	NA	NA	NA	NA	NA	NA	0.07	0.17	57 (+)
10	10/01/2015	295.93	146.70	50 (−)	NA	NA	NA	NA	NA	NA	13.80	32.53	58 (+)
11	12/02/2015	67.49	13.46	80 (−)	NA	NA	NA	NA	NA	NA	0.66	2.31	72 (+)
12	22/02/2015	352.03	88.70	75 (−)	3.08	2.79	9 (−)	0.33	0.06	83 (−)	50.37	42.79	15 (−)
13	04/05/2015	188.66	5.79	97 (−)	7.57	2.46	67 (−)	0.14	0.01	92 (−)	7.57	2.46	67 (−)
14	12/06/2015	36.19	8.71	76 (−)	1.49	0.57	62 (−)	0.02	0.01	41 (−)	0.87	8.50	90 (+)
15	03/12/2015	93.72	1.42	98 (−)	3.61	0.21	94 (−)	0.04	0.00	95 (−)	3.63	1.13	69 (−)
16	11/12/2015	48.80	4.99	90 (−)	2.76	0.78	72 (−)	0.03	0.01	78 (−)	1.08	5.71	81 (+)
17	01/01/2016	263.82	82.14	69 (−)	12.35	10.62	14 (−)	0.17	0.10	41 (−)	17.77	39.48	55 (+)
	Mean	151.36	39.76	78 (−)	5.14	2.91	53 (−)	0.12	0.03	72 (−)	9.22	15.16	38 (+)

2011) and larger catchment scales (Burns and McDonnell, 1998). Based upon results presented herein (Section 3.2), H2: that beaver dams significantly alter flow regimes resulting in attenuated flow is supported. Related work by colleagues emphasises the value of baseline data (Luscombe et al., 2016) in assessing the impact of landscape restoration techniques upon hydrology and the unavoidable lack of pre-beaver baseline in this study must be acknowledged as a limitation, which should be addressed in future studies. The flow attenuating response of beaver activity, observed both in this study and previous research (Green and Westbrook, 2009; Gurnell, 1998; Pollock et al., 2007), indicates that water is being trapped or at least slowed as it moves through beaver impacted sites. In a previous study, Green and Westbrook (2009) found that the removal of a sequence of beaver dams resulted in an 81% increase in flow velocity. The slow movement of water in beaver impacted sites is attributed to two main causes (1) increased water storage and (2) stream discontinuity and reduced longitudinal hydrological connectivity. Firstly, the increase in storage provided by beaver ponds and associated wetlands (Grygoruk and Nowak, 2014; Gurnell, 1998; Woo and Waddington, 1990) increases water retention times and reduces the velocity of the water. This in turn can increase the duration of the rising limb of the flood hydrograph which, in turn, can reduce the peak discharge of floods (Burns and McDonnell, 1998; Green and Westbrook, 2009; Nyssen et al., 2011). Finally, water stored in the site is released slowly as the leaky dams are drawn-down following rainfall, resulting in elevated baseflows from the site relative to flows into the site.

Water levels in ponds varied significantly as a result of meteorological conditions. Consequently, seasonal variations in water storage were observed as demonstrated by Majerova et al. (2015). It may be therefore expected that the attenuating impact of flow due to storage will be less during wet periods. However, results showed that the flow attenuation impact of the beaver site persisted through the winter months, when pond levels were higher. 14 of the 16 largest events were during the wettest part of the hydrological year and showed no significant reduction in flow attenuation when compared with all flow events (Figs. 3 and 4). That beaver activity still attenuates flow during large events, is supported elsewhere by Nyssen et al. (2011) who conducted one of the few in-channel hydrological studies of Eurasian beaver (*C. fiber*); finding that flow attenuation was greatest during larger events. The connectivity of landscapes is increasingly recognised as being a key control over their hydrological function (Bracken and Croke, 2007; Puttock et al., 2013). It is argued that the observed discontinuity or reduced downstream hydrological connectivity resulting from beaver dam building activity (also shown by Butler and Malanson, 2005), is a key reason for the flow attenuation impact observed herein, which persists even for larger events during the wetter, winter months.

It is important to acknowledge that beaver dam building activity is not a uniform activity and depends on the existing habitat, building material availability and channel characteristics (Collen and Gibson, 2000). Woo and Waddington (1990) identified multiple ways in which dam structure will influence flow pathways and that stream flow can overtop or funnel through gaps in the dams, leak from the bottom of the dams or seep through the entire structure. Whilst some of these pathways (through flow and underflow) were attributed to abandoned dams, visual observations made during this study found that all of these flow pathways can occur together. Whilst, the impact of dam structure upon connectivity and therefore, flow velocity will differ (Hering et al., 2001; Woo and Waddington, 1990), all dams will increase channel roughness and therefore, deliver a flow attenuation effect. In addition to dam structural variations, it is important to observe that the 13 dam and pond structures at the study site were not acting in isolation, but that the differences in hydrological function observed at Above Beaver and Below Beaver was rather a cumulative effect of the overall site structure. Previous studies also discuss the importance of the number of dams in a reach, with beaver dams having the greatest impact on hydrology when they occur in a series (Beedle, 1991; Gurnell, 1998). Sequences of debris dams in 3rd order, Northern Indiana streams were found to increase the retention time of water by a factor of 1.5–1.7 (Ehrman and Lamberti, 1992). Ponds located in series provide both greater storage and greater roughness, resulting in a greater reduction in flow velocities as shown by Green and Westbrook (2009). In another study, pond sequences have been shown to reduce the peak flows of 2-year return floods by 14% whereas individual dams reduced flood peaks of similar events by only 5.3% (Beedle, 1991).

Results presented herein provide strong evidence for the role that beaver dams or similar engineered woody-debris dams (Thomas and Nisbet, 2012), can play a role in flood-defence focused catchment management strategies. There is growing policy support for such 'working with nature' strategies in the UK (Environment Agency, 2014), whilst applied research in the USA has shown how beaver damming activity could be encouraged in locations that suffer from flooding (Pollock et al., 2014). Whilst it appears that such strategies would best be implemented in headwater, low-order tributaries, or in areas where traditional flood defences such as walls cannot be constructed (Wilkinson et al., 2010), further mechanistic understanding of how beaver damming should be encouraged and how many beaver dams would be required to achieve desired results, at different scales, is required (Pollock et al., 2014). Furthermore, as highlighted by Wilkinson et al. (2010) nature based solutions to flooding may potentially provide additional benefits such as water quality improvements. Catchment management strategies should therefore consider these multiple benefits, afforded by soft engineering approaches, alongside the traditional hard engineering flood defence approach (Wilkinson et al., 2014).

4.3. Water quality

4.3.1. Sediment dynamics

The hydrological changes in water storage and flow are likely to have implications for the chemical composition of water leaving the site (Naiman et al., 1986), in addition to stores and downstream fluxes of sediment and associated nutrients (Butler and Malanson, 1994; Lizarralde et al., 1996). Storm event monitoring of water quality at the study site showed lower concentrations and loads of suspended sediment leaving the site in contrast to sediment concentrations/loads entering the site. It is therefore suggested that beaver dams and ponds can exert a significant influence over channel sediment budgets, akin to the dam and woody debris that once played a vital role in the evolution of river networks and floodplains, through the storage of sediment and creation of riparian wetland and woodland. With the intensification of agriculture and the decline of beaver across Europe, in addition to geomorphological alterations such as damming and channelisation (Petts and Gurnell, 2005; Sear et al., 1995) the sediment storage capacity of rivers has declined. Many of these rivers are now experiencing significant rates of incision (Hering et al., 2001). Sedimentation has been reported in many studies of beaver dam morphology. In lower order streams, debris dams have been shown to account for up to 87% of sediment storage (Hering et al., 2001). Sediments, transported from upstream, are deposited in beaver ponds due to the sudden decrease in velocity associated with the decrease in stream power (Butler and Malanson, 1994). An additional benefit is that downstream of beaver dams, channel beds may be less impacted by sediment which has positive implications for the spawning of salmonids and the overall ecological status of the freshwater (Kemp et al., 2012).

The cumulative impact of beaver dams also seems noteworthy in terms of sediment-related water quality. Qualitative observations made at the site demonstrate that the majority of sediment is being trapped in the first few upstream ponds. Over time, sediment may continue to accumulate until each pond fills completely and sediments are colonised by plants forming beaver meadows (Polvi and Wohl, 2012) or the dam collapses (Butler and Malanson, 2005). The rate of sediment accumulation and the long term fate of these deposits will depend on the availability and composition of deposited sediment, the flow regime and the maintenance of the dam structures (Butler and Malanson, 2005; de Visscher et al., 2014).

It has also been argued that beavers can contribute to downstream sediment budgets; through the excavation of canal networks and bank burrows (de Visscher et al., 2014; Lamsodis and Ulevičius, 2012), in addition to the release of sediment following dam outburst floods (Curran and Cannatelli, 2014; Levine and Meyer, 2014). That enhanced fluxes resulting from beaver building activity were not observed herein, suggests that the structure and density of the dams was enough to mitigate the sediment fluxes observed from the intensively managed grasslands upstream over the monitoring period. Such landscapes have previously been shown to export significant amounts of sediment during high-energy storm events (Bilotta et al., 2010; Granger et al., 2010; Peukert et al., 2014), demonstrating the potential role that beaver dams could play in combatting diffuse pollution from agriculture. As with flow, a pre-beaver baseline would be desirable. However, based on the presented differences Above Beaver and Below Beaver it is argued that for suspended sediment, H3 – that Beaver ponds act as sinks for diffuse pollutants significantly improving water quality downstream can be accepted, with significant implications for addressing some of the problems attributed to loss of sediment from intensively farmed landscapes (Brazier et al., 2007).

4.3.2. Chemical water quality

Beaver activity can influence water chemistry and therefore downstream water quality via both abiotic and biotic processes (Cirmo and Driscoll, 1996; Johnston et al., 1995). It is believed that two key mechanisms affected the difference in water quality observed in the system reported herein: (1) flow was slowed resulting in the physical deposition of sediment and associated nutrients (2) the site increased in wetness altering the biogeochemical cycling of nutrients. Previous studies have found that when beaver dams inhibit the transport of fine sediments, this results in the storage of large volumes of organic and inorganic compounds within beaver ponds (Rosell et al., 2005), including nitrogen, phosphorus and particulate bound carbon (Lizarralde et al., 1996; Naiman et al., 1994). This structural change increases the volume of anoxic sediments and provides organic material to aid microbial respiration. Sediments and their associated nutrients are temporarily immobilised in pond sediments and taken up by aquatic plants, periphyton and phytoplankton. Increases in plant available nitrogen, phosphorus, carbon and increased light availability (due to canopy reduction) favour the growth of instream and riparian vegetation, thus further immobilising nutrients within plant biomass (Rosell et al., 2005).

Results presented in Section 3.3. showed TON and PO_4 to be significantly lower leaving the site, both in terms of concentrations and loads, indicating that beaver activity at the site created conditions for the removal of nitrogen and phosphorus entering the site. Correll et al. (2000) found that prior to dam construction, TON concentrations were significantly correlated with river discharge but after dam construction, no significant relationship was observed, although there was a correlation between discharge and nitrate. Similarly, Maret et al. (1987) identified reductions in Total Kjeldahl Nitrogen (TKN) downstream of beaver dams during high flows. It has also been shown that beaver ponds are particularly effective at nitrate retention (Devito et al., 1989). It is suggested therefore, that in agriculturally dominated catchments, particularly those located in Nitrate Vulnerable Zones, beaver ponds are potentially effective tools to manage N-related diffuse pollution problems from intensive agriculture upstream (Lazar et al., 2015).

Results suggest that beaver ponds can also act as sinks for phosphorus associated with sediments. Interestingly, Maret et al. (1987) identified that suspended sediment was the primary source of phosphorus found leaving a beaver pond; therefore, during conditions when more sediment is retained behind the dam than is released, total phosphorus retention is likely to increase. In a study of a beaver impacted and non-beaver impacted catchment, Dillon et al. (1991), found total phosphorus export was higher in the non-impacted catchment suggesting that phosphorus was being stored somewhere within the catchment – most probably in the beaver ponds. Lizarralde et al. (1996) also reported that whilst phosphorus concentrations were significantly higher in riffle sediments, due to extensive wetland creation, total storage was highest in Patagonian beaver ponds. Whilst results here demonstrated a steeper relationship between discharge and phosphate loads in water entering the site, when compared to water leaving the site, previous studies have focused primarily on the relationship between discharge and phosphorus concentrations and yields leaving ponds, with inconclusive results. Devito et al. (1989) reported a strong positive correlation between phosphorus loads and stream discharge. However, Maret et al. (1987) report a negative correlation between phosphorus concentrations and discharge and (Correll et al., 2000) report no correlation between nutrient flushing and stream discharge following dam construction. Climatic and seasonal changes (Devito and Dillon, 1993; Klotz, 2007) and organic matter availability (Klotz, 2007, 2013) have been shown to affect in-pond phosphorus-dynamics. However, with regard to downstream impact, the key consensus, that is supported by the correlation between suspended sediment and phosphate concentrations observed herein is that beaver ponds are most effective at retaining phosphorus associated with high sediment loads (Devito et al., 1989; Maret et al., 1987).

In contrast to the trends observed for nitrogen and phosphate, which correlated with suspended sediment, concentrations and loads of DOC increase on leaving the site, meaning that H3 (beaver activity significantly improves water quality), cannot be accepted for all three macronutrients. The increase in DOC concentrations observed were perhaps to be expected. The increase in sediment and nutrient storage discussed above, in-addition to the overall increase in wetland extent created an environment rich in organic matter, as previously shown by Vecherskiy et al. (2011). Similarly, Law et al. (2016), using colour as a proxy for DOC, observed increased concentrations below a series of beaver dams. Such ecosystems contrast starkly with the carbon depleted, intensively managed agricultural landscape upstream, a landscape that prevails across much of the western UK (Bilotta et al., 2010; Glendell and Brazier, 2014; Peukert et al., 2014, 2016) for examples. Therefore, the dams may trap sediment-bound particulate carbon meaning that ponds may act as net stores of carbon (Correll et al., 2000; Lizarralde et al., 1996; Naiman et al., 1986). However, as a consequence of this overall increase in carbon availability, significant exports of DOC have been observed either downstream (Correll et al., 2000; Naiman et al., 1994) or in comparison with non-beaver impacted catchments (Błędzki et al., 2011). Several authors have speculated that the cause of this DOC release relates to: (i) incomplete decomposition processes making DOC more available for loss (Cirmo and Driscoll, 1996); (ii) enhanced production during primary productivity; (iii) a product of enhanced microbial respiration (Correll et al., 2000) (iv) retention of particulate organic carbon and litter entering the site and subsequent decomposition (Law et al., 2016).As in other organic matter rich environments, DOC release may be expected to vary seasonally due to altering decomposition and production rates (Grand-Clement et al., 2014; Margolis et al., 2001). This also applies to pH which has been shown to be a first order control on DOC production and transport elsewhere (Clark et al., 2007; Grand-Clement et al., 2014). However, another study (Cirmo and Driscoll, 1996) found that a beaver impacted catchment contained higher levels of DOC both before and after $CaCO^3$ treatment when compared with a non-impacted catchment, suggesting that pH plays a limited role in the production of DOC.

This study showed pH to be marginally (but significantly $p < 0.05$) more alkaline in water leaving the site, which is in agreement with other studies showing higher pH levels in beaver ponds and immediately downstream (Cirmo and Driscoll, 1993, 1996; Margolis et al., 2001). However, whether this change in pH was of a large enough magnitude (mean 6.25 ± 0.20 Above Beaver and 6.56 ± 0.29 Below Beaver) to alter within site nutrient cycling is unclear.

Our study demonstrates that concentrations of DOC were significantly higher downstream, but overall losses of DOC were more variable due to the impact of lower, attenuated flows at Below Beaver. Whether losses of DOC from beaver impacted areas are a problem or simply a side effect of a landscape which otherwise acts as an increased carbon store (Johnston, 2014; Wohl, 2013), needs further investigation, in conjunction with an understanding of the impact of beavers upon gaseous carbon fluxes (Klotz, 2013; Wohl, 2013). Much of the existing research focuses on the potential for flushing from beaver ponds and impacts upon in-pond and downstream dynamics with inconclusive results (Correll et al., 2000; Devito et al., 1989; Maret et al., 1987). There is far less research on the potential for beaver ponds to trap or mitigate diffuse pollution from upstream, in agriculturally dominated catchments such as the site studied here, where sediment and associated nutrient losses have been identified as a key problem (Peukert et al., 2014).

5. Conclusion

The results presented within this study represent a significant contribution to our understanding of how Eurasian beaver can impact upon ecosystem structure, with major implications for environmental function, management and the provision of environmental ecosystem services. Specifically in the wooded site, upon a first-order tributary, beaver activity was shown to create a diverse wetland environment, dominated by a sequence of 13 pond and dam structures. The decreased downstream connectivity resulting from this change in ecosystem structure is highly likely to be responsible for the observed attenuating impact upon flood flows across a range of storm event sizes. Furthermore, for a range of key water quality determinands including; suspended sediment, total oxidised nitrogen and phosphate, both concentrations and loads were shown to be significantly lower downstream of the beaver impacted site.

The hydrological impacts of beaver activity are likely to be highly scale and site specific, depending on a range of factors including channel characteristics, food availability and population pressure. Therefore, further research across a range of temporal and spatial scales is required. However, given the widespread reintroduction of Eurasian beaver across Europe, in conjunction with the requirement for improved catchment and land management strategies, this research forms a solid base, from which to develop an understanding of how beavers may form a 'nature based solution' to the land management, water resource and flooding problems faced by society.

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Appendix 2. Sediment and nutrient storage in a beaver engineered wetland

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Sediment and nutrient storage in a beaver engineered wetland

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ESPL
Earth Surface Processes and Landforms

ABSTRACT: Beavers, primarily through the building of dams, can deliver significant geomorphic modifications and result in changes to nutrient and sediment fluxes. Research is required to understand the implications and possible benefits of widespread beaver reintroduction across Europe. This study surveyed sediment depth, extent and carbon/nitrogen content in a sequence of beaver pond and dam structures in South West England, where a pair of Eurasian beavers (*Castor fiber*) were introduced to a controlled 1.8 ha site in 2011. Results showed that the 13 beaver ponds subsequently created hold a total of 101.53 ± 16.24 t of sediment, equating to a normalised average of 71.40 ± 39.65 kg m^2. The ponds also hold 15.90 ± 2.50 t of carbon and 0.91 ± 0.15 t of nitrogen within the accumulated pond sediment.

The size of beaver pond appeared to be the main control over sediment storage, with larger ponds holding a greater mass of sediment per unit area. Furthermore, position within the site appeared to play a role with the upper-middle ponds, nearest to the intensively-farmed headwaters of the catchment, holding a greater amount of sediment. Carbon and nitrogen concentrations in ponds showed no clear trends, but were significantly higher than in stream bed sediment upstream of the site.

We estimate that >70% of sediment in the ponds is sourced from the intensively managed grassland catchment upstream, with the remainder from *in situ* redistribution by beaver activity. While further research is required into the long-term storage and nutrient cycling within beaver ponds, results indicate that beaver ponds may help to mitigate the negative off-site impacts of accelerated soil erosion and diffuse pollution from agriculturally dominated landscapes such as the intensively managed grassland in this study.

KEYWORDS: Eurasian beaver; ecosystem engineering; sediment storage; nutrient storage; soil erosion

Introduction

In the UK intensively managed grasslands, soil erosion rates of between 0.5 and 1.2 t ha^{-1} yr^{-1} have been reported (Bilotta *et al.*, 2010; Gregory *et al.*, 2015), and agricultural erosion rates can exceed 140 t ha^{-1} yr^{-1} (Chambers and Garwood, 2006). Such rates exceed typical soil formation rates of 0.1 t ha^{-1} yr^{-1} under intensive land use (Verheijen *et al.*, 2009), which constitutes a net soil loss (Montgomery, 2007). In 2009, the cost of soil erosion in the UK was estimated at £45 million per annum, much of which was due to the off-site impacts associated with sediment and nutrient pollution (DEFRA, 2009). To manage the environmental problems faced in the landscape there is an increasing interest in 'working with natural processes' (Environment Agency, 2017) one such option in the UK is the reintroduction of the Eurasian beaver (*Castor fiber*).

Beavers are often termed ecosystem engineers (Jones *et al.*, 1994). They can extensively modify riparian and river systems to create habitats more suitable for habitation (McKinstry *et al.*, 2001; Nyssen *et al.*, 2011; Nummi and Holopainen, 2014). The most significant geomorphic impact of beavers results from their dam building ability and the consequent impoundment of large volumes of water and potentially associated sediment and nutrient accumulation in ponds (Naiman *et al.*, 1988; Butler and Malanson, 2005; Hood and Bayley, 2008). Dam and pond features can alter hydrological regimes, both locally and downstream (Polvi and Wohl, 2012; Burchsted and Daniels, 2014). The resulting increased structural heterogeneity of the environment (Rolauffs *et al.*, 2001) also creates a diverse range of habitats (Rosell *et al.*, 2005) with an increasingly recognised potential as a habitat restoration tool (Law *et al.*, 2017). In addition to increasing biodiversity (Law *et al.*, 2017), it has been suggested that, due to their engineering activity, beavers could play a role in the management of river catchments (Puttock *et al.*, 2017).

Beaver damming can cause major changes in landscape connectivity to occur; increasing water storage on floodplains and reconnecting floodplains with channels (Macfarlane *et al.*, 2015). Beaver dams can also reduce channel flow velocity (Burchsted and Daniels, 2014) and attenuate storm event hydrographs (Nyssen *et al.*, 2011) with positive impacts on flood risk alleviation, attributed to the increased storage capacity (Collen and Gibson, 2000) and reduced downstream connectivity (Puttock *et al.*, 2017). Beaver pond–dam complexes have been reported to act as sediment traps, due to the rapid decrease in velocity when water enters a pond (Butler and Malanson, 1995; Klotz, 2007). The altered flow regimes also modify nutrient and chemical cycling in ponds and rivers which, combined with trapping and storage of sediment, can impact upon downstream water quality (Naiman *et al.*, 1986; Dillon *et al.*, 1991).

Previous research by the authors, monitoring water quality above and below a sequence of beaver dams, found a reduction in downstream concentrations and loads of nitrogen, phosphate and suspended sediment during storm flows (Puttock *et al.*, 2017). The work highlighted the role that beaver reintroduction might play in managing degraded agricultural landscapes. Another recent study of beaver activity in UK agricultural landscapes has shown similar downstream reductions in nitrogen and phosphorus concentrations (Law *et al.*, 2016).

The extent to which beavers alter river systems depends on habitat suitability, population numbers and catchment characteristics (Butler and Malanson, 2005). By promoting deposition, beaver dams can lead to the infilling of beaver ponds with sediment which, over time, can be colonised and stabilised by vegetation and are referred to as beaver meadows (Naiman *et al.*, 1988; Burchsted and Daniels, 2014; Johnston, 2014). As such, sediment storage has been shown to increase with beaver pond age (Gurnell, 1998). However, it must also be recognised that this beaver meadow end state is not reached in all situations and beaver dams can fail (Butler and Malanson, 2005). Typically during high energy rain events (Klimenko and Eponchintseva, 2015) beaver dam failure can result in releases of sediment (Polvi and Wohl, 2012, de Visscher *et al.*, 2014) meaning that sediment storage in ponds can be transient (Levine and Meyer, 2014).

The combined impact of a beaver dam sequence on flow dynamics results in a change in deposition and storage dynamics downstream through a sequence of ponds. Furthermore, while it has been identified that beaver dams can store large amounts of sediment (Lamsodis and Ulevičius, 2012), it has also been shown that beaver activity (i.e. burrowing) can remobilise sediment (Butler and Malanson, 1995) and that in-pond erosion can occur and constitute a source (de Visscher *et al.*, 2014). As such, it cannot be assumed that all sediment within a beaver pond sequence originates from upstream and therefore sediment source must also be considered.

Eurasian beavers were once widespread across Europe (Halley and Rosell, 2002). However, populations were greatly reduced by human activities (Collen and Gibson, 2000) with beaver being effectively absent from the UK by the 16th century (Conroy and Kitchener, 1996). Recent reintroduction programs have seen the re-establishment of colonies across much of their previous European geographical range (de Visscher *et al.*, 2014). Yet, due in part to the contemporary absence from European countries, most existing research has focused on the North American beaver (*Castor canadensis*), rather than the Eurasian beaver (*Castor fiber*). Perhaps more importantly, North American research has been undertaken across very different landscapes to the intensively-farmed land that is typical of Europe and, with notable exceptions (Stefan and Klein, 2004, de Visscher *et al.*, 2014), is understudied in Europe (Puttock *et al.*, 2017). European landscapes are characterised by a long history of intensive agriculture, high human population density and dense networks of infrastructure (Brown *et al.*, 2018) meaning beaver impacts cannot be presumed directly comparable with North American studies (Gurnell, 1998). As a consequence, further understanding of how beavers impact on the environment is required. Such information will inform policy regarding both their reintroduction into countries like the United Kingdom and the wider management of these animals across Europe.

The aim of this paper is to present results from a controlled monitoring experiment to improve understanding of the impacts of the Eurasian beaver on sediment and nutrient storage within intensively managed agricultural landscapes. To meet this aim, the study addresses the following hypotheses:

Hypothesis 1 (Sediment and nutrient storage) Individual beaver ponds create significant sediment and nutrient stores, in excess of local channel storage.

Hypothesis 2 (Storage downstream) In a sequence of beaver ponds, in-pond sediment and associated nutrient storage significantly changes downstream.

Hypothesis 3 (Storage and age) Sediment and nutrient storage in beaver ponds is positively correlated with age as older ponds accumulate more sediment over time.

Hypothesis 4 (Sediment source) Sediment and nutrients stored in ponds is sourced from both in-site redistribution by beaver activity and sediment eroded from intensively managed grassland upstream, but is dominated by the latter.

Methods

Study site

Surveying and sampling was undertaken at the Mid-Devon Beaver Project controlled reintroduction site in Devon, South West England (DWT, 2013). The site is situated on a first-order stream in the headwaters of the River Tamar catchment. The site has a 20 ha upstream catchment area dominated by intensively managed grassland. Drainage ditches around the perimeter hydrologically isolate the site, ensuring that the stream is the only flow in and out of the site and the only fluvial source of sediment and nutrients. Since beaver introduction, the site has changed from *c* 75% woodland cover (*Salix cinerea – Galium palustre* woodland) to a fen-meadow dominated community (*Molinia caerulea – Cirisium dissectrum* fen meadow) (DWT, 2013). The site experiences a temperate climate with a mean annual temperature of 14°C and mean annual rainfall of 918 mm (Met Office, 2015). A pair of Eurasian beavers was introduced to the 1.8 ha enclosure, which includes a 183 m stretch of channel in 2011. As illustrated in Figure 1, prior to beaver reintroduction there were no ponds apart from pond 8, which was created to allow beaver reintroduction to the site. In the presented figures this constructed pond is displayed as Pond 8a and has since expanded to cover the area labelled 8b, which are analysed herein together as pond 8. Beaver activity has created a complex wetland environment, dominated by ponds, dams and an extensive canal network (DWT, 2013; Puttock *et al.*, 2015). The age of ponds is detailed in Table I.

Site survey and sample collection

As the site is constantly changing due to beaver activity, in addition to the long-term monitoring of structural change delivered by annual surveys (shown in Figure 1), a survey was undertaken at the time of sediment sampling (October, 2016) to create a detailed ‘snapshot’ of the site structure. Pond extents were surveyed using a differential global positioning system (DGPS - Leica GS08plus system). Sediment and water volumes within each pond were calculated via sampling at each node on a 2×2 m grid using a ranging pole (marked with mm increments). At each survey point the pole was gently inserted

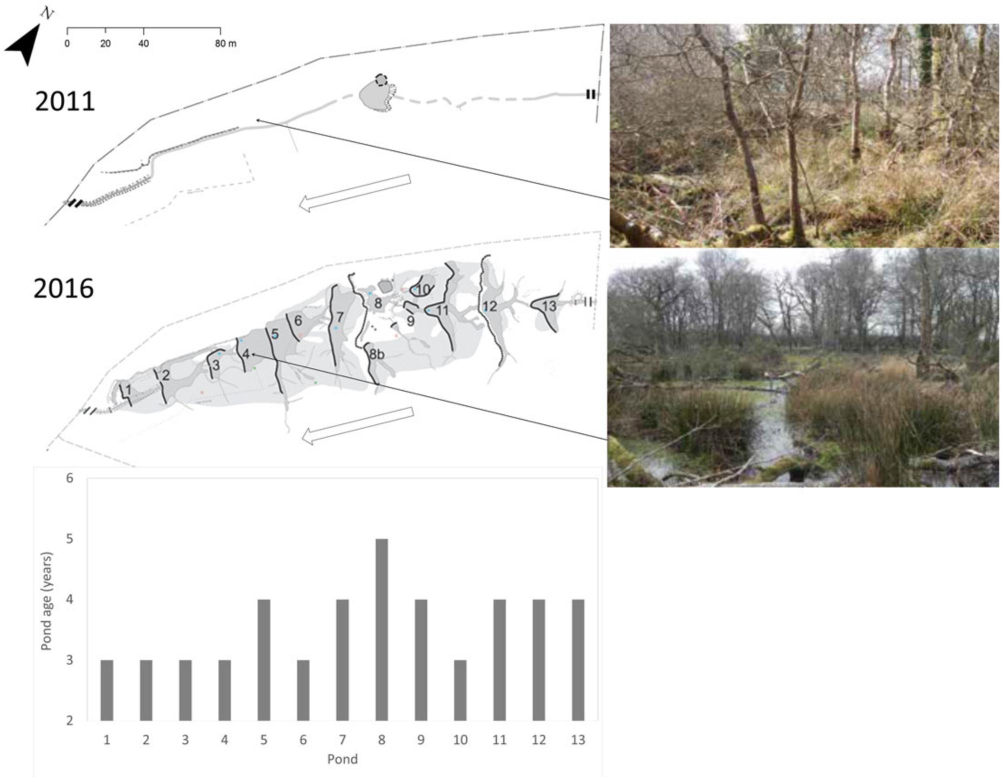

Figure 1. Schematic showing change in site structure between 2011 (immediately prior to beaver introduction) and 2016. Solid black lines signify dam position and extent while dark grey areas are impounded water and light grey areas are wet areas resulting from raised water table. Pond 8 was artificially constructed to allow for humane beaver release. Black and grey arrow indicates downstream flow direction through the site. Bottom graph illustrates age of ponds in years. Site schematics provided by South West Archaeology and included with permission. [Colour figure can be viewed at wileyonlinelibrary.com]

until the tip reached the top of the sediment layer, which was recorded as water depth. The pole was then gently pushed through the unconsolidated sediment until it reached a compacted layer, which was recorded as sediment depth as per Butler and Malanson (1995), Stefan and Klein (2004) and de Visscher *et al*. (2014). This method assumes the unconsolidated sediment layer to be material that has accumulated post-pond creation while the compacted/consolidated layer is the pre-pond surface. Surveying on a 2 m grid (at each node) resulted in a minimum of n = 12 (maximum n = 29) points being collected per pond.

At three randomly selected points within each of the 13 ponds, a core was taken through the sediment layer, using a beeker corer (Uwitec, Austria). Sediment was deposited into plastic bags and transported back to the University of Exeter's laboratories for analysis. In addition, the volume of samples was recorded allowing calculation of bulk density. For all variables, mean values for each pond were calculated using the

Table I. Summary pond characteristics alongside; mean, sum and normalised by area values of sediment (S) total nitrogen (N), total carbon (C), bulk density (BD). All errors are standard deviation (± SD). Pond positions are illustrated relative to data in Figures 2(a) and 3(a)

Pond and age (years)	Area 2016 (m^2)	S Depth (m)	Volume S (m^3)	C (%)	N %	BD ($g\,cm^{-3}$)	Sediment (t)	Carbon (t)	Nitrogen (t)
Pond 1 (3)	47.23	0.19±0.26	9.01±12.14	8.88±2.28	0.56±0.16	0.23±0.01	2.08±2.80	0.18±0.25	0.01±0.02
Pond 2 (3)	181.65	0.17±0.15	30.68±26.7	16.00±2.12	0.92±0.12	0.23±0.01	7.06±2.90	1.13±0.3	0.06±0.02
Pond 3 (3)	158.91	0.13±0.08	20.18±12.49	15.06±2.03	0.97±0.24	0.25±0.01	5.01±3.82	0.75±0.54	0.05±0.03
Pond 4 (3)	150.71	0.14±0.12	20.78±17.94	17.66±2.07	1.06±0.09	0.25±0.01	5.16±5.33	0.91±0.84	0.05±0.05
Pond 5 (4)	169.47	0.20±0.20	33.80±33.76	14.72±3.74	0.96±0.22	0.26±0.02	8.84±5.28	1.30±0.83	0.08±0.05
Pond 6 (3)	119.52	0.23±0.20	27.29±23.79	18.06±0.94	1.01±0.02	0.25±0.01	6.81±5.17	1.23±0.82	0.07±0.05
Pond 7 (4)	198.26	0.27±0.20	52.85±40.41	20.85±6.92	1.06±0.39	0.27±0.01	14.20±5.06	2.96±0.8	0.15±0.05
Pond 8 (5)	116.17	0.42±0.26	49.06±30.13	11.84±3.24	0.62±0.18	0.27±0.02	13.39±4.94	1.59±0.78	0.08±0.04
Pond 9 (4)	30.42	0.51±0.21	15.62±6.24	14.88±0.59	0.96±0.02	0.24±0.01	3.67±4.73	0.55±0.75	0.04±0.04
Pond 10 (3)	40.12	0.56±0.34	22.6±13.53	16.00±1.25	1.03±0.03	0.28±0.01	6.34±4.52	1.01±0.72	0.07±0.04
Pond 11 (4)	207.72	0.29±0.23	59.51±48.66	17.85±2.39	0.95±0.05	0.29±0.01	17.32±4.39	3.09±0.69	0.16±0.04
Pond 12 (4)	110.76	0.30±0.19	33.15±20.92	10.41±2.10	0.68±0.05	0.29±0.01	9.51±4.39	0.99±0.68	0.06±0.04
Pond 13 (4)	60.50	0.12±0.10	7.33±6.31	9.41±0.92	0.57±0.03	0.29±0.01	2.15±4.30	0.20±0.69	0.01±0.04
Mean (±SD)	122.42±61.77	0.27±0.15	29.37±16.28	14.74±3.65	0.87±0.19	0.26±0.02	7.81±4.72	1.22±0.9	0.07±0.05
Sum (±SD)	1591.44		381.87±93.02				101.53±16.24	15.90±2.50	0.91±0.15
Sum Normalised by Area (m^2)			0.24				0.06	0.01	0.00

three samples and are presented alongside standard deviation (Table I). For total values (i.e. total sediment mass), a square root of the sum of squared SD values for each pond was used (i.e. total SD^2 = (pond 1 SD^2 + pond 2 SD^2 +...)) to present a compiled SD value.

Laboratory analysis

Upon collection, samples were oven dried (1 week at 40°C). The sample from a known volume was then dry weighed to calculate bulk density: (BD (g cm^3) = dry sediment weight (g)/ sediment volume (cm^3). Samples were then sieved (<2 mm) and finely ground. Samples were analysed for carbon and nitrogen via dynamic flash combustion using a Flash 2000 Series and compared with standards of known value.

Data processing and statistical analysis

To address Hypothesis 1 (Sediment and nutrient storage), sediment and nutrient volumes and mass within ponds, as well as the entire pond system, were calculated. As in Stefan and Klein (2004) and Butler and Malanson (1995), mean depths per pond (m) were combined with surveyed spatial extent (m^2) allowing calculation of sediment and water volume at time of sampling. Mass of sediment was calculated by multiplying volume of sediment by bulk density and converted into tonnes (t):

$$Sm = (V \times BD) \quad (1)$$

where Sm = sediment mass (g), V = volume (m^3), BD = bulk density (g m^3).

Further analysis was undertaken to understand storage of sediment within the site. As in previous studies (Butler and Malanson, 1995; Stefan and Klein, 2004), annual accumulation rates were calculated by dividing average sediment depth (m) by age (years). Normalised by area (m^2) values were calculated by dividing volume and mass calculations by surface area of each pond. The total pond volume at time of sampling was calculated as the sum of water and sediment volumes to understand the remaining potential storage capacity of ponds at time of sampling.

Percentage carbon and nitrogen values for each pond were used to calculate carbon-to-nitrogen ratios (C:N) and also total mass of carbon and nitrogen stored within each pond. As in previous studies (Peukert *et al.*, 2012; Glendell *et al.*, 2014), nutrient stocks (carbon and nitrogen) were calculated by multiplying mean pond decimal percentage concentrations (%, n = 3), with bulk density (g m^3) and volume (m^3) and then converting to tonnes:

$$Ns = (V \times BD \times (n \div 100)) \quad (2)$$

where Ns = nutrient stock (carbon or nitrogen (g), V = volume (m^3), BD = bulk density (g m^3) and n = nutrient percentage concentration (carbon or nitrogen).

To address Hypothesis 2 (Storage downstream) and Hypothesis 3 (Storage and age), statistical analysis was undertaken between ponds (n = 13). Exploratory analysis illustrated that data were not normally distributed and were therefore log transformed for normality. To establish whether observed variance between ponds was statistically significant, an independent two-tailed heteroscedastic *t*-test was used. The tests assumed unequal variance between samples and was carried out at the 95% confidence level ($P < 0.05$). Relationships between measured pond variables were tested using linear regression while correlations between downstream pond position and measured variables were undertaken on non-normalised data using the non-parametric Spearman's rank correlation. All tests were undertaken using SPSS v23 (SPSS Inc, IBM, USA). Unless otherwise stated, all errors are standard deviations around the mean (detailed for measured variables in Table I and Table II).

It has been shown that there will be some sediment sourced from beaver building activity and within site erosion (Lamsodis and Ulevičius, 2012; de Visscher *et al.*, 2014; Hood and Larson, 2014). Sediment partitioning or source determination was not undertaken as part of this study. Over such small contributing areas (20 ha headwater catchment in this case) there is very little discriminatory power in existing techniques and considerable uncertainty associated with estimates of sediment source (Smith and Blake, 2014). Instead, to address the source of sediment in ponds (Hypothesis 4), data describing sediment mass in ponds recorded in this study, were combined with hydrological and water quality data previously published from the site (Puttock *et al.*, 2017) to estimate upstream catchment contributions to the quantities of sediment and nutrients stored in the beaver ponds.

In previous work undertaken at the study site (see Puttock *et al.*, 2017, for full details), 226 water quality samples were collected between 2014 and 2015. These samples were collected through a full range of flow conditions (from baseflow

Table II. An illustration of total pond volume and remaining storage capacity at a point in time (October 2016) if the system was to remain static. All errors are standard deviation (±SD). Pond positions are illustrated relative to data in Figures 2(a) and 3(a)

Pond and age (years)	Volume Water (m^3)	Volume Sediment (m^3)	Total Pond Volume (m^3)	% Remaining Capacity Volume	Extra sediment capacity (t)
Pond 1 (3)	16.45±6.51	9.01±12.14	25.46±11.45	64.61±23.04	3.8±1.5
Pond 2 (3)	77.81±31.5	30.68±26.7	108.49±32.05	71.72±20.21	17.91±7.25
Pond 3 (3)	44.49±17.41	20.18±12.49	64.68±21.74	68.8±12.7	11.05±4.32
Pond 4 (3)	60.68±29.56	20.78±17.94	81.46±24.44	74.49±21.09	15.06±7.34
Pond 5 (4)	43.12±32.79	33.8±33.76	76.92±42.21	56.06±27.42	11.28±8.57
Pond 6 (3)	34.2±25.75	27.29±23.79	61.49±31.71	55.62±21.95	8.53±6.42
Pond 7 (4)	43.62±24.18	52.85±40.41	96.46±45.29	45.22±24.36	11.72±6.49
Pond 8 (5)	27.06±11.2	49.06±30.13	76.13±31.48	35.55±21.11	7.39±3.06
Pond 9 (4)	10.65±4.48	15.62±6.24	26.26±10.29	40.54±5.35	2.5±1.05
Pond 10 (3)	14.51±0.86	22.6±13.53	37.11±13.51	39.1±16.24	4.07±0.24
Pond 11 (4)	62.32±33.3	59.51±48.66	121.83±59.7	51.15±23.63	18.13±9.65
Pond 12 (4)	29.02±15.62	33.15±20.92	62.17±23.47	46.67±26.63	8.32±4.48
Pond 13 (4)	15.8±5.36	7.33±6.31	23.12±7.72	68.31±15.73	4.63±1.57
Mean (±SD)	36.90±20.09	29.37±15.64	66.28±30.69	55.22±12.83	9.58±5.02
Sum (±SD)	479.72±77.86	381.87±93.02	861.58±111.90		124.39±2.03

to peak flow) across 11 storm events both for water entering the site 'Above Beaver' and water leaving the site after travelling through the pond complex 'Below Beaver'. This sampling, while giving an insight into the differences in water quality entering and leaving the site, did not give enough temporal coverage to calculate total sediment loadings for the duration of the 5 years since beaver introduction, for example, using Walling and Webb (1985) method. Therefore, the difference between mean suspended sediment values Above Beaver (112.42 ± 71.47 mg L^{-1}) and Below Beaver (39.15 ± 36.88 mg L^{-1}), combined with annual discharge entering the site over the monitoring period (2014–2015) was used to approximate sediment yield from the upstream catchment (Equation (3)) and furthermore, calculate an estimated annual erosion rate (Equation (4)).

$$SC = \left(\frac{SS \times Q}{1e^{+09}}\right) \times T \tag{3}$$

where *SC* = sediment from catchment (t); *SS* = difference in suspended sediment Above Beaver and Below Beaver (mg L^{-1}) *Q* = discharge for a 1 year period (L) and *T* = time beavers have been at the site (years).

$$AR = \left(\frac{SC}{C}\right) / T \tag{4}$$

where *SC* = sediment from catchment (t); *AR* = mean annual erosion rate (t ha^{-1} yr^{-1}); *C* = catchment size (ha) and *T* = time beavers have been at site (years).

Results

Total sediment and nutrient storage

Ponds covered a total of 1591 ± 61.77 m^2 of the 1.8 ha study site (i.e. surface water covered 9% of the land area). The 13 ponds had a mean total depth of 0.58 ± 0.16 m, a mean water depth of 0.31 ± 0.07 m and a mean sediment depth of 0.27 ± 0.15 m. Given the site had been active for 5 years at the time of sampling (although there is some variation in pond age from 3 to 5 years), this equates to an average annual accumulation rate of 5.4 ± 3.0 cm yr^{-1}. In total, the ponds stored 381.87 ± 16.28 m^3 of sediment which, when combined with bulk density values (mean 0.26 ± 0.02 g cm^3) equated to a total of 101.53 ± 16.24 t of sediment within the 13 ponds. As shown in Figure 1, prior to beaver reintroduction, there were no ponds at the site and even if Pond 8, which was artificially created to facilitate beaver introduction to the site is not included, this represents a sediment storage increase of 88.14 t in 5 years. Normalised per ponded area, the site stores an average of 71.40 ± 39.65 kg of sediment per m^2 of pond. The ratio of remaining storage capacity to measured water level was also calculated, with the assumption that the site was to remain static with no further beaver engineering. Results presented in Table II indicate that, overall the pond system had a remaining 55.7% potential storage capacity, equating to 124.4 t of sediment.

Analysis of this sediment showed mean percentage concentrations of 14.74 ± 3.65% total carbon and 0.87 ± 0.19% total nitrogen, equating to total storage of 15.90 ± 2.50 t of carbon and 0.91 ± 0.15 t of nitrogen within the ponds.

Changes in sediment and nutrient storage through the pond sequence

It was hypothesised that, in a sequence of ponds, sediment and nutrient storage would change downstream (Hypothesis 2). Variability, between ponds and downstream through the pond sequence, was investigated. Table I summarises survey results quantifying the surface area of ponds, in addition to the quantity of sediment and water being stored at the time of fieldwork.

Figure 2(B) illustrates how factors contributing to total sediment and nutrient storage (pond area, sediment depth and bulk density) change downstream throughout the sequence of 13 ponds. Neither surface area nor depth showed a significant relationship with downstream position ($P > 0.05$). In contrast, bulk density showed an overall marginal, but statistically significant downstream increase ($P < 0.05$, $r^2 = 0.67$). The amount of sediment in individual ponds related closely to the surface area of ponds with bigger ponds storing more sediment ($P < 0.05$, $r^2 = 0.45$), regardless of location within the site.

To explore further how sediment storage varies with distance downstream, normalised sediment storage values per ponded surface area (m^3 per m^2 and kg per m^2) were calculated. Overall, there was no significant correlation between normalised pond sediment values and downstream position ($P > 0.05$). However, as can be seen from Figure 2(C) normalised sediment per m^2 and sediment depth showed a notable spike being significantly higher ($P < 0.05$) between ponds 12 and 7, compared with the first pond (13) and downstream ponds (6–1). The downstream ponds also showed a significantly higher ($P < 0.05$) mean remaining storage capacity (65.2%) than the site as a whole (55.7%).

As outlined in Hypothesis 3, it was hypothesised that the age of each pond could impact upon sediment storage, with older ponds having had more time to accumulate sediment. The age of ponds (Figure 1) was determined from previous surveys undertaken at the site. The ponds that had been present longest (4–5 years), showed significantly higher total amounts of sediment ($P < 0.05$) and higher (but not significantly, $P > 0.05$) normalised sediment values than newer ponds (≤3 years).

Nutrient stores associated with sediment also varied significantly across the study site. As illustrated in Figure 3(B), mean percentage concentrations of both carbon and nitrogen in pond sediment (C = 14.74 ± 2.35; *N* = 0.87 ± 0.12, *n* = 39) were significantly higher ($P < 0.05$) than mean percentage concentrations of channel bed sediment, both upstream and downstream of the beaver-impacted site (C = 1.56 ± 0.20%; *N* = 0.13 ± 0.02%, *n* = 6). In addition, both carbon and nitrogen showed higher percentage concentrations in sediment entering the site Above Beaver (AB; C = 2.40 ± 0.33%; *N* = 0.18 ± 0.03%, n = 3), compared with Below Beaver (BB; C = 0.72 ± 0.06%; *N* = 0.08 ± 0.003%, n = 3).

Significant differences in mean percentage concentrations of carbon and nitrogen were observed between ponds ($P < 0.05$). However, for both nutrients, there was no significant correlation with downstream position or volume/mass of sediment in ponds ($P > 0.05$). Total mass of carbon and nitrogen in ponds (Figure 3(D)) showed a significant positive correlation ($P < 0.05$) with pond surface area and also volume/mass of sediment ($P < 0.05$) although the latter cannot be considered as an independent variable.

For both concentrations and total mass, carbon and nitrogen showed a strong positive relationship with each other ($P < 0.001$). C:N ratios showed no significant difference throughout the pond sequence ($P > 0.05$). However, within pond C:N ratios were slightly higher within pond sediment than sediment

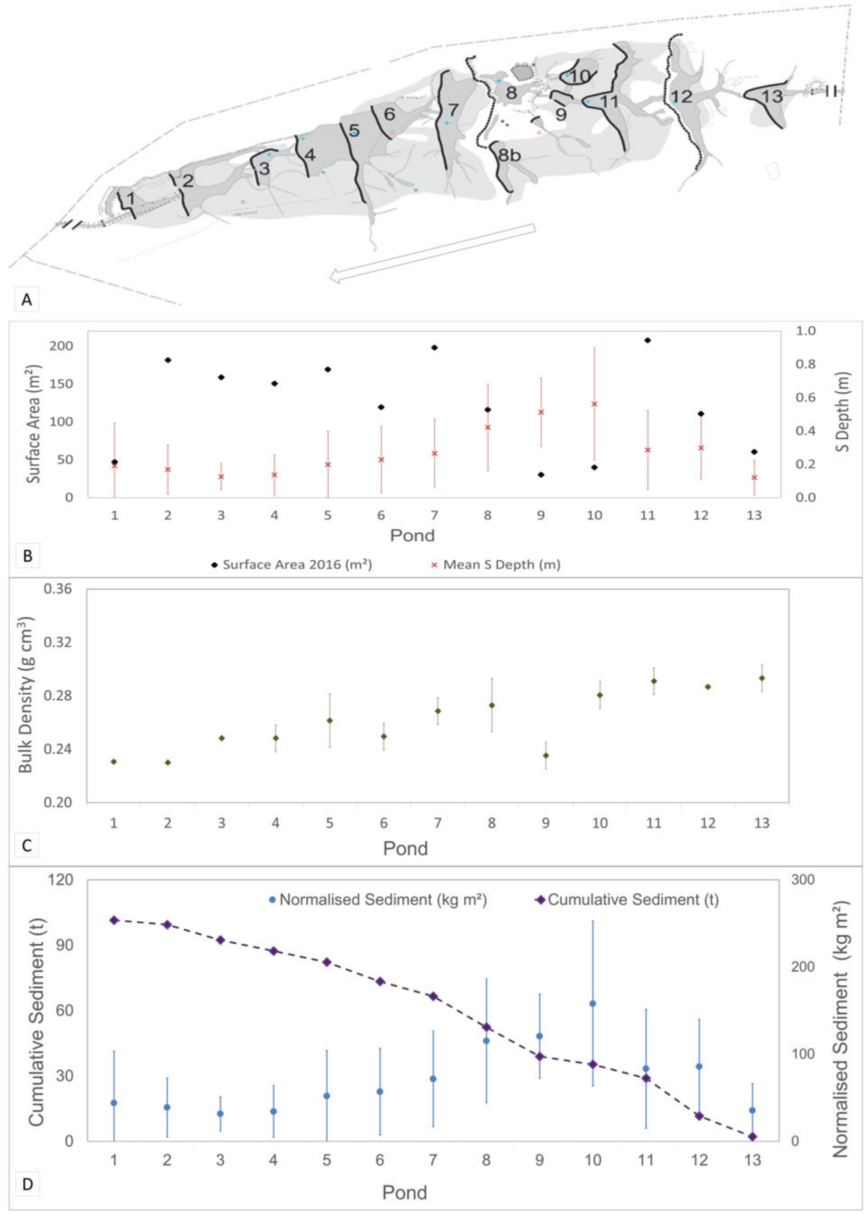

Figure 2. Pond sediment survey results. (a) 2016 pond schematic with ponds numbered and arrow indicating flow direction. Provided by South West Archaeology and included with permission; (b) pond characteristics including sediment depth and surface area; (c) bulk density throughout the pond sequence; and (d) cumulative sediment throughout the sequence and normalised sediment per m^2 surface area. [Colour figure can be viewed at wileyonlinelibrary.com]

above ($P > 0.05$) and significantly higher than sediment below the pond sequence ($P < 0.05$).

Source of sediment in beaver ponds

If the beaver ponds had a trapping efficiency of 100% and 100% of sediment trapped in the beaver ponds (101.53 t) was sourced from the upstream catchment this would equate to 20.3 t yr^{-1} being lost from the 20 ha catchment, over the 5 year period since beaver introduction (or an erosion rate of 0.98 t ha yr^{-1}). However, zit was hypothesised that sediment and nutrients stored in ponds is sourced from both in-site redistribution and sediment eroded from intensively managed grassland upstream, but is dominated by the latter (Hypothesis 4).

In previous research at the site, mean suspended sediment values of 112.42 ± 71.47 mg L^{-1} were reported in water entering the site and a mean of 39.15 ± 36.88 mg L^{-1} in water leaving the site (Puttock *et al.*, 2017). These results suggest a net trapping efficiency (or overall downstream reduction in suspended sediment concentrations) of 65.17%.

Applying Equation (3), given a difference in suspended sediment of 73.35 mg L^{-1} and a total annual discharge of 1.95E+08 L (Puttock *et al.*, 2017) for the monitoring period, equates to an estimated 71.42 t or 70.34% of the total sediment in ponds being sourced from the catchment upstream. Applying Equation (4) to this 71.42 t of sediment, estimated to have originated from the upstream catchment (of 20 ha), results in an estimated annual rate of 0.71 t ha^{-1} yr^{-1} over a 5 year period.

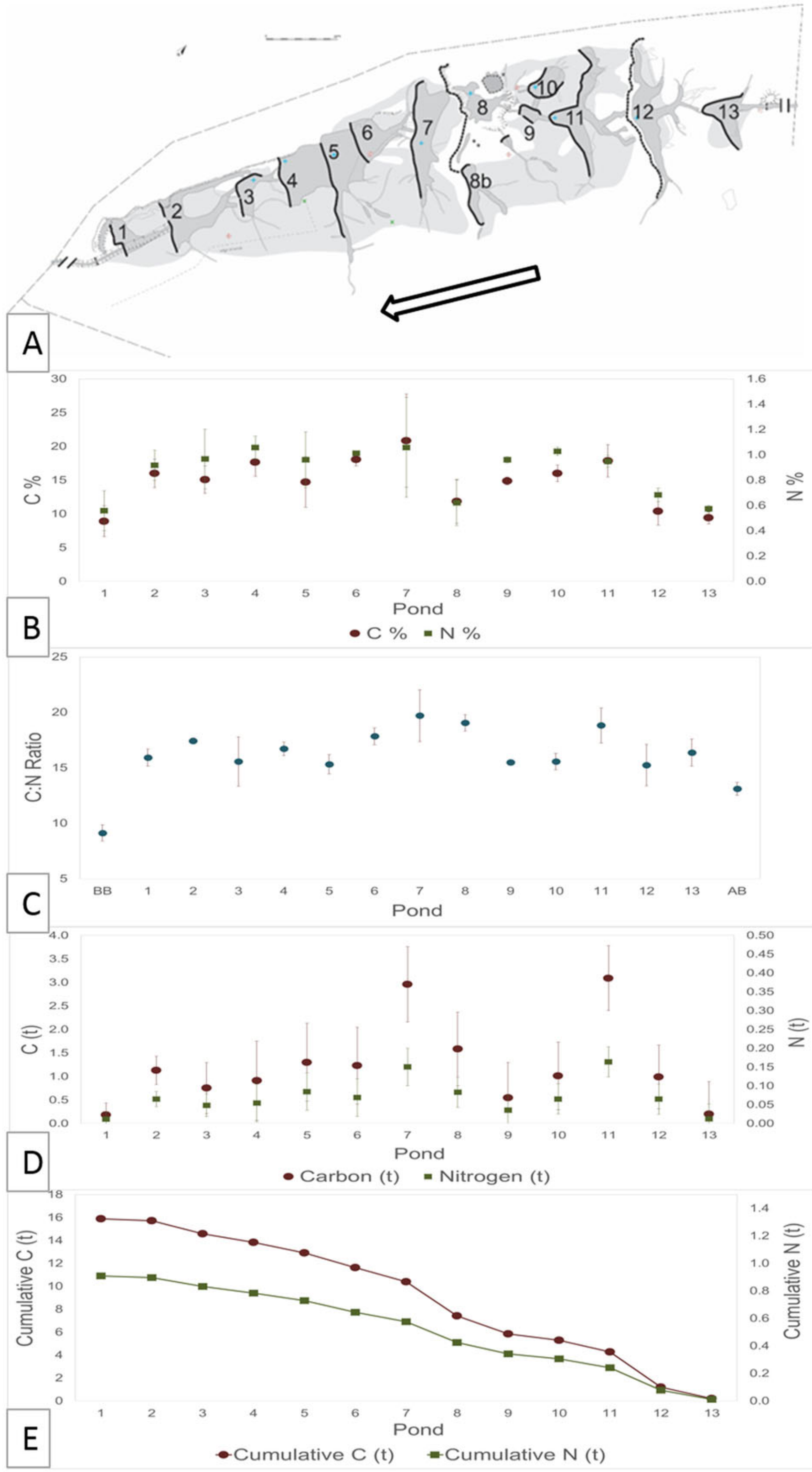

Figure 3. Pond sediment carbon and nitrogen content results. Top (a) 2016 pond schematic with ponds numbered and arrow indicating flow direction. Provided by South West Archaeology and included with permission; middle top (b) C:N ratios throughout the pond sequence and above the site (AB) and below the site (BB); (c) carbon and nitrogen concentrations throughout the pond sequence and above the site (AB) and below the site (BB); middle bottom (d) total carbon and nitrogen within each pond; bottom (e) cumulative total carbon and nitrogen throughout the pond sequence. [Colour figure can be viewed at wileyonlinelibrary.com]

Discussion

Total sediment and nutrient storage

It is clear that beaver activity at the study site has resulted in dramatic structural change and significant amounts of both sediment and nutrients being stored within the 13 ponds. The total of over 100 t of sediment combined with almost 16 t of carbon and 1 t of nitrogen supports Hypothesis 1 that beaver ponds act as large sediment and nutrient stores. This supports previous research finding that beaver impoundments create localised sediment deposits, having the ability to accumulate large volumes of sediment and associated nutrients (Butler and Malanson, 2005; Law *et al.*, 2016). It is further evident that beaver ponds change not just the hydrological regime of small channels, by slowing flow and enhancing water storage (Puttock *et al.*, 2017), but also create landscapes with depositional sediment regimes (Burchsted *et al.*, 2010), as signified by the large sediment volumes recorded in this study.

Data herein illustrates nutrient storage associated with beaver pond development, both in terms of carbon and nitrogen deposition. These results support the existing body of research showing that wetlands, in the broad sense, act as valuable sediment and nutrient stores (Johnston, 1991), particularly in contrast to anthropogenic degraded landscapes (Nahlik and Fennessy, 2016). Furthermore, results indicate that beaver engineered wetlands are exemplars of such valuable wetlands and can successfully exist or be created within intensively managed European agricultural landscapes (Law *et al.*, 2017; Puttock *et al.*, 2017).

The large mass of sediment (101.53 ± 4.72 t or 71.40 ± 39.65 kg per m^2 of ponded extent) being stored in a relatively small area (1.8 ha) in this study is in agreement with previous studies, primarily from North America. Low order streams, containing dams have previously been shown to account for up to 87% of sediment storage at reach scales (Hering *et al.*, 2001), while the removal of a sequence of beaver dams in Sandon Creek, British Colombia, led to the mobilisation of 648 m^3 of stored sediment (Butler and Malanson, 1995, 2005). Butler and Malanson *et al.* (1995) also reported a range of 2–28 cm yr^{-1} of sediment accumulated in several beaver ponds in Glacier National Park, Montana, while for six different ponds (also in Glacier National Park, similar rates of *c.* 4–39 cm yr^{-1} were reported (Butler and Malanson, 1994). Values of sediment accumulation from North American beaver systems indicate the estimated average accumulation value of 5.4 cm yr^{-1} presented in this study may be at the lower end of what is possible in bigger dam–pond complexes or systems with a more plentiful sediment supply. In one of the few studies in European landscapes, De Visscher *et al.* (2014), studied sediment accumulation in two beaver pond sequences in predominately extensively-managed forest/meadow ecosystems of the Chevral River, Belgium. de Visscher *et al.* (2014) estimated the total sediment mass deposited in the dam sequences at 495.9 t. From the two pond sequences, average pond area was 200.4 m^2, average sediment depth 25.1 cm and average sediment mass of 14.6 t, equating to a normalised mass of 72.65 kg of sediment m^2. These values are very similar to the mean sediment depth of 27 cm and mean normalised mass of 71.40 kg m^2 reported in this study from the UK, albeit from entirely different ecosystems. The sediment accumulation values presented both in this study and others, also demonstrate that beaver ponds can exhibit high sediment accumulation values in comparison with other wetland systems. As an example, in a review of sediment accumulation rates in freshwater wetlands (Johnston, 1991) a mean annual accumulation rate of 0.69 cm yr^{-1} was reported across 37 different wetland types, ranging from riparian forest to wet meadows.

As long as supply continues, sediment will continue to accumulate until either the pond infills and sediments are colonised by plants forming a beaver meadow (Polvi and Wohl, 2012) or a dam collapses releasing sediment (Butler and Malanson, 2005). In catchments with high stream power, and associated risk of dam failure, there may be lower and less stable long-term sediment associated stores of nutrients than presented herein (Błędzki *et al.*, 2011). However, where local factors, such as channel gradient, support the stable construction of dams and the resulting stream discontinuity, nutrients may be retained in sediments as shown in this study. Plant colonization and the creation of beaver meadows can further immobilise these sediments and associated nutrients (Naiman *et al.*, 1994). Furthermore, as a considerable volume of potential storage capacity within the 13 yet remains (> 55%), without accounting for ongoing dam building, it may be expected that beaver damming continues to enhance or at least maintain a dynamic equilibrium of sediment storage at the site (Giriat *et al.*, 2016).

It is notable that, at the site reported here, dam failures and resulting sediment releases have not been observed since beaver release. However, dam failures, particularly in high energy environments, may cause infrequent but significant pulses of sediment (Butler and Malanson, 2005). Such pulses may, in some cases, exert significant impacts upon river geomorphology (Bigler *et al.*, 2001; Butler and Malanson, 2005). However, different sediment retention dynamics have been reported following dam collapse. Giriat *et al.* (2016) found that there were very minimal losses of sediment from the Beaver ponds studied, following a dam collapse. Similarly, Butler and Malanson (2005) reported that the majority of sediments were retained in ponds and subsequently stabilised following colonisation and dam reconstruction. Levine and Meyer (2014) reported large sediment losses but the remnants of the dam structure were found to trap sediment, which was rapidly colonised by plants and stabilised. In contrast, other studies have observed rapid loss of pond sediments following dam collapse (Curran and Cannatelli, 2014; Levine and Meyer, 2014). It is likely that, as with the site studied, where closely-spaced, multi-dam complexes exist, these will provide a major buffering effect, reducing the likelihood of dam failure and, in so doing, also reducing the downstream release of sediment from any single dam failure. It is clear from the literature that significant uncertainty regarding dam failure dynamics exists (Anderson and Shaforth, 2010; Klimenko and Eponchintseva, 2015) and is an area in need of further research.

Research undertaken in this study suggests that sediment is enriched in both carbon and nitrogen (average across all ponds of 14.74% C and 0.87% TN), resulting in a notable store of nutrients within the landscape. This summary is supported by previous research and is commonly attributed to the same factors such as channel discontinuity and flow velocity reduction that result in sediment deposition and storage of associated nutrients (Naiman *et al.*, 1986; Devito *et al.*, 1989; Lizarralde *et al.*, 1996; Klotz, 2013). Wohl (2013) estimated that even relict beaver dam-related storage can account for 8% of total carbon storage within the landscape and actively maintained beaver wetlands up to 23%.

Compared with semi-natural ecosystems, intensive agricultural landscapes are often depleted in carbon (Webb *et al.*, 2001; Quinton *et al.*, 2006). The proportions of nutrients in sediment entering the site (carbon 2.4 ± 0.3% nitrogen 0.18

± 0.03%) are lower, but comparable with those reported in Peukert *et al.* (2016) for three intensively managed grassland field systems on similar soil types and in comparable topographic locations, in the South West UK (total carbon range: 3.5–5.0% and total nitrogen range 0.4–0.6%). Such findings, in addition to high within-site storage values, suggest that even when agricultural source areas are depleted in carbon, beaver ponds can still play a role in enhancing carbon storage in the landscape. Therefore, beaver dams may recreate valley bottom wetlands, which would have historically been nutrient rich (Wohl, 2013).

There is only a limited amount of research into the nutrient storage associated with sediment stored in beaver ponds and even less from intensively-managed agricultural landscapes. A key area that is unclear and beyond the scope of this study, is how the impoundment of water, sediments and associated nutrients in ponds affects biogeochemical cycling and the resulting transfers of nutrients in both gaseous and dissolved forms. Previous research at the study site (Puttock *et al.*, 2017) showed that compared with water entering the site, water leaving the site had lower levels of both suspended sediment and also nitrogen. Naiman *et al.* (1994) found that following the build-up of large nitrogen stocks in ponds, there is some removal through both transport and local cycling; however, the majority of nitrogen is retained in pond sediments and taken up by plants. Similarly Correll *et al.* (2000) showed that, before dam construction, nitrogen concentrations were significantly correlated with river discharge but, after dam construction, no significant relationship was observed; perhaps due to enhanced plant uptake or degassing of CH_4 and N_2O.

In contrast to nitrogen values, dissolved organic carbon levels have been shown to be higher leaving the site than entering (Puttock *et al.*, 2017). This was attributed to the greater carbon stocks within site in contrast to the relatively carbon depleted soils in the agricultural catchment upstream. This finding is supported by previous work showing beaver ponds retain organic matter (Law *et al.*, 2016) and consequently act as net carbon stores (Lizarralde *et al.*, 1996; Correll *et al.*, 2000), but attributing increased dissolved organic carbon (DOC) downstream of beaver ponds to increased primary production in ponds (Correll *et al.*, 2000). Beaver ponds have also been shown to result in increased carbon dioxide and methane fluxes compared with non-impacted river reaches (Vecherskiy *et al.*, 2011; Lazar *et al.*, 2015), although It has been suggested that the sequestration of carbon-rich sediment in ponds may help offset any increase in gaseous carbon emissions associated with ponds (Johnston, 2014). From previous studies there is some inconsistency in the reporting of retention, production and release of both carbon and nitrogen in beaver ponds with climatic and seasonal variation in temperature and discharge, pond age and level of plant colonisation likely to be key controls (Devito *et al.*, 1989; Naiman *et al.*, 1994).

Changing sediment and nutrient storage through the pond sequence

Beaver pond sequences are heterogeneous and the number, characteristics and distribution of ponds may have significant implications for sediment and nutrient storage. The distribution and properties of sediments within ponds and along pond complexes is discussed by several authors (Gurnell, 1998; Walsh *et al.*, 1998; Meentemeyer and Butler, 1999; Bigler *et al.*, 2001; de Visscher *et al.*, 2014), though there is notable variability between studies. Beaver pond size will depend on the characteristics of the catchment, building material available, as well as the size of stream in which they occur (Butler and Malanson, 1995; de Visscher *et al.*, 2014). Previous research has determined that pond infilling can also be a function of dam age (Meentemeyer and Butler, 1999; Bigler *et al.*, 2001), with older ponds typically accumulating more sediment (Gurnell, 1998). Herein, the older ponds appeared to hold more sediment, supporting Hypothesis 3 that storage is positively correlated with age, but this relationship was non-significant. This is probably due to the relatively low number of ponds and low difference between maximum ages with ponds at similar successional stages (Naiman *et al.*, 1988).

A common finding in previous studies is that larger ponds (by surface area) hold more sediment (Butler and Malanson, 1995; Walsh *et al.*, 1998; Giriat *et al.*, 2016). Herein, no matter where the ponds are located behind the sequence of 13 dams, larger ponds not only hold significantly more total sediment, but also hold more sediment per unit area. These results suggest that larger ponds may exert a greater influence on flow dynamics and sedimentation patterns, with de Visscher *et al.* (2014) explaining this via velocity gradients across ponds.

In addition to size, the position of each pond within a series of ponds may play a role in sediment and nutrient storage (Hypothesis 2). Studies have identified that there is a downstream decrease in storage between ponds, with the most upstream ponds storing more than those downstream (Butler and Malanson, 1995; Stefan and Klein, 2004). This has been attributed to high energy upstream catchments providing a sediment supply which accumulated more rapidly in the upstream ponds. In a lower energy environment, no difference in sedimentation might be observed between ponds because the majority of sediment would be fine and transported in suspension; therefore, larger ponds were found to retain the largest volumes (Butler and Malanson, 1995). Being in a first order, headwater tributary, it may be anticipated that the study site examined herein falls into the latter category, as supported by the relationship between sediment and pond size. However, as illustrated in Figure 2, sediment mass normalised by area shows a distinctive pattern with a peak in the middle ponds. Water entering the site during storm events (when sediment loads are highest) may have the energy to carry sediment through the first pond, before it is slowed in subsequent ponds depositing sediment. Water entering the downstream ponds is sediment depleted resulting in less sediment being deposited in the lower ponds and lower concentrations of suspended sediment leaving the site (Puttock *et al.*, 2017). Therefore, results suggest that, in addressing Hypothesis 2, downstream position does play a role in sediment storage.

Bulk density values reported in previous research range from $0.47 \pm 0.05\ g\ cm^3$ by Naiman *et al.* (1994) to $0.29 \pm 0.05\ g\ cm^3$ by de Visscher *et al.* (2014), with the mean values reported in this study ($0.26 \pm 0.02\ g\ cm^3$), being marginally lower than this range. Previous studies including that by Naiman *et al.* 1994), also recorded no significant change in bulk density throughout the pond sequence. In this study a small, but statistically significant downstream increase in bulk density was observed, which combined with the previously discussed reduction in sediment depth in the lower ponds, adds to a picture of sediment being preferentially trapped and deposited in the upper to middle ponds (Butler and Malanson, 1995), with less sediment in lower ponds.

Total carbon and nitrogen at the study site varied with the size of pond and mass of sediment. Nutrient concentrations within sediment showed no discernible change throughout the pond sequence. Both carbon and nitrogen concentrations in ponds were significantly higher ($P < 0.05$) than samples taken from within channel locations above and below the beaver-impacted site. Concentrations and C:N ratios in sediment above the pond sequence were higher than those leaving the site, indicating preferential in-site carbon retention. Lizarralde *et al.* (1996) found that sediment trapped in beaver ponds contained a greater concentration of nutrients, including carbon, than riffle environments in the same reach. Similarly, Johnston (2014) found beaver ponds to exhibit higher nutrient concentrations than adjacent unimpounded soils.

Sources of sediment in beaver ponds and wider implications

While the source of much of the beaver pond sediment appears to be the upstream catchment, beaver activity within the site has undoubtedly contributed. It has been shown that beaver activity can constitute a sediment source primarily through the contribution of excavated material from burrows and canals (Lamsodis and Ulevičius, 2012). Attempts have been made to quantify such sources; for example, Lamsodis and Ulevicius (2012) investigated the contribution of beaver (*C. fiber*) excavation to sedimentation in lowland agricultural ditches in Lithuania. They found that, in a given 1 km reach of beaver-impacted channel, a mean of 53 burrows were observed which could generate an estimated 80 m^3 of sediment (approximate volume of 1.49 m^3 per burrow). Another study (focusing on *C. canadensis*), by Butler and Malanson (1995) suggests a lower, but still noteworthy value of 0.4 m^3 per burrow (Butler and Malanson, 1995). Similarly, in a study of *C. canadensis* in 16 US wetlands, it was found that the contribution of sediment from beaver canals to rivers was significant (Hood and Larson, 2014). The authors show that, over a 13 km^2 area in the Miquelon Lake Provincial Park, Canada, an estimated 22 315 m^3 of sediment was released into the watercourse. Erosion from within ponds (de Visscher *et al.*, 2014) or dam failure (Butler and Malanson, 2005) upstream in a dam sequence may also contribute sediment of a mixed source to ponds downstream.

It is probable that the ratio between beaver sourced sediment and other sources of sediment, such as anthropogenic soil erosion, will vary greatly as a function of land use, existing channel characteristics and beaver population densities. Similarly, the overall contribution of beaver activities to reach or catchment scale sediment budgets will vary greatly depending on the extent and nature of beaver engineering activities. It may be hypothesised that in reaches where extensive and stable dam structures exist, the ability of beaver activity to act as a sediment sink may be significant. In contrast, in areas where beavers exist but are not damming, their burrowing and other activities may act as a sediment source that is rarely quantified in existing monitoring and management strategies.

The results presented here support the acceptance of Hypothesis 4 (Sediment source), they show that over 70% (or *c.* 70 t) of the sediment stored in the ponds was sourced from the upstream intensively-managed grassland catchment over the course of 5 years. The calculated annual rate of 0.71 t ha^{-1} yr^{-1} equates closely to that of 0.72 t ha^{-1} yr^{-1}, which was reported as a mean annual erosion rate for intensively managed grasslands (from nine studies) in a recent compilation of UK soil erosion studies (Benaud *et al.*, 2017).

Globally, soil erosion and degradation of predominately agricultural land is both an environmental and economic threat (Gregory *et al.*, 2015). Erosion is also a serious issue for downstream water quality leading to siltation, habitat destruction and eutrophication (Bilotta *et al.*, 2008). While beaver channel modification cannot prevent agricultural soil erosion, the reintroduction of beavers into headwaters may provide a means by which to trap sediment (and associated nutrients) in ponds and reconnect floodplains, limiting negative downstream impacts. For example, in North America beavers are increasingly used as a cost-effective restoration tool to restore incised and eroding stream systems (Pollock *et al.*, 2014) and also to restore channel heterogeneity and fish habitat (Bouwes *et al.*, 2016). Results presented herein go some way to demonstrating that this could also be a viable strategy within the agricultural landscapes which prevail in Western Europe.

In the UK, the value of wetland recreation is recognised (Braskerud *et al.*, 2005; Deasy *et al.*, 2009), with recommendations for wetland creation across 2% of catchments having being made (Millhollon *et al.*, 2009). Others have suggested smaller, strategically placed features could play a key role (Braskerud *et al.*, 2005; Ockenden *et al.*, 2014). However, such work commonly focuses on anthropogenic features with associated construction and maintenance costs (Ockenden *et al.*, 2012). Allowing the recreation of more natural environments, may provide a cost-effective strategy (i.e. when beavers constantly maintain active dam sequences to maintain water storage capacity), while additionally providing a host of other benefits such as biodiversity and habitat restoration (Law *et al.*, 2017), flow attenuation and water quality improvements (Puttock *et al.*, 2017). The estimated sediment accumulation rates, presented for the pond sequence in our study (0.71 t ha^{-1} yr^{-1}), compares closely with those presented by Ockenden *et al.* (2012) for 10 different wetlands constructed with the aim of sediment retention (range 0.01–0.8 t ha^{-1} yr^{-1}).

Conclusion

Results presented in this paper illustrate that beavers can exert a significant impact upon sediment and nutrient storage. Beaver ponds were shown to hold large volumes of sediment and associated nutrients. Results also suggest that, whilst pond age and deposition in a dam–pond sequence may play a role in sediment and nutrient storage, the clearest control was pond size, with larger ponds holding more sediment per unit area.

Unlike most previous work, this study focused on a site located within an intensively managed grassland landscape. It was inferred that the majority of sediment trapped in the ponds originated from erosion in the upstream intensively managed grassland catchment, therefore, beaver dams mitigated the loss of this sediment downstream. While further understanding of the long-term stability of sediment and nutrient storage in beaver ponds is now required, findings presented in this study have important implications for understanding the role beavers may play as part of catchment management strategies.

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Appendix 3. Beaver: Nature's ecosystem engineers

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OVERVIEW

WIREs WATER WILEY

Beaver: Nature's ecosystem engineers

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Abstract

Beavers have the ability to modify ecosystems profoundly to meet their ecological needs, with significant associated hydrological, geomorphological, ecological, and societal impacts. To bring together understanding of the role that beavers may play in the management of water resources, freshwater, and terrestrial ecosystems, this article reviews the state-of-the-art scientific understanding of the beaver as the quintessential ecosystem engineer. This review has a European focus but examines key research considering both *Castor fiber*—the Eurasian beaver and *Castor canadensis*—its North American counterpart. In recent decades species reintroductions across Europe, concurrent with natural expansion of refugia populations has led to the return of *C. fiber* to much of its European range with recent reviews estimating that the *C. fiber* population in Europe numbers over 1.5 million individuals. As such, there is an increasing need for understanding of the impacts of beaver in intensively populated and managed, contemporary European landscapes. This review summarizes how beaver impact: (a) ecosystem structure and geomorphology, (b) hydrology and water resources, (c) water quality, (d) freshwater ecology, and (e) humans and society. It concludes by examining future considerations that may need to be resolved as beavers further expand in the northern hemisphere with an emphasis upon the ecosystem services that they can provide and the associated management that will be necessary to maximize the benefits and minimize conflicts.

This article is categorized under:

- Water and Life > Nature of Freshwater Ecosystems

KEYWORDS

beaver, catchment management, ecological restoration, ecosystem engineers, hydrology

1 | INTRODUCTION

Over millions of years, beavers (*Castoridae)* have developed the ability to modify ecosystems profoundly to meet their ecological needs. In doing so, they also provide valuable habitats for many other species that thrive in wetlands. They engineer ecosystems by building dams, which retain ponds, full of sediment, nutrients, plants, and wildlife. These dams slow the flow of water, reducing peak flows downstream (Puttock, Graham, Cunliffe, Elliott, & Brazier, 2017), storing and gently releasing water in times of drought (Hood & Bayley, 2008). Beavers excavate canals, laterally across floodplains, to access and transport food and building resources, enhancing floodplain connectivity, and geomorphic dynamism (Gorczyca, Krzemień, Sobucki, & Jarzyna, 2018; Pollock et al., 2014). They coppice trees, providing deadwood habitat and allowing sunlight to reach understory vegetation which in turn responds in abundance and diversity (Law, Gaywood, Jones, Ramsay, & Willby, 2017), providing rich habitat for insects, birds, bats, and amphibians (Dalbeck, Hachtel, & Campbell-Palmer, 2020; Stringer & Gaywood, 2016; Willby, Law, Levanoni, Foster, & Ecke, 2018). Beavers were once present throughout Europe, Asia, and North America in large numbers, managing water resources, working with natural processes, supporting the healthy functioning of freshwaters—the very definition of a keystone species.

Consider the potential implications of removing such an animal from our ecosystems. Large areas of stored surface water are lost, rivers flow faster, becoming flashy in times of flood and with lower baseflows in times of drought. Woody debris, carbon in water—an essential building block of life in ponds, streams, rivers, estuaries, and marine environments is reduced, undermining the food-chains that it supported. Wetlands dry up, wildlife move on, or are possibly lost from ecosystems entirely. During the Anthropocene, our catchments have largely become a product of human activity that realizes all of these implications, with associated additional pressures including; hydrological extremes, diffuse pollution, and soil erosion (Hewett, Wilkinson, Jonczyk, & Quinn, 2020). The natural disturbance and dynamic equilibrium maintained by beaver activity drives geomorphic and ecological complexity, in their absence, riparian ecosystems have taken on a simpler form both in terms of their structure and their function (Brown et al., 2018).

In the Northern hemisphere, beavers were hunted to near extinction and extirpated entirely in countries such as Great Britain (GB) about 400 years ago (Conroy & Kitchener, 1996). Thus, our living memory of what beaver-lands were like, is limited, in landscapes where natural recolonizations or reintroductions are now taking place. Our understanding of how *other* species co-existed with beavers, many of them dependent upon wetlands such as beaver ponds, is similarly limited. There is thus a requirement to understand the impact of beavers in contemporary ecosystems, particularly in landscapes that, since their extirpation, have been over-exploited, degraded, and altered by intensive farming and urban development.

To bring together understanding of the role that beavers may play in the management of water resources, freshwater, and terrestrial ecosystems, this paper reviews the state-of-the-art scientific understanding of the beaver as the quintessential ecosystem engineer. We focus upon research considering both *Castor fiber*—the Eurasian beaver and *Castor canadensis*—its North American counterpart, as they re-establish in ecosystems within which their numbers were decimated and are reintroduced or return to ecosystems from where they were extirpated, due to their high-value fur (for hats), castoreum (as a painkiller and perfume)—Nolet and Rosell (1998), and their scaly tail, which led the Catholic church to classify beavers as a fish—fit for consumption on Fridays and Saints days (Coles, 2006; Kitchener & Conroy, 1997; Manning et al., 2014).

The remaining two species of beaver are related to pre-historic *Castoridae* which included as many as 40 species, for example, the giant beaver (*C. Castorides spp*; Martin, 1969) and the terrestrial *C. Paleocastor spp*, famed for its spiralized burrows (Martin & Bennett, 1977). Today, the two extant species of beaver are genetically distinct with differing numbers of chromosomes (Kuehn, Schwab, Schroeder, & Rottmann, 2000). Despite their genetic and minor physiological differences, there are many similarities between the species. For example, they are visually similar and difficult to differentiate by sight alone (Kuehn et al., 2000). Until relatively recently, it was considered that the North American beaver had a tendency to build dams and lodges more frequently and of a greater size than the Eurasian beaver, but it has now been shown by Danilov and Fyodorov (2015) that, under the same environmental conditions, the building behavior of the two species does not differ.

In recent decades species reintroductions across Europe, followed by natural expansion has led to the return of *C. fiber* to much of its Eurasian range (Halley, Rosell, & Saveljev, 2012) with a recent review of national population studies, estimating that the *C. fiber* population in Europe numbers over 1.5 million individuals (Halley et al., 2012). As such, there is an increasing need for understanding of the impacts of beaver in intensively populated and managed modern European landscapes. This review focuses on Europe and *C. fiber* but draws on relevant research into *C. canadensis* in North America. The review summarizes how beaver impact: (a) ecosystem structure and geomorphology, (b) hydrology and water resources, (c) water quality, (d) freshwater ecology, and (e) humans and society. It concludes by examining future scenarios that may need to be considered as beavers expand in the northern hemisphere with an emphasis upon the ecosystem services that they can provide and the associated management that will be necessary to maximize the benefits and minimize conflicts.

2 | BEAVER IMPACT UPON THE ENVIRONMENT—CONTEMPORARY UNDERSTANDING

2.1 | Impacts of beaver upon geomorphology

2.1.1 | Overview

We take this opportunity to revisit Gurnell's (1998) review on the hydrogeomorphological effects of beaver, which provides an excellent foundation for our understanding. Beavers, as ecosystem engineers, have a marked influence upon the terrestrial and riverine environments that they occupy (Westbrook, Cooper, & Baker, 2011). Beavers are primary agents of zoogeomorphic processes; here we acknowledge their influence upon river form and process (Johnson et al., 2020) and discuss recent literature on the impacts of beaver on hydrogeomorphology.

2.1.2 | Canal and burrow excavation

Beavers are well known for their construction of impressive lodges, sometimes as tall as 3 m (Danilov & Fyodorov, 2015), but beavers, especially in river systems, typically excavate bank burrows in which to establish dwellings (Collen & Gibson, 2000; Rosell, Bozer, Collen, & Parker, 2005). Beavers often excavate multiple burrows in a single territory, which can contribute significant volumes of sediment to a watercourse (de Visscher, Nyssen, Pontzeele, Billi, & Frankl, 2014; Lamsodis & Ulevičius, 2012) and also create areas of weakness which can lead to localized erosion and, in some instances, the collapse of earthen flood embankments (Harvey, Henshaw, Brasington, & England, 2019).

Beavers commonly dig shallow channels, often referred to as canals, which extend laterally from beaver ponds. These structures enable beavers to access food and building resources more easily (Butler, 1991; Gurnell, 1998). Often developing into dense networks, these canals contribute significantly to the local hydrogeomorphology of floodplains, creating hydraulic roughness, tortuous flow paths, and complex topography in otherwise planar landscapes (Hood & Larson, 2015). Like burrows, these canals may act as a source of fine sediment (Lamsodis & Ulevičius, 2012; Puttock, Graham, Carless, & Brazier, 2018) or, in the event of significant overbank flows and floodplain inundation, sites of deposition. It is interesting to consider that early humans might have moved over (crossing channels on beaver dams) and through beaver landscapes crisscrossed by canals, observing beaver transporting woody building materials by water with ease, and subsequently learning to do so themselves (Coles, 2006).

2.1.3 | Woody debris contribution

Woody debris is a key driver of geomorphic complexity, has been shown to be a fundamental aspect of "natural" stream geomorphology and a critical habitat for aquatic life (Collen & Gibson, 2000; Gurnell, Piégay, Swanson, & Gregory, 2002; Harvey, Henshaw, Parker, & Sayer, 2018; Thompson et al., 2018; Wohl, 2014, 2015). Beaver increase the rate of both large and small woody material contribution to river systems (Gurnell et al., 2002). In small streams, the large woody material (for example felled trees) is less mobile and often remains in place, exerting a strong influence on geomorphic processes, increasing bed heterogeneity through promoting localized scour and deposition (Gurnell et al., 2002). The contribution of smaller woody fragments or cuttings has been shown to significantly increase willow (*Salix spp*) recruitment due to the provision of propagules, which can establish on gravel/sand bars (Levine & Meyer, 2019). This increases the stability of depositional features and promotes rates of aggradation and bed/bank stability.

2.1.4 | Dam building

Beavers have a preference for habitats with deep, slow-flowing water, to feel safe from predators (Collen & Gibson, 2000; Hartman & Tornlov, 2006; Swinnen, Rutten, Nyssen, & Leirs, 2019). Therefore, their dam-building activity is typically restricted to lower-order streams where stream power is limited (Graham et al., 2020; Gurnell, 1998; Macfarlane et al., 2015; Rosell et al., 2005) and water depths may not be sufficient (normally <0.7 m depth) for beaver movement and security. When dam building does occur, it increases the area of lentic (still freshwater) habitats in systems that are typically dominated by lotic (free-flowing freshwater) habitats (Hering, Gerhard, Kiel, Ehlert, & Pottgiesser, 2001). Damming typically reduces downstream connectivity, and conversely increase lateral connectivity, forcing water sideways into neighboring riparian land, inundating floodplains, and creating diverse wetland environments (Hood & Larson, 2015) as well as contributing to soil and groundwater recharge (Westbrook, Cooper, & Baker, 2006). Dams vary significantly in their size and structure depending on physical factors such as hydrology, topography, and building materials but also ecological factors (Graham et al., 2020). Hafen, Wheaton, Roper, Bailey, and Bouwes (2020) found that primary dams, that maintained a lodge pond, were significantly larger than secondary dams, which are used to improve mobility and the transport of woody material, concluding that beaver ecology, in addition to channel characteristics, exerts a primary control on dam size.

2.1.5 | Agents of erosion

Erosion often occurs at the base of dams, due to a localized increase in gradient and stream power (Gurnell, 1998; Lamsodis & Ulevičius, 2012). Woo and Waddington (1990) observed that flow across the dam crest may be concentrated in gaps, enhancing erosion of the stream bed and banks downstream of the dam, forming plunge pools, and widening the channel, respectively. Lamsodis and Ulevičius (2012) observed the geomorphic impacts of 242 dams in lowland agricultural streams in Lithuania; of which, 13 (5.4%) experienced scour around the periphery of the dam.

Beaver dams are also key sites for channel avulsion (Giriat, Gorczyca, & Sobucki, 2016; John & Klein, 2004), as shown in Figure 1. John and Klein's (2004) study investigated the geomorphic impacts of beaver dams on the upland valley floor of the third-order River Jossa (Spessart/Germany). Due to the creation of valley-wide dams, which extended beyond the confines of the bank, multi-thread channel networks developed across the floodplain. Newly created channels would deviate from the main stream channel, re-entering the river some way downstream. At the point where the newly created channel enters the stream, a difference in elevation results in the development of a knickpoint. This knickpoint then propagates upstream through head-cut erosion, eventually relocating the main stem of the channel.

2.1.6 | Agents of aggradation

Hydrogeomorphic changes, due to beaver engineering, are likely to have implications for stores and downstream fluxes of sediment and associated nutrients (Butler & Malanson, 1994; Lizarralde, Deferrari, Alvarez, & Escobar, 1996). Sediments mobilized and transported from upstream are deposited in beaver ponds, due to a decrease in velocity associated with a reduction in water surface gradient (Giriat et al., 2016) and consequently stream power (Butler & Malanson, 1994).

Pollock, Lewallen, Woodruff, Jordan, and Castro (2017) showed lower concentrations and loads of suspended sediment leaving a beaver site in contrast to those entering the site, while Puttock et al. (2018) showed that within the same site the beaver pond sequence was storing 100 t of sediment combined with an associated 16 t of carbon and 1 t of nitrogen. It is therefore suggested that beaver dams and ponds can create landscapes with depositional sediment regimes exerting a significant influence over channel sediment budgets, akin to the pre-anthropocene dam and woody debris that once played a vital role in the evolution of river networks and floodplains, through the storage of sediment and nutrients and creation of riparian wetland and woodland (Brown et al., 2018).

The large mass of sediment (over 70 kg per m^2 of ponded extent) being stored in a relatively small area (1.8 ha) reported by Puttock et al. (2018) represents similar levels of aggradation to those reported in studies, primarily from North America. Beaver dam sequences on low order streams have previously been shown to account for up to 87% of sediment storage at reach scales, while the removal of a sequence of beaver dams in Sandon Creek, British Colombia, leads to the mobilization of 648 m^3 of stored sediment (Butler & Malanson, 1994, 1995; Page et al., 2005). Butler and Malanson (1994, 1995), also reported sediment accumulation rates of 2–28 and 4–39 cm $year^{-1}$ for different beaver pond sequences in Glacier National Park, Montana. Values of sediment accumulation from North American beaver systems indicate the estimated average accumulation value of 5.4 cm $year^{-1}$ presented by Puttock et al. (2018) in Great Britain may be at the lower end of what is possible in bigger dam–pond complexes or systems with a more plentiful sediment supply. In one of the few other studies in European landscapes, de Visscher et al. (2014) studied sediment accumulation in two beaver pond sequences in the Chevral River, Belgium. de Visscher et al. (2014) estimated the total

FIGURE 1 Examples of dam construction and channel avulsion resulting from beaver dam construction from the River Otter catchment, England. Panel (a) shows an example where a divergent flow path has re-entered the main channel resulting in head-cut erosion. Panel (b) shows the type of multi-thread channel form that occurs downstream of dams in wide, low gradient floodplains. Panel (c) shows a beaver dam on a 4th order stretch of river. (Reproduced with permission from Photos © Hugh Graham and Alan Puttock)

sediment mass deposited in the dam sequences at 495.9 t. From the two pond sequences, average pond area was 200.4 m^2, average sediment depth 25.1 cm, and average sediment mass of 14.6 t, equating to a normalized mass of 72.65 kg of sediment deposited per m^2 of the pond. These values are very similar to the mean sediment depth of 27 cm and mean normalized mass of 71.40 kg m^2 reported from the intensively managed grassland catchment in the UK (Puttock et al., 2018).

The sediment data published also demonstrate that beaver ponds can exhibit high sediment accumulation rates in comparison with other wetland systems. As an example, in a review of sediment accumulation rates in freshwater wetlands (Johnston, 1991) a mean annual accumulation rate of 0.69 cm $year^{-1}$ was reported across 37 different wetland types, ranging from riparian forest to wet meadows. As with the biodiversity benefits of beaver ponds (see Willby et al., 2018 and Section 3 below) the high sediment accumulation rate of beaver ponds in relation to other freshwater wetlands, may reflect the highly dynamic nature of beaver systems, their constant evolution, and sustained maintenance (i.e., continuous dam-building).

The long-term fate of sediment will depend on the availability and composition of deposited sediment, the flow regime, and the preservation of dam structures (Butler & Malanson, 2005; de Visscher et al., 2014). Over many years, sediment may continue to accumulate until each pond fills completely and sediments are colonized by plants forming beaver meadows (Polvi & Wohl, 2012). However, beavers can also contribute to downstream sediment budgets; through the excavation of canal networks and bank burrows (de Visscher et al., 2014; Lamsodis & Ulevičius, 2012), in addition to the release of sediment following dam outburst floods (Curran & Cannatelli, 2014; Levine & Meyer, 2014). Beaver dam failure can result in releases of sediment (Polvi & Wohl, 2012) meaning that sediment storage in ponds can be transient (de Visscher et al., 2014). However, different sediment retention dynamics have been reported following dam collapse. For example, Giriat et al. (2016) found that there were very minimal losses of sediment from beaver ponds studied in Poland, following a dam collapse. Similarly, the majority of sediments were retained in ponds and subsequently stabilized following dam reconstruction (Curran & Cannatelli, 2014; Levine & Meyer, 2014) most likely reducing the downstream release of sediment from any single dam failure within the complex (Butler & Malanson, 2005; Puttock et al., 2018). While recent studies in North America involving extensive survey work have expanded knowledge of beaver dam persistence significantly (Hafen et al., 2020), including persistence during large rainstorm events (Westbrook, Ronnquist, & Bedard-Haughn, 2020), resilience, failure, and associated sediment dynamics are likely to be highly spatially and temporally variable. As identified in Section 2.2 for both hydrological, geomorphic, and associated sediment/water quality impacts a greater mechanistic understanding of dam failure is therefore still required.

Finally, high levels of nutrient-rich sediment have also been shown to result in further biogeomorphic alterations, that is, colonization by homogeneous patches of herbaceous or shrubby species, adding roughness to topography, reduced water velocities, and encouraging further deposition of sediments. Additionally, partial felling and submergence of woody debris disrupts flows and when felled in-channel, creates reinforcement for existing dam structures (Curran & Cannatelli, 2014).

2.1.7 | Impacts of dams on river profile

Beaver dams have two main effects on river profile; (a) long-profile is altered such that a stepped profile develops with sections of reduced gradient, that promote aggradation, upstream of dams separated by hydraulic jumps, created by flow over the dams, which initiates erosion. (b) Channel planform typically increases in complexity with many studies reporting; greater sinuosity, channel width, and the development of a multi-thread planform (Ives, 1942; John & Klein, 2004; Pollock et al., 2014; Wegener, Covino & Wohl, 2017). These increases in cross-profile complexity are driven by an increase in the heterogeneity of flow direction, which drives lateral flow, increasing bank erosion, channel widening, and subsequent localized deposition (Gorczyca et al., 2018).

2.1.8 | Agents of river restoration

In an undisturbed or near-pristine riverine system, the engineering behavior of beaver may simply maintain an evolving geomorphic structure, sustaining a state of dynamic equilibrium in river function. In degraded landscapes (which are much more common), where river planforms are incised, single thread, straightened, even dredged, and lacking in geomorphic diversity, beaver have a dramatic impact on channel planform at multiple scales. In North America, beaver dams and their human-constructed counterparts, known as beaver dam analogs, have been shown to restore degraded river systems (Pollock, Beechie, & Jordan, 2007), primarily through the aggradation of channel beds, leading to greater channel-floodplain connectivity (Macfarlane et al., 2015; Pollock et al., 2014).

Dams, however, are not rigid structures—they influence and are influenced by flow regimes (Johnston & Naiman, 1987) as is evidenced in Figure 2 (after Pollock et al., 2014). In narrow, incised channels, typical of degraded landscapes, beaver dams will capture some sediment but predominantly provide a foci for erosion. In these confined channels, unit stream power is high and therefore dams will frequently blow-out and erode laterally. The resultant effect is a widening of the channel, which leads to a concomitant decline in stream power, thus allowing for greater aggradation rates and less frequent blow-outs altering the sediment regime from net erosional to net depositional (Butler, 1995; Butler & Malanson, 2005). Over time, incised, straightened streams can be restored to complex multi-threaded channel systems that represent a return to the pre-anthropocene streams and rivers that were once common across north-west Europe (Brown et al., 2018). In Poland, beaver initiated geomorphic processes were shown to alter artificially homogenized river reaches and thus it has been suggested that they may have a substantial role to play in the renaturalization of river systems (Gorczyca et al., 2018).

2.1.9 | Summary of geomorphic impacts

- Beaver damming activity is mostly limited to ≤fifth-order streams as low stream power is favorable for dam-building and persistence, with a reduction in the frequency of blowouts.
- Beavers drive a transition in sediment dynamics from dominantly erosional to net depositional, while increasing the spatial variability of both erosional and depositional features.
- Geomorphic change due to beaver is often characterized by changes in channel planform, longitudinal profiles, water surface and channel bed slope, increased sinuosity, and enhanced floodplain connectivity and surface roughness.

2.1.10 | Gaps in geomorphic understanding

- At present, the majority of geomorphology-facing beaver research is from North America. Several studies from Europe indicate strong parallels between the geomorphic impacts between continents. However, geomorphic impacts are strongly influenced by local geography and therefore further monitoring is necessary to complement these findings.
- Research on the impacts of beaver on geomorphic processes is required at larger spatial extents and longer temporal scales. At present, most research focuses on site/reach scale observations, which must be continued in dialogue with long-term, catchment scale monitoring and modeling to build understanding at landscape scales.
- The effects of beaver activity on short-term sediment storage/mobilization due to bank-burrowing and canal excavation, has not yet been substantially investigated.

2.2 | Impacts of beaver upon hydrology

2.2.1 | Overview

There is an increased need to recognize the influence of biology upon river form and process (Johnson et al., 2020) and beavers as recognized ecosystem engineers are a key example of the ability of an animal to influence hydrological functioning. While other beaver engineered structures discussed in Section 2.1, such as burrows and canals, have a measurable impact (Grudzinski, Cummins, & Vang, 2019), the biggest (and most studied) hydrological impact of beavers results from their dam-building ability and the consequent impoundment of large volumes of water in ponds (Butler & Malanson, 1995; Hood & Bayley, 2008). Dam and pond features can alter hydrological regimes, both locally and downstream (Burchsted & Daniels, 2014; Polvi & Wohl, 2012). Beaver activity can reduce downstream hydrological connectivity, and conversely increase lateral connectivity, forcing water sideways into neighboring riparian land, inundating floodplains, and creating diverse wetland environments (Macfarlane et al., 2015), while also contributing to soil and groundwater recharge (Westbrook et al., 2006).

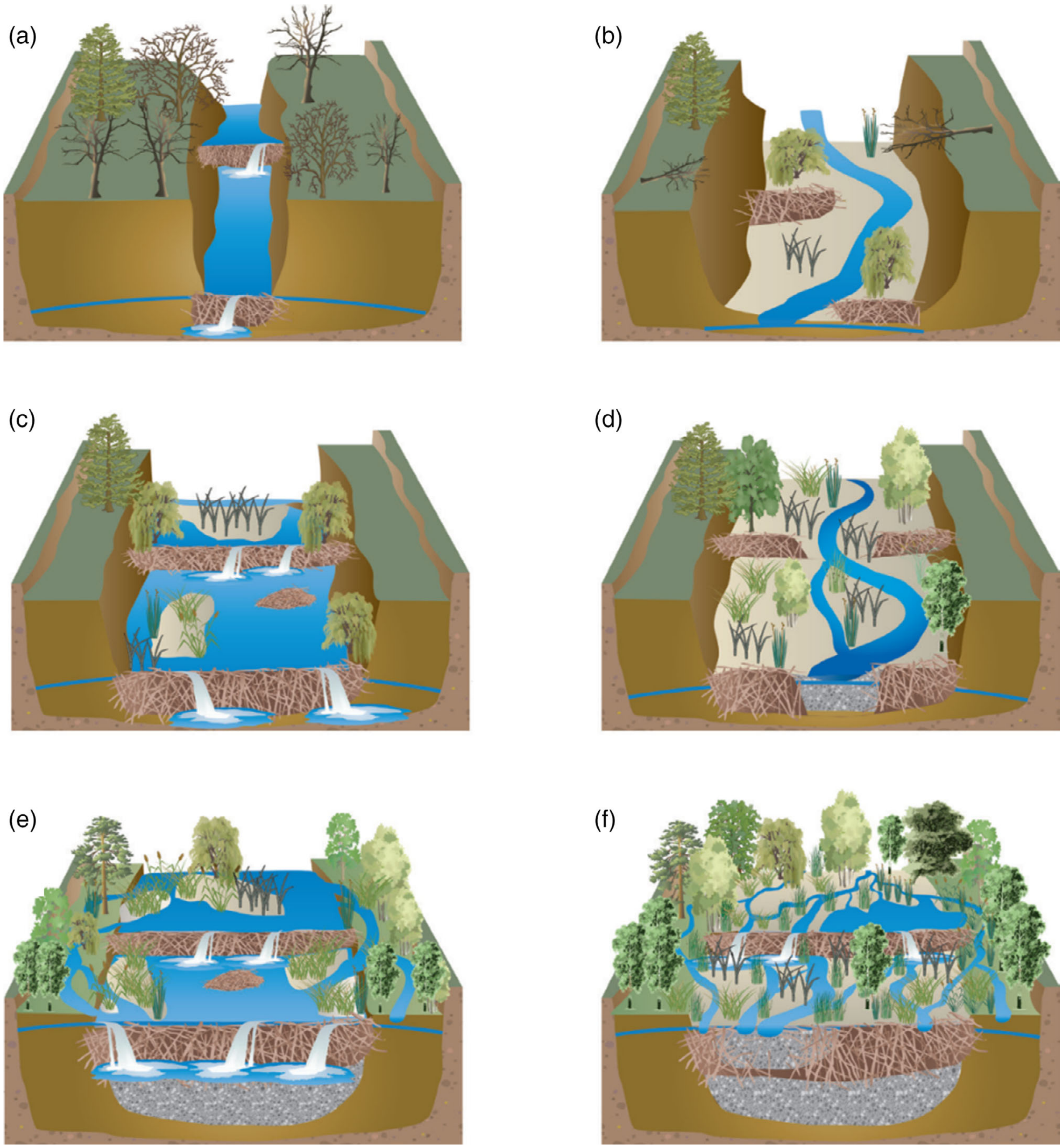

FIGURE 2 The influence of beaver activity on the geomorphology of incised streams: (a) low-flow damming of confined channels with high-flow blowouts causes overtopping, bank widening, and excavation of the channel bed; (b) sediment becomes more mobile and the channel reconfigures with vegetation establishment; (c) channel widening reduces high-flow peak stream power and this provides suitable conditions for wider, more stable dams; (d) sediment accumulates in ponds and raises the height of the channel with dams overtopped and small blow-outs occurring where dams are abandoned; (e) process repeats until dams are rebuilt, channel widens and the water table rises sufficiently to reconnect river channel to the floodplain; and (f) high heterogeneity occurs with vegetation and sediment communities establishing themselves, multi-threaded channels and ponds increase reserves of surface water and dams and dead wood reduce flows and provide wetland habitats. (Reproduced with permission from Pollock et al., 2014)

Multiple studies have identified beaver dam sequences and wetlands as a cause of flow attenuation—so-called "slowing the flow" (Green & Westbrook, 2009; Gurnell, 1998; Pollock et al., 2007). This impact has been attributed to the increase in water storage in beaver pond sequences, relative to undammed reaches (Westbrook et al., 2020), and increased hydrological roughness from the creation of dams and complex wetlands (Puttock et al., 2017), resulting in water being trapped or slowed as it moves through, over and around beaver dams. For example, Green and Westbrook (2009) found the removal of a sequence of beaver dams resulted in an 81% increase in flow velocity. The slow movement of water in beaver impacted sites is attributed to two main mechanisms: (a) increased water storage and (b) stream discontinuity and reduced longitudinal hydrological connectivity (Puttock et al., 2017). The increase in storage provided by beaver ponds and wetlands (Grygoruk & Nowak, 2014; Gurnell, 1998; Woo & Waddington, 1990) lengthens water retention times and reduces the velocity of the water. This in turn can increase the duration of the rising limb of the flood hydrograph which can reduce the peak discharge of floods (Burns & McDonnell, 1998; Green & Westbrook, 2009; Nyssen, Pontzeele, & Billi, 2011). Additionally, water stored in beaver ponds is released slowly as the porous dams gently leak both during and following rainfall, elevating stream base flows even during prolonged dry periods (Majerova, Neilson, Schmadel, Wheaton, & Snow, 2015; Puttock et al., 2017; Woo & Waddington, 1990), increasing environmental resilience to risks including drought and fire (Fairfax & Whittle, 2020).

Water levels in ponds vary significantly as a result of meteorological conditions both over long (i.e., seasonal) and short (i.e., inter-event) timeframes (Puttock et al., 2017; Westbrook et al., 2020). Consequently, seasonal variations in water storage have been observed (see Majerova et al., 2015 for example). It might be expected that the attenuating impact of flow due to storage will be less during wet periods. However, it has been proven that beaver activity still attenuates flow during large events. For example, see Nyssen et al. (2011) who conducted one of the few in-channel hydrological studies of Eurasian beaver; finding that flow attenuation was in fact greatest during largest events. In 2013, Westbrook et al. (2020) monitored the largest recorded flood in the Canadian Rocky Mountains west of Calgary, Alberta, challenging the commonly held assumption that dams fail during large floods (the majority fully or partially persisted) and showing that water storage offered by beaver dams (even failed ones) delayed downstream flood peaks. Therefore, it has been argued that the observed discontinuity or reduced downstream hydrological connectivity resulting from beaver dam-building activity—also shown by Butler and Malanson (2005), is a key reason for the flow attenuation impact persisting even for larger events during wetter periods (Puttock et al., 2017).

Of course, beaver dam construction is highly variable and depends on the existing habitat, building material availability, and channel characteristics (Collen & Gibson, 2000; Woo & Waddington, 1990). Woo and Waddington (1990) identified multiple ways in which dam structure will influence flow pathways and that streamflow can overtop or funnel through gaps in the dams, leak from the bottom of the dams or seep through the entire structure. While the impact of dam structure upon connectivity and therefore, flow velocity will differ (Hering et al., 2001; Woo & Waddington, 1990), all dams will increase channel/hydraulic roughness and therefore, deliver some flow attenuation effect, which can be most significant when a suite of dams in close proximity are constructed (for example see Puttock et al., 2017 case study). Thus, in addition to dam structural variations, it is important to note that the number of dams and their density will strongly influence any observed differences in hydrological function. Existing work has also discussed the importance of the number of dams in a reach, with beaver dams having the greatest impact on hydrology when they occur in a series (Beedle, 1991; Gurnell, 1998). Similarly, sequences of (non-beaver) debris dams in third order, Northern Indiana (USA) streams were found to increase the retention time of water by a factor of 1.5–1.7 (Ehrman & Lamberti, 1992). Ponds located in series provide both greater storage and greater roughness, resulting in a greater reduction in flow velocities as shown by Green and Westbrook (2009). In another study, pond sequences have been shown to reduce the peak flows of 2-year return floods by 14% whereas individual dams reduced flood peaks of similar events by only 5.3% (Beedle, 1991).

There are very few hydrological modeling studies into the impacts of beaver dam sequences upon flow regimes. In European landscapes, this perhaps reflects the fact that until recently there has been both a dearth of beaver dams themselves and also a lack of empirical understanding of the impact on hydrological functioning. In a notable exception, Neumayer, Teschemacher, Schloemer, Zahner, and Rieger (2020) undertook hydraulic modeling of beaver dam sequences and evaluated their impacts during flood events. Utilizing surveys of beaver dam cascades in Bavaria and 2D hydraulic modeling, Neumayer et al. (2020) predicted that during small flood events, beaver dams can deliver significant impacts upon peak flows (up to 13% reductions) and lag/translation times (up to 2.75 hr). But, Neumayer et al. (2020) also predicted that during larger floods (return period $\geq$2 years), the impact upon peak flows of a single dam sequence may be smaller (ca. 2%) and perhaps negligible at the catchment outlet. However, Neumayer et al. (2020) modeled the impacts of beaver dams on channels larger than those that other research has shown might support the greatest densities of dams (i.e., Graham et al., 2020 show that dams rarely persist on >fifth-order streams) and thus it is suggested that further modeling work is required into the downstream hydrological impacts of small streams with high dam densities. In addition, further research is required to understand what the cumulative catchment outlet effects might be if beavers return to being widespread and catchments contain multiple dam sequences (i.e., hundreds of dams) in all headwater streams.

2.2.2 | Summary of hydrological impacts

- Beavers can reduce longitudinal (downstream) connectivity, while simultaneously increasing lateral connectivity, pushing water sideways.
- Beavers can increase surface water storage within ponds and canals, while also elevating the water table and contributing to groundwater recharge.
- Beaver dam sequences and wetlands can attenuate flow during both high and low flow periods.

2.2.3 | Gaps in understanding: Hydrology

- A greater mechanistic understanding of the hydrological impacts of beaver dams and also critically sequences of beaver dams across scales and land uses to inform hydrological modeling, management, and policy decision making.
- Conditions of dam failure and consequences.
- Greater understanding of beaver landscape engineering upon low flow conditions and wetland maintenance during drought.

2.3 | Impacts of beaver upon water quality

The altered flow regimes and water storage capacity discussed in Section 2.2 can also modify sediment regimes and nutrient and chemical cycling in freshwater systems. As a consequence of reduced downstream connectivity and a change from lotic to lentic systems, beaver activity is believed to alter both local and downstream sediment dynamics, and water quality via both abiotic and biotic processes (Cirmo & Driscoll, 1996; Johnston, Pinay, Arens, & Naiman, 1995). It has been argued that two key mechanisms affect the difference in sediment dynamics of water quality observed in beaver systems: (a) slowing of flow resulting in the physical deposition of sediment (reviewed in Section 2.1) and associated nutrients/chemicals, (b) an increase in both ponded water and a local rise in water tables, results in an overall increase in wetness altering the biogeochemical cycling of nutrients (Puttock et al., 2017).

2.3.1 | Impacts on nutrient cycling

When beaver dams inhibit the transport of fine sediments, large volumes of organic and inorganic compounds become stored within beaver ponds (Rosell et al., 2005), including; nitrogen, phosphorus, and particulate (bound) carbon (Lizarralde et al., 1996; Naiman, Pinay, Johnston, & Pastor, 1994). This change increases the volume of anoxic sediments and provides organic material to aid microbial respiration. Nutrients are temporarily immobilized in pond sediments and taken up by aquatic plants, periphyton, and phytoplankton. Increases in plant-available nitrogen, phosphorus, carbon, and increased light availability (due to canopy reduction) favor the growth of instream and riparian vegetation, thus further immobilizing nutrients within plant biomass that re-establishes local nutrient cycles (Rosell et al., 2005). In addition to the impacts of large volumes of sediment, the reduction in free-flowing water and increased decomposition has been shown to increase anaerobic conditions in both pond surface water and saturated soils (Ecke et al., 2017; Rozhkova-Timina, Popkov, Mitchell, & Kirpotin, 2018).

Lazar et al. (2015) show that beaver ponds have a denitrification impact while results from Puttock et al. (2017) showed Total Oxidized Nitrogen (TON) and Phosphate (PO_4-P) to be significantly lower in waters leaving a beaver impacted site compared with water quality entering. These reductions manifest both in terms of concentrations and loads of nutrients, suggesting that beaver activity at the site created conditions for the removal of diffuse pollutants from farmland upstream. Correll, Jordan, and Weller (2000) found that prior to dam construction, TON concentrations were significantly correlated with river discharge but after dam construction, no significant relationship was observed, although there was a correlation between discharge and nitrate (NO_3-N). Similarly, Maret, Parker, and Fannin (1987) identified reductions in Total Kjeldahl Nitrogen (TKN) downstream of beaver dams during high flows. It has also been shown that beaver ponds are particularly effective at NO_3-N retention (K. J. Devito, Dillon, & Lazerte, 1989). It is suggested, therefore, that in agriculturally dominated catchments where diffuse pollution rates are high, beaver ponds may be effective tools to manage N-related diffuse pollution problems from intensive agriculture upstream (Lazar et al., 2015).

Puttock et al. (2017) show that beaver ponds can also act as sinks for phosphorus associated with sediments, while Maret et al. (1987) identified that suspended sediment was the primary source of phosphorus found leaving a beaver pond; therefore, during conditions when more sediment is retained behind the dam than is released, total phosphorus retention will increase. In a study of a beaver impacted and non-beaver impacted catchment (Dillon, Molot, & Scheider, 1991), found total phosphorus export was higher in the non-impacted catchment suggesting that phosphorus was being stored somewhere within the catchment—most probably in the beaver ponds. Lizarralde et al. (1996) also reported that while phosphorus concentrations were significantly higher in riffle sediments, due to extensive wetland creation, total storage was highest in Patagonian beaver ponds. Previous studies have focused primarily on the relationship between discharge and phosphorus concentrations and yields leaving ponds, with inconclusive results. Devito et al. (1989) reported a strong positive correlation between phosphorus loads and stream discharge. However, Maret et al. (1987) report a negative correlation between phosphorus concentrations and discharge and Correll et al. (2000) report no correlation between nutrient flushing and stream discharge following dam construction. Climatic and seasonal changes (Devito & Dillon, 1993; Klotz, 2007) and organic matter availability (Klotz, 2007, 2013) have been shown to affect in-pond phosphorus-dynamics. With regard to downstream impact, the key consensus, that is supported by the correlation between suspended sediment and phosphate concentrations observed in Puttock et al. (2017) is that beaver ponds are effective at retaining phosphorus associated with high sediment loads (Devito et al., 1989; Maret et al., 1987).

Ecke et al. (2017) suggest age dependency as a factor in nitrogen and phosphorus dynamics, with older, more solid dams increasing retention compared to younger more leaky dams. In a review of beaver impacts upon nitrogen and phosphorus content in ponds and downstream, Rozhkova-Timina et al. (2018) cite contradictory information and study results as showing there is a strong contextual dependence and it is clear that further research into the controlling mechanisms of nutrient retention is required.

In contrast to the trends observed for nitrogen and phosphorus, multiple studies, that is, Puttock et al. (2017) and Cazzolla Gatti et al. (2018) found concentrations and loads of Dissolved Organic Carbon (DOC) increase due to beaver activity. This increase is attributed to enhanced sediment and nutrient storage in addition to the overall increase in wetland extent creating an environment rich in organic matter, as previously shown by Vecherskiy, Korotaeva, Kostina, Dobrovol'skaya, and Umarov (2011). Similarly, Law, McLean, and Willby (2016), using color as a proxy for DOC, observed increased concentrations below a series of beaver dams. Dams trap sediment-bound particulate carbon meaning that ponds can act as net stores of carbon (D. Correll et al., 2000; Lizarralde et al., 1996; Naiman, Melillo, & Hobbie, 1986). However, as a consequence of this overall increase in carbon availability, significant exports of DOC have been observed either downstream (D. Correll et al., 2000; Naiman et al., 1994) or in comparison with non-beaver impacted catchments (Błędzki, Bubier, Moulton, & Kyker-Snowman, 2011). Several authors have speculated that the cause of this DOC release relates to (a) incomplete decomposition processes making DOC more available for loss (Cirmo & Driscoll, 1996); (b) enhanced production during primary productivity; (c) a product of enhanced microbial respiration (D. Correll et al., 2000); and (d) retention of particulate organic carbon and litter entering the site and subsequent decomposition (Law et al., 2016). Based upon research in western Siberia, Cazzolla Gatti et al. (2018) argue that beaver activity simultaneously increases nutrient cycling and DOC availability at the same time as increasing carbon sequestration as carbon is accumulated in sediment and removed from the short-term carbon cycle.

pH has been shown to be a first-order control on DOC production and transport in other wetlands (Clark, Lane, Chapman, & Adamson, 2007; Grand-Clement et al., 2014). However, Cirmo and Driscoll (1996) found that a beaver impacted catchment contained higher levels of DOC both before and after $CaCO_3$ treatment (to reduce acidity) when compared with a non-impacted catchment, suggesting that pH plays a limited role in the production of DOC in beaver ponds. Puttock et al. (2017) showed pH to be marginally more alkaline in water leaving the site, which is in agreement with other studies showing more acidic waters in beaver ponds than immediately downstream (Cirmo & Driscoll, 1993; Cirmo & Driscoll, 1996; Margolis, Castro, & Raesly, 2001). However, whether these changes in pH were of a large enough magnitude to alter within site biogeochemical cycling is as yet unclear.

Increased water availability in beaver systems, in addition to a change in chemistry associated with a transformation from lotic to lentic waters, has also been ascribed by multiple studies to control increased leaching of heavy metals from soils and increased concentrations in waters downstream. Releases from pond or increases in downstream concentrations of calcium, iron, and magnesium (for example) were observed by Naiman et al. (1994) and C. A. Johnston et al. (1995), while Levanoni et al. (2015) and Margolis et al. (2001) also observed downstream increases in manganese and observed increasing methylmercury concentrations both downstream of beaver sites and in macroinvertebrates within beaver sites. In a meta-analysis review, Ecke et al. (2017) found young ponds to be a source for methylmercury in water, while old ponds were not, again highlighting that beaver systems are complex and dynamic with a high degree of context-dependence required to understand their impacts upon water quality.

2.3.2 | Summary of water quality impacts

- Beaver wetlands and dam sequences can change parts of freshwater ecosystems from lotic to lentic systems impacting upon sediment regimes and biogeochemical cycling.
- By slowing the flow of water, suspended sediment and associated nutrients are deposited, with ponds shown to be large sediment and nutrient stores.
- Increased water availability, raised water tables, and increased interaction with aquatic and riparian vegetation have all been shown to impact positively upon biogeochemical cycling and nutrient fluxes.

2.3.3 | Water quality gaps in understanding

- Sediment and nutrient dynamics within dam sequences as opposed to individual dams and ponds.
- A greater understanding is required of the contributing source of sediment and nutrients to beaver ponds.
- How long-term beaver dam sequences and wetland dynamics contribute to downstream water quality.
- How the impoundment of water, sediments, and associated nutrients in ponds affects biogeochemical cycling and resulting transfers of nutrients in both gaseous and dissolved forms to understand the contribution of beavers to overall nutrient budgets in both the carbon and nitrogen cycles.

3 | BEAVER IMPACTS UPON LIFE—CONTEMPORARY UNDERSTANDING

3.1 | Impacts of beaver upon aquatic ecology

Enhancement of natural processes, floodplain inundation, lateral connectivity, and structural heterogeneity in beaver-impacted environments creates a diverse mosaic of habitats. Such habitats are underpinned by greater provision of food, refuge, and colonizable niches, which form the cornerstone of species-rich and more biodiverse freshwater wetland ecosystems (Brazier et al., 2020; Campbell-Palmer et al., 2016; Gaywood et al., 2015; Gurnell, 1998; Rosell et al., 2005; Stringer & Gaywood, 2016). Readers are directed to three reviews on this topic: Stringer and Gaywood (2016), which provides a comprehensive overview of the impacts of beaver on multiple species, Dalbeck et al. (2020) which considers the impacts of beavers on amphibians in temperate European environments and Kemp, Worthington, Langford, Tree, and Gaywood (2012) which provides a valuable meta-analysis of the impacts of beaver on fish. This section builds on these reviews to summarize the findings of research into the impacts of beaver activity on aquatic plants, invertebrates, and fish. We focus on these groups as they are widely considered to be strong indicator species of freshwater health and function (Herman & Nejadhashemi, 2015; Law et al., 2019; Turley et al., 2016).

3.1.1 | Aquatic vegetation (macrophytes)

Beavers affect aquatic vegetation through direct and indirect mechanisms over a range of spatial and temporal scales (Rosell et al., 2005). Natural disturbances, including; herbivory, food caching, tree-felling (Campbell-Palmer et al., 2016; Harrington, Feber, Raynor, & Macdonald, 2015), and/or dam-induced extension of wetland area (Gurnell, 1998; Puttock et al., 2017) can aid macrophyte recruitment (Levine & Meyer, 2019), regenerate riparian areas (Jones, Gilvear, Willby, & Gaywood, 2009), and enhance plant biodiversity from the local to the landscape scale (Law, Bunnefeld, & Willby, 2014; Law, Jones, & Willby, 2014; Law, Levanoni, Foster, Ecke, & Willby, 2019; Willby et al., 2018). Canopy-opening and floodplain inundation creates wetland areas with reduced shading (Donkor & Fryxell, 2000; Johnston & Naiman, 1990), providing opportunities for shade-intolerant, opportunistic, and wetland plant species (Law et al., 2016, 2017; Law, Levanoni, et al., 2019; Marshall, Hobbs, & Cooper, 2013). Early successional shifts in newly created wetted zones promote emergent vegetation (Ray, Rebertus, & Ray, 2001), while transitional edges form around pond margins, characterized by rich, diverse, and structurally complex plant communities (McMaster & McMaster, 2001).

Over time, beaver wetland creation, maturation, and abandonment, can result in the siltation of ponds, creating novel habitats in marshy beaver meadows characterized by spatial variability in moisture-regimes which drives higher plant species richness (Polvi & Wohl, 2012; Ray et al., 2001; Wright, Flecker, & Jones, 2003; Wright, Jones, & Flecker, 2002). As beaver meadows mature, terrestrial succession often occurs, leading to herbaceous encroachment, typically comprising grasses, shrubs, and sedges, with studies showing evidence of an eventual return to open, forested, stream environments (Johnston, 2017; Little, Guntenspergen, & Allen, 2012; McMaster & McMaster, 2001; Naiman, Johnston, & Kelley, 1988; Pollock et al., 1995; Ray et al., 2001).

3.1.2 | Invertebrates and amphibians

Beaver increase the heterogeneity of stream depth, flow velocity, and benthic habitats such as silty substrates, woody material (Clifford, Wiley, & Casey, 1993; France, 1997; Rolauffs, Hering, & Lohse, 2001), and both submerged and emergent vegetation, which separately support unique invertebrate species and assemblages (Benke, Ward, & Richardson, 1999; Bush & Wissinger, 2016; Law, Levanoni, et al., 2019; Wissinger & Gallagher, 1999). Beaver ponds support more lentic species (Collen & Gibson, 2000; Margolis et al., 2001; Rosell et al., 2005) and typically demonstrate increased invertebrate abundance (Czerniawski & Sługocki, 2018; Osipov, Bashinskiy, & Podshivalina, 2018; Strzelec, Białek, & Spyra, 2018; Willby et al., 2018), biomass (Osipov et al., 2018) and/or density (McDowell & Naiman, 1986). Beaver ponds may harbor unique assemblages, dominated by collector-gatherers, shredders, and/or predators (Law et al., 2016; McDowell & Naiman, 1986; Robinson, Schweizer, Larsen, Schubert, & Siebers, 2020; Strzelec et al., 2018). However, diversity may be reduced due to the typically homogeneous benthic habitat within ponds resulting from increased fine sediment deposition (Descloux, Datry, & Usseglio-Polatera, 2014; Pulley, Goubet, Moser, Browning, & Collins, 2019). At broader scales, varying successional stages in beaver wetlands, as well as longitudinal variability in habitat type along with beaver dam-pond sequences (e.g., Margolis et al., 2001), increases the taxonomic, trophic, and/or β-diversity of aquatic invertebrate communities compared to environments lacking beaver modification. This is primarily due to the heterogeneity of habitat benefiting a range of both lotic and lentic species (Bush, Stenert, Maltchik, & Batzer, 2019; Law et al., 2016; Pollock et al., 2017; Willby et al., 2018). Furthermore, the storage of sediment and nutrients within beaver ponds improves water quality (Puttock et al., 2017) downstream and therefore enhances habitat for pollution-sensitive species (Rosell et al., 2005; Strzelec et al., 2018).

The gradual release of water from beaver ponds maintains flows during dry periods (Section 2.1), thereby increasing invertebrate resilience to drought by providing refuge pools and greater post-drought recolonization potential (Wild, 2011; Wissinger & Gallagher, 1999). High-head dams promote high velocity and turbulent water over, through, or around dams in side-channels, creating habitat suitable for lotic species, which can otherwise be rare in low-gradient stream reaches (Clifford et al., 1993; Law et al., 2016). In addition, cold hyporheic upwelling and lower stream temperatures downstream of high-head dams, and at depth in beaver ponds, has been shown to benefit the reproductive success of invertebrate species such as mayflies (Fuller & Peckarsky, 2011).

Beaver-engineered woody structures, such as dams and lodges, offer key invertebrate habitats resulting in greater abundance (France, 1997), biomass, density (McDowell & Naiman, 1986; Rolauffs et al., 2001), productivity, richness (France, 1997; Rolauffs et al., 2001), and diversity (Benke, Van Arsdall, Gillespie, & Parrish, 1984) compared to beaver ponds and free-flowing streams. Direct benefits for invertebrates arise from physical complexity, such as the interstices of dams, lodges, bank burrows, and canals, which offer spaces suitable for novel microhabitats (Hood & Larson, 2015; Willby et al., 2018), refuge from predators (Benke & Wallace, 2003), egg-laying (oviposition) sites (Gaywood et al., 2015), and emergent metamorphosis (Wallace, Grubaugh, & Whiles, 1993). These woody structures also provide attachment sites for filter-feeding organisms and foraging resources for species that feed on woody material (xylophagous) and those that feed on the epixylic biofilms which grow on woody surfaces (Godfrey, 2003; Hering et al., 2001; Strzelec et al., 2018). For example, deadwood-eating (saproxylic) beetles are known to occupy beaver-impacted habitats (Horák, Vávrová, & Chobot, 2010; Stringer & Gaywood, 2016). In addition, the retention of organic particulate matter in beaver ponds enhances foraging opportunities for aquatic invertebrates, particularly gatherers and shredders

(Johnston, 2014; Law et al., 2016; Wohl, 2013). Organic drift can also bring wider benefits within catchments, increasing the abundance and/or richness of invertebrates in areas both downstream (Redin & Sjöberg, 2013) and upstream (Rolauffs et al., 2001) of beaver-modified sites.

Dalbeck et al. (2020) conclude that beavers and their habitat creating activities can be pivotal determinants of amphibian species richness, particularly in the headwater streams. The creation of lentic zones in beaver modified wetlands is cited as an essential breeding habitat for amphibian species, but can also be important for entire life history requirements (Cunningham, Calhoun, & Glanz, 2007), with beaver ponds offering sites where reliable spawning and early metamorphosis can take place, in instances comprising exclusive ovipositional sites within wider wetlands (Dalbeck, Janssen, & Luise Völsgen, 2014). Beaver modifications, which increase lentic-rich habitat heterogeneity and/or raise light levels and solar radiation, warming patches of water, in turn, support healthier amphibian assemblages. Such improvements manifest via greater species-richness (Cunningham et al., 2007), diversity (Bashinskiy, 2014; Cunningham et al., 2007; Dalbeck, Lüscher, & Ohlhoff, 2007), colonization rates and abundance (Anderson, Paszkowski, & Hood, 2015; Dalbeck et al., 2014; Stevens, Paszkowski, & Foote, 2007), older-pond density (Stevens et al., 2007), size and productivity compared to unmodified habitats, with connectivity between ponds and through beaver canals reducing distances between breeding and foraging sites (Anderson et al., 2015). Woody complexes which form lodges and dams may also provide valuable habitat which amphibians can use for larval food provision and development (Tockner, Klaus, Baumgartner, & Ward, 2006), potential overwintering hibernation sites (Stevens et al., 2007) or cover from predators (Tockner et al., 2006), with cover options offering predatorial and larval protection by areas of shallow emergent-vegetated pond margins (Dalbeck et al., 2007; Vehkaoja & Nummi, 2015). Conversely, lotic obligate species may be negatively affected by beaver activity (Stringer & Gaywood, 2016), although studies have demonstrated the persistence and high abundance of stream-dependent species on the unimpounded reaches of beaver modified streams (e.g., Cunningham et al., 2007).

3.1.3 | Fish

Beavers and fish have cohabited for millennia (Malison & Halley, 2020) and have previously been shown to coexist positively (Kemp et al., 2012). As such, it is no surprise that beaver-induced habitat changes, particularly increased heterogeneity, can benefit fish populations (Figure 3). Documented benefits include increased: growth rates (Malison, Eby, & Stanford, 2015; Pollock, Heim, & Werner, 2003; Rosell & Parker, 1996), survival (Bouwes et al., 2016), biomass (Bashinskiy & Osipov, 2016), density (Bouwes et al., 2016; Wathen et al., 2019), productivity (Osipov et al., 2018; Pollock et al., 2003; Pollock, Pess, Beechie, & Montgomery, 2004), species richness (Snodgrass & Meffe, 1998), and diversity (Smith & Mather, 2013). Additional benefits to fish include the creation of juvenile rearing habitat (Johnson & Weiss, 2006; Leidholt-Bruner, Hibbs, & McComb, 1992; Pollock et al., 2004), overwintering habitat (Chisholm, Hubert, & Wesche, 1987; Cunjak, 1996; Malison et al., 2015), migratory respite (Virbickas, Stakėnas, & Steponėnas, 2015), enhanced spawning habitat (Bylak, Kukuła, & Mitka, 2014), greater invertebrate food availability (Rolauffs et al., 2001), and refugia from low-flows (Hägglund & Sjöberg, 1999), high discharge (Bouwes et al., 2016), temperature extremes (Wathen et al., 2019), and predation (Bylak et al., 2014). It is for these reasons, that recent approaches in the US have used beaver reintroduction to enhance habitat in support of salmonid reintroduction and/or conservation (Bouwes et al., 2016).

Due to the wide range of changes that beavers bring about, the benefits listed above will likely manifest for a variety of freshwater fish species through a wider understanding of these impacts is required as most research has focused upon interactions between beaver and salmonid species. Salmonids, particularly anadromous species (migrating from the sea to spawn in rivers) hold significant financial, cultural, and recreational value from a fisheries perspective (Butler, Radford, Riddington, & Laughton, 2009). Unfortunately, for a variety of reasons, which have nothing to do with beavers, populations of salmonid populations in Europe are in decline, and the two most abundant native salmonids, the Atlantic salmon (*Salmo solar*) and the Brown/Sea trout (*S. trutta*) are under threat (Forseth et al., 2017). Research in the US has largely shown that beaver reintroduction aids the recovery of salmonid populations (e.g., Bouwes et al., 2016; Wathen et al., 2019); however, despite the long-term coexistence of these species, the expansion and reintroduction of beavers across European landscapes, now substantially altered due to anthropogenic activity, has raised concerns regarding the potential impact that beaver activity may have on salmonid species (Malison & Halley, 2020).

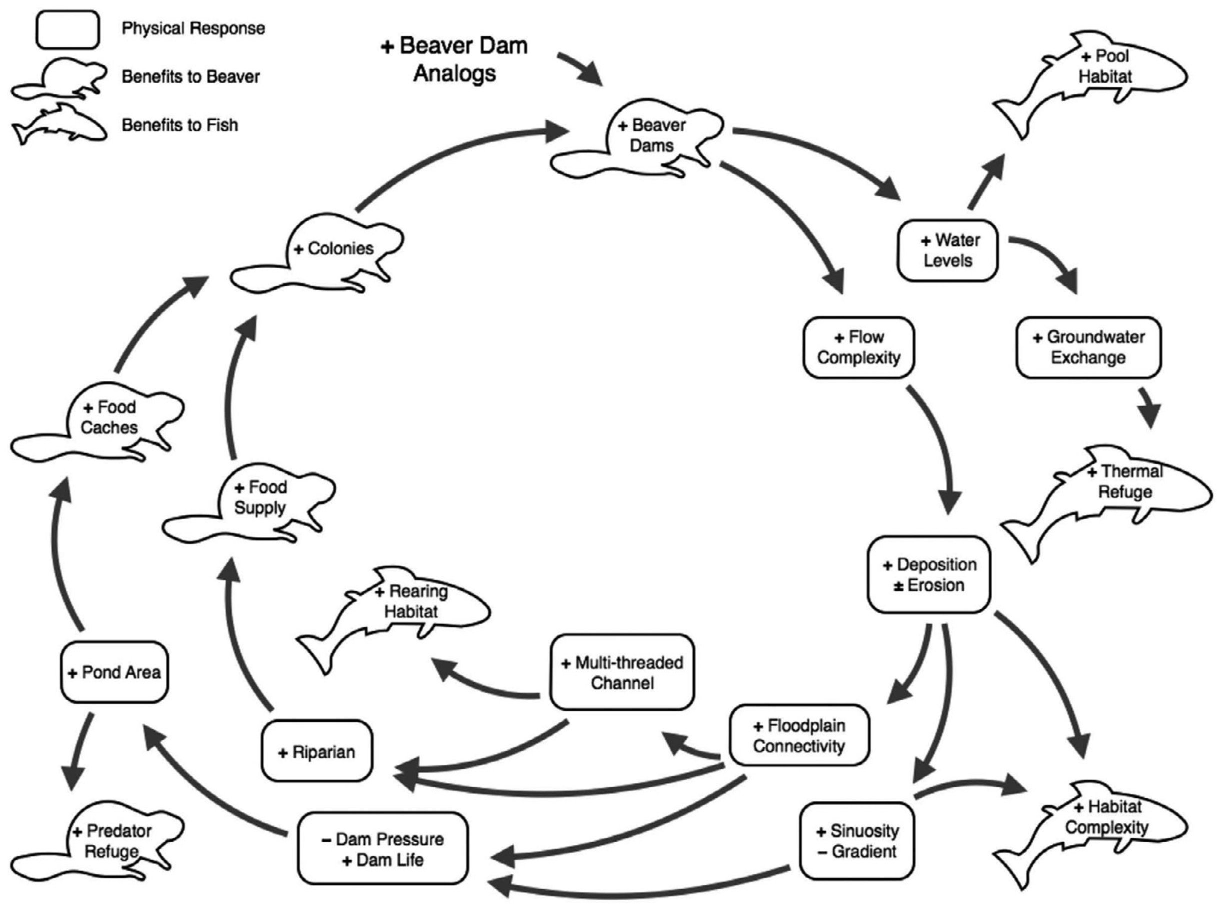

FIGURE 3 Flow Diagram of expected change following beaver return. (Reproduced with permission from Bouwes et al., 2016)

Two recent studies have investigated the impacts of beaver on salmonid habitat and populations in upland streams (Bylak & Kukuła, 2018; Malison & Halley, 2020). Both of these studies report increased habitat patchiness and heterogeneity in river systems that are typically dominated by fast-flowing habitat. Neither study found evidence to suggest that beaver dams prevented fish movement either upstream or downstream. However, Malison and Halley (2020) did find that the presence of beaver dams affected the frequency of movement between stream reaches, suggesting that either beaver dams may act to restrict daily home ranges of salmonids, or the increased local habitat complexity around beaver dams reduces the need for salmonids to travel greater distances. A conflicting finding of these studies is that of the use of ponds by salmonids. In agreement with numerous studies that found beaver ponds to provide valuable rearing habitat (Malison, Lorang, Whited, & Stanford, 2014; Weber et al., 2017) and habitat niches for different stages of salmonid life cycles (Bouwes et al., 2016; Wathen et al., 2019), Bylak and Kukuła (2018) observed that brown trout used different beaver-created habitats throughout their life stages. However, Malison and Halley (2020) reported that they did not observe beaver ponds being used as salmon rearing habitat. Both studies report either no significant effect of beaver on fish populations (Malison & Halley, 2020) or a positive impact on the community composition and patch dynamics (Bylak & Kukuła, 2018).

Virbickas et al. (2015) studied the impacts of beaver on two lowland Lithuanian streams. Unlike, the studies from upland streams, Virbickas et al. (2015) found evidence to suggest that beaver dam sequences do restrict upstream movement of salmonids with reaches below and between ponds being used but no salmonids or redds (spawning sites) being observed upstream of beaver dam complexes. While the presence of beavers did enhance community evenness upstream of dams, this effect was attributed to the exclusion of salmonids, which typically dominated fish communities downstream of dams.

The scale of such studies should be considered carefully in the context of mobile and dynamic species of fish. Bylak and Kukuła (2018) present data from the longest period of monitoring in Europe. They show that the response of fish to beaver activity enhances metacommunity resilience but consequently localized fish communities may alter for short periods of time. However, in these upland systems, high flows capable of "blowing out" dams are more frequent (Macfarlane et al., 2017) thus allowing unimpeded fish movement during these periods. In lowland systems, such as those investigated by Virbickas et al. (2015) the increased hydrological stability may result in a longer lasting separation of fish communities up and downstream of beaver dams. In low gradient systems, where spawning habitat is located solely in the upper reaches of a catchment, the presence of dams could potentially limit access to these reaches, affecting spawning success or resulting in the formation of new spawning habitat, such as the clean gravel bars which commonly form at the tail end of beaver ponds and immediately downstream of dams (Bouwes et al., 2016).

Further research on the impacts of fish across varied European landscapes is required. These studies should seek to understand the effect of beaver on fish communities at the catchment scale. It is well established that fish can navigate beaver dams (Bouwes et al., 2016; Bylak & Kukuła, 2018; Malison & Halley, 2020; Virbickas et al., 2015). However, a greater understanding is required to quantify the importance of any reduced longitudinal movement of fish alongside the known benefits including an increase in food availability and greater habitat diversity.

3.1.4 | Aquatic ecology summary

- Beaver activity extending wetland areas aids aquatic plant recruitment, abundance, and species diversity.
- Nutrient-rich beaver meadows result in mature beaver managed landscapes, contributing diverse plant life, and increasing patchiness in otherwise homogeneous (especially intensively farmed) landscapes.
- Heterogeneity of beaver habitat leads to greater diversity of invertebrates, benefitting both lotic, and lentic species.
- Slow release of water from beaver ponds elevates baseflow downstream supporting greater aquatic life, improving resilience especially in times of drought.
- A multitude of benefits accrue for fish due to beaver activity such as increased habitat heterogeneity and food availability.
- It is established that salmonid species can navigate beaver dams, though there is evidence that the presence of dams does alter the way they move within river networks. The impact of dams on salmonid movement is highly dependent on location and upstream movement may be reduced in low gradient, low energy systems.

3.1.5 | Aquatic ecology gaps in understanding

- Community level, catchment scale understanding of beaver interactions with fish of all species is required to determine whether the changes seen—returning freshwaters to something akin to pre-anthropocene conditions, are overall positive (as current literature suggests) or negative and thus requiring management interventions.
- The narrow, riparian landscapes of many European countries, wherein intensive agriculture encroaches on freshwaters, need further research into the impacts of beavers on both existing vegetation and that which may emerge if more space for water and beavers is made.
- Changes to the ecological status of freshwaters inhabited by beavers are inevitable and research to understand the impact on goals of the Water Framework Directive is needed, to contextualize what is meant by "good" ecological status now that beavers are present.

3.2 | Human–beaver interactions

The potential benefits and impacts of beaver reintroduction (outlined above for the environment) can also manifest for humans. Notably, flow attenuation resulting from beaver damming will be likely to reduce potential for flooding of properties downstream. There is a further socioeconomic benefit not as yet explored in this article; as beavers bring more wildlife to ecosystems, beaver lands can become a focus of wildlife tourism, where humans interact with wild animals or with animals in enclosures (Higginbottom, 2004; Moorhouse, D'Cruze, & Macdonald, 2017). Wildlife tourism is a growing global trend which can engage people with nature, with their experiences often contributing toward local communities, providing benefits for mental health and well-being, and incentivizing nature conservation behaviors

(Curtin, 2009; Curtin & Kragh, 2014; Higginbottom, 2004; Lackey et al., 2019; Newsome, Rodger, Pearce, & Chan, 2019; Skibins, Powell, & Hallo, 2013).

Much wildlife tourism is centered upon "charismatic species" (Curtin, 2010; Skibins et al., 2013), but some are motivated by the intention to support wider biodiversity rather than charismatic species alone (Hausmann, Slotow, Fraser, & Minin, 2017). Beavers are often considered charismatic and, as a keystone species, are associated with biodiverse landscapes, which they create and maintain. Thus, they exhibit both those traits that motivate wildlife tourism. Beaver tourism activities that currently exist in Europe include "beaver safaris", guided tours of beaver-modified landscapes, and information centers (Campbell, Dutton, & Hughes, 2007; Halley et al., 2012; Rosell & Pedersen, 1999). Beaver tourism and associated support for local communities is therefore often cited as one of the reasons for reintroduction where beavers are not yet present (Campbell et al., 2007; Gaywood, 2018; Gurnell et al., 2009; Jones, Halley, Gow, Branscombe, & Aykroyd, 2012; Moran & Lewis, 2014).

There are, however, a number of challenges experienced where beaver and humans interact. In Europe, these are observed mostly where beaver impacts interact with human interests within the riparian zone (Campbell-Palmer et al., 2016; Halley et al., 2012; Heidecke & Klenner-Fringes, 1992), particularly in upper and marginal reaches of watercourses where beaver will undertake the largest-scale habitat alteration (Graham et al., 2020; Halley et al., 2012). For example, where water is stored behind beaver dams, it may inundate land owned by humans which could lead to a financial cost, especially when associated with agriculture or forestry (Campbell-Palmer et al., 2016; Gaywood et al., 2015; Morzillo & Needham, 2015; Parker et al., 1999). Other notable impacts can include beaver burrow collapse and bank erosion in agricultural land (Campbell-Palmer et al., 2016; Gurnell, 1998), beaver grazing on arable crops (Campbell-Palmer et al., 2016, p.; McKinstry & Anderson, 1999), or the felling of particular trees of human importance (Campbell-Palmer et al., 2016; Campbell-Palmer, Schwab, & Girling, 2015). Perhaps not surprisingly, beaver are perceived more negatively by people where these conflicts occur (Enck et al., 1992; Jonker et al., 2010; McKinstry & Anderson, 1999; Payne & Peterson, 1986).

Practical management interventions exist that can be employed to address these factors, including dam removal, bank stability management, flow device installation (to lower water levels), tree protection, restoration of riparian zone as management, supported further by compensation or positive incentive payments (Campbell-Palmer et al., 2015; Campbell-Palmer et al., 2016; Morzillo & Needham, 2015; Pollock et al., 2017). To reduce the potential for further conflicts, however, particularly those that occur between people over species management (Marshall, White, & Fischer, 2007; Redpath, Bhatia, & Young, 2015), it is recognized that engaging with affected individuals and sharing in the decision-making processes for management of beaver is vital (Coz & Young, 2020; Decker et al., 2015, 2016; Redpath et al., 2015).

A recent study of local peoples' attitudes toward beaver in Romania and Hungary demonstrated that beaver was often viewed negatively when related to provisioning ecosystem services but positively regarding regulatory or cultural services. As such the study called for recognition of this complexity in perceptions to minimize conflicts, through "reciprocal learning" between conservationists and locals in adaptive management (Ulicsni, Babai, Juhász, Molnár, & Biró, 2020). For beaver, there are a number of management frameworks which seek to engage with affected parties across Europe in a variety of ways, for example: in Bavaria (Germany), regional authorities employ two beaver managers to oversee a network of volunteer beaver consultants throughout the region (Pillai & Heptinstall, 2013; Schwab & Schmidbauer, 2003); in the Netherlands, the government monitors the beaver population and provides management advice to landowners (Pillai & Heptinstall, 2013); in France, the state authorities provide an advisory service at a catchment scale (Campbell-Palmer et al., 2015; Campbell-Palmer et al., 2016; River Otter Beaver Trial, 2019). However, although engagement is a key component of management strategies, there are to date, few European studies describing attitudes towards beaver (Ulicsni et al., 2020).

The case is different in Great Britain where beaver is currently being reintroduced at a politically devolved level (with the reintroduction status at varying stages throughout the nations) as there have been a number of studies of attitudes towards the species. This may be because an understanding of social factors is a requirement of reintroduction according to the guidelines set by the International Union for the Conservation of Nature (IUCN & SSC, 2013); these guidelines were published in 2013 after many of the reintroduction projects in mainland Europe (Halley et al., 2012), and of course, these guidelines do not apply to established or naturally dispersing populations of beaver that were not therefore "reintroduced". Additionally, there is a recent increase in recognition in the literature that the human dimension of environmental projects is a key component of their success or failure (Bennett et al., 2017a, 2017b; Chan et al., 2007; IUCN & SSC, 2013; Redpath et al., 2015). For example, conflicts between humans and wildlife, or between humans about wildlife, may result in threats to species populations or the future success of any attempted species reintroduction (Dickman, 2017; Manfredo & Dayer, 2004; O'Rourke, 2014).

The British studies of attitudes may have limitations (most notably the ability to which they can be deemed representative of a wider population), but they have consistently demonstrated a majority in favor of beaver projects, ranging between 63 and 95.19% of respondents (Auster, Puttock, & Brazier, 2019). However, the intricacies of the social debate run deeper than a simple "for or against" question. A nationwide survey found an association between support for reintroduction and a positive view of potential impacts, and vice versa (Auster et al., 2019). The respondents from the occupational sectors of "Farming and Agriculture" or "Fisheries and Aquaculture" were less likely to have a favorable view of beaver impacts and were thus often (though not unanimously) opposed to beaver reintroduction, which is in line both with other studies conducted in Great Britain (Auster, Barr, & Brazier, 2020a; Crowley, Hinchcliffe, & McDonald, 2017; Gaywood, 2018; Lang, 2004; Scott Porter Research and Marketing Ltd, 1998) and the aforementioned conflict challenges which have been observed across mainland Europe.

Socially, when whomever gains or losses from beaver reintroduction is examined it is concluded that (in certain scenarios) those people who experience the benefits may differ from those who experience the costs (Brazier et al., 2020; Gaywood, 2018). Although it is often cited that the potential benefits of beavers will outweigh the costs (Brazier et al., 2020; Campbell et al., 2007; Gaywood, 2018; Gaywood et al., 2015; Gurnell et al., 2009; Jones et al., 2012; Tayside Beaver Study Group, 2015), the costs that do occur may be attributed to a small number of people who themselves derive little or no direct financial benefit. This distinction between potential beneficiaries and the negatively impacted parties is perhaps most easily demonstrated in the case of beaver damming, where a downstream community may benefit significantly from flood alleviation while the landowner upstream may experience flooding on their property. Thus, strategic management decisions will need to consider how to bridge this disconnect and address potential conflict issues while allowing for the potential opportunities for biodiversity, flow attenuation, water quality, and ecotourism to be maximized.

It is highlighted herein, that to enable maximization of the opportunities from beaver reintroduction that are reviewed above, these conflicts will need to be appropriately recognized; the best management strategies are those where issues are mutually addressed between wildlife management authorities and stakeholders (Auster, Barr, & Brazier, 2020b; Redpath et al., 2015; Rust, 2017; Treves, Wallace, & White, 2009). There are real opportunities resulting from beavers, as discussed above, but there are real conflict challenges to be addressed as well, and they should be considered as one within a holistic approach with a closed-loop between the beneficiaries and the negatively affected. Further, in the case of reintroduced beavers, such management considerations will need early attention if the potential for later conflicts is to be reduced, particularly as challenges may not yet exist but could occur post-introduction (Auster et al., 2019; Conover & Decker, 1991; Coz & Young, 2020).

Finally, holistic management strategies will need to incorporate effective communication to aid the reduction of potential conflict issues. In a case from Poland, beavers had been reported as of concern by fishery managers, who cited damage to pond levees. Some of the participants had received compensation for reported damage, but a number of fishery managers had undertaken both authorized and unauthorized beaver culls as the beavers were viewed as problematic. In this scenario, it was reported that "poor communication" by conservation bodies was a particular part of the problem, with a lack of information on management measures and unresponsiveness from government agencies being factors which were suggested to have exacerbated conflict (Kloskowski, 2011). However, the literature recognizes that, when stakeholders are appropriately engaged and communication is effective, trust can be fostered between stakeholders and the wildlife management authorities (Decker et al., 2015, 2016; Redpath et al., 2015; Rust, 2017; Treves et al., 2009). This in turn can enable an environment within which, as Redpath et al. remarked in 2013, wildlife management issues and decisions can be "shared as one" (Redpath et al., 2015).

3.2.1 | Summary of human–beaver interactions

- There are real opportunities for humans provided by beavers, as well as real potential conflicts between humans and the activity of beavers. The opportunities may be realized by different people to those who incur the costs in certain contexts.
- Effective management strategies should consider the beneficiaries and cost-bearers in a holistic manner, bridging the distinctions within a closed-loop management system.

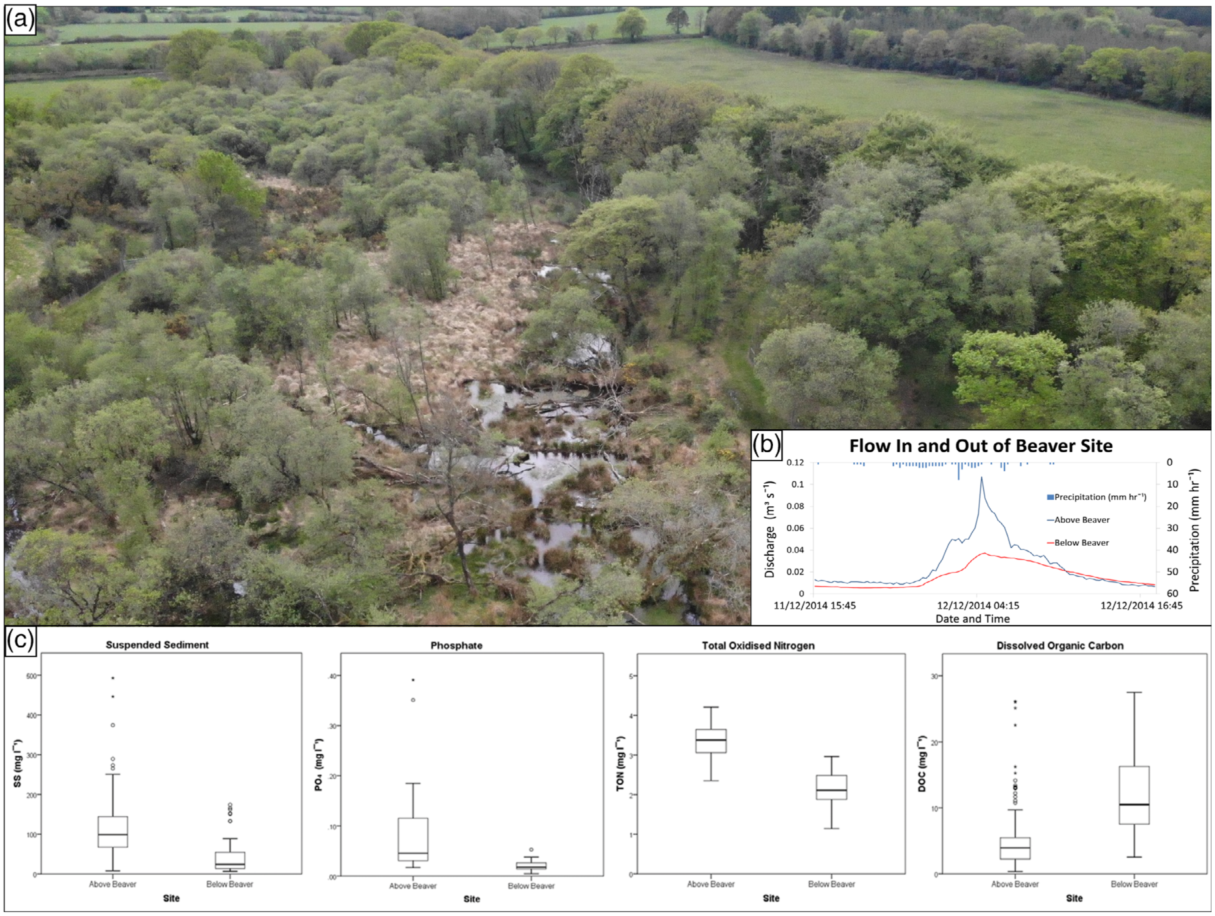

FIGURE 4 A summary figure for the Devon Beaver Project: (a) aerial photo showing the beaver wetland nestled amongst an agriculturally dominated landscape; (b) an example hydrograph showing the contrast in flow regime between water entering the site (blue) and water leaving the site (red); (b) summary water quality results from the site for each figure "Above Beaver" to the left is the concentration entering the site and "Below Beaver" to the right is concentration leaving the site. From left to right: suspended sediment, phosphate, total oxidized nitrogen, and dissolved organic carbon

- Management strategies require clear communication to gain trust between stakeholders and the wildlife management authority, thus providing an environment that is conducive toward addressing issues as a collective and reducing the potential for conflict between parties.

3.2.2 | Human–beaver gaps in understanding

- Where they are reintroduced, living with beavers (and associated management) will be a new concept. How do people learn and adapt to this change?
- In policy, what is the best approach for a closed-loop management framework that maximizes opportunities, for example, ecosystem service provision, while minimizing the potential for conflicts?
- What is the best way to disseminate information regarding approaches to management?

4 | CONCLUSION: FUTURE SCENARIOS AND CONSIDERATIONS

The beaver is clearly the very definition of a keystone species. The myriad ways in which it alters ecosystems to suit its own needs, which in turn supports other species around it, demonstrate its value in re-naturalizing the heavily

BOX Case study: Hydrology and water quality—Devon Beaver project

Puttock et al. (2017) undertook research at an enclosed and therefore controlled beaver reintroduction site in Devon, South West England. The site is situated on a first-order stream. In March 2011, a pair of Eurasian beavers were released into a 3 ha enclosure, dominated by mature willow and birch woodland, in addition to gorse scrub. Upstream, the site was fed by a 20 ha catchment area dominated by intensively-managed grassland. As illustrated in Figure 4, beaver activity at the site created a complex wetland, dominated by 13 ponds, dams, and canal networks (Puttock, Cunliffe, Anderson, & Brazier, 2015). Flow was monitored upstream and downstream of the beaver ponds.

Monitoring of the site between 2013 and 2016 showed that the 13 ponds covered >1,800 m^2 and stored >1 million liters of water. Across 59 rainfall-runoff storm events, the outflow below the beaver impacted site showed a more attenuated response relative to water entering the site. Events exhibited on average 34% lower total event discharges, 30% lower peak discharges, and 29% longer lag times below the beaver dam sequence, in contrast, to flow entering the site. Critically, Puttock et al. (2017) analyzed a sub-set of the largest flood events of greatest interest from a flood risk management perspective. Results showed the flow attenuation impact to persist. Additionally, while the inflow to the site was ephemeral, drying up during drought periods, the outflow from the site never dried up during the monitoring period, highlighting the ability of increased water storage in beaver wetland environments to maintain base flow in river systems.

Analysis was undertaken into sediment storage within the site and water quality entering and leaving the site. A site survey (Puttock et al., 2018) showed that ponds held over 100 t of sediment, 15 t of carbon, and 1 t of nitrogen. Pond size was shown to be the greatest control over storage, with larger ponds holding more sediment per unit area. Source estimates indicated that >70% of the sediment trapped in the ponds was from the upstream agriculturally dominated catchment. A summary of water quality results taken during rainfall-runoff events (see Puttock et al., 2017) showed that on average, compared to water entering the site, water downstream of the beaver dam sequence contained 3 times less sediment, 0.7 times less nitrogen, 5 times less phosphate, but twice the dissolved organic carbon content. Associated flow attenuation was shown to result in further reductions in total loads.

degraded environments that we inhabit and have created. The impacts of beaver reintroduction reviewed herein; to deliver changes to ecosystem structure and geomorphology, hydrology and water resources, water quality, freshwater ecology and humans, and society are profound. Beaver impacts are not always positive, at least from a human perspective, thus it remains critical that the knowledge gaps identified above are addressed as beaver populations grow, to ensure that improved understanding coupled with clear communication of beaver management can prevail.

Where beavers do deliver positive change, on balance benefits are shown to outweigh the costs associated with beaver reintroduction or management. It is unlikely that any other species, including humans, will deliver these changes, thus it would seem rational to conclude that beaver population expansion should be supported, wherever habitat is suitable and the species naturally occurred historically. Indeed, it is suggested that reintroducing beavers, is a genuine example of "working with natural processes" or implementing "nature-based solutions", which are both low cost and multi-faceted. As such, beaver reintroduction can underpin approaches to reverse the decline of species extinctions while also delivering ecosystem services, which may increase resilience to climate change and mitigate associated risks such as flooding and drought.

Of course, such an environmentally progressive approach needs to be implemented hand-in-hand with an appropriate management regime, ideally funded by Government, to capitalize on the environmental goods and services that beavers provide, and established as part of a national (or even international) strategy for the reintroduction of the beaver. Such management approaches have been normalized in places such as the German state of Bavaria, where beavers now deliver the wide range of ecosystem services reviewed above, with a pragmatic and flexible approach towards beaver management to support people who experience negative impacts while supporting a favorable conservation status of the species (Pillai & Heptinstall, 2013; Schwab & Schmidbauer, 2003). Other countries, including GB where beaver populations are in their infancy, but expanding, would do well to adopt similar management strategies (e.g., see the River Otter Beaver Trial, 2019) to ensure that successful reintroduction of beavers maximizes the environmental opportunities and minimizes the social conflicts that may manifest (Box 1).

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

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Richard Brazier: Writing-original draft; writing-review and editing. **Alan Puttock:** Writing-original draft; writing-review and editing. **Hugh Graham:** Writing-original draft; writing-review and editing. **Roger Auster:** Writing-original draft; writing-review and editing. **Kye Davies:** Writing-original draft; writing-review and editing. **Chryssa Brown:** Writing-original draft; writing-review and editing.

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Appendix 4. Beaver dams attenuate flow: A multi-site study

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RESEARCH ARTICLE

WILEY

Beaver dams attenuate flow: A multi-site study

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Abstract

Beavers can profoundly alter riparian environments, most conspicuously by creating dams and wetlands. Eurasian beaver (*Castor fiber*) populations are increasing and it has been suggested they could play a role in the provision of multiple ecosystem services, including natural flood management. Research at different scales, in contrasting ecosystems is required to establish to what extent beavers can impact on flood regimes. Therefore, this study determines whether flow regimes and flow responses to storm events were altered following the building of beaver dams and whether a flow attenuation effect could be significantly attributed to beaver activity. Four sites were monitored where beavers have been reintroduced in England. Continuous monitoring of hydrology, before and after beaver impacts, was undertaken on streams where beavers built sequences of dams. Stream orders ranged from 2nd to 4th, in both agricultural and forest-dominated catchments. Analysis of >1000 storm events, across four sites showed an overall trend of reduced total stormflow, increased peak rainfall to peak flow lag times and reduced peak flows, all suggesting flow attenuation, following beaver impacts. Additionally, reduced high flow to low flow ratios indicated that flow regimes were overall becoming less "flashy" following beaver reintroduction. Statistical analysis, showed the effect of beaver to be statistically significant in reducing peak flows with estimated overall reductions in peak flows from −0.359 to −0.065 $m^3\ s^{-1}$ across sites. Analysis showed spatial and temporal variability in the hydrological response to beaver between sites, depending on the level of impact and seasonality. Critically, the effect of beavers in reducing peak flows persists for the largest storms monitored, showing that even in wet conditions, beaver dams can attenuate average flood flows by up to ca. 60%. This research indicates that beavers could play a role in delivering natural flood management.

KEYWORDS
beaver, beaver dams, catchment management, flood peaks, flow attenuation, flow regimes, hydrology, natural flood management

1 | INTRODUCTION

Beavers have the capacity to modify freshwater ecosystems extensively (McKinstry et al., 2001), creating diverse wetland habitats with significant biodiversity benefits (Brazier, Elliott, et al., 2020; Law et al., 2016; Rosell et al., 2005; Willby et al., 2018). Beavers are considered a keystone species due to their engineering, notably the construction of dams and impoundment of large volumes of water

(Hood & Bayley, 2008). Such alterations to ecosystem structure impact upon hydrological functioning by increasing water storage (Grygoruk & Nowak, 2014; Westbrook et al., 2020) but also a change in downstream connectivity (Macfarlane et al., 2015). The impact upon hydrological functioning can be summarized as an increase in lateral connectivity, with dams pushing water out sideways onto floodplains (Puttock et al., 2017). Such a change has been shown to result in flow attenuation characterized by increased water retention and increased rainfall to peak flow lag times (Burchsted & Daniels, 2014; Green & Westbrook, 2009; Westbrook et al., 2020) and reduced flows (Beedle, 1991; Burchsted & Daniels, 2014) downstream of beaver sites. These impacts result due to increased water storage and increased structural roughness created by dams reducing downstream connectivity during storm flow events (Puttock et al., 2017). Conversely, water storage in ponds and overall flow regime attenuation can also result in a persistence of downstream hydrological connectivity during low flow or drought periods via the slowed release of water and maintenance of base flows (Fairfax & Small, 2018; Pilliod et al., 2017).

Flooding is an economically and socially costly natural hazard, predicted to increase under future climate scenarios (Dadson et al., 2017). There is also a growing recognition of the multiple benefits of working with natural processes to deliver ecosystem services with societal benefits including flood risk reduction (Lane, 2017). Natural flood management or hybrid “soft” engineering approaches may provide holistic, catchment-based flood management options (Hewett et al., 2020; Lane, 2017; Wilkinson et al., 2014), increasing the resilience or effectiveness of existing conventional “hard” engineering defences and delivering wider environmental and societal benefits (Lane, 2017). They may also provide alternatives at the local scale where hard engineering is not viable or affordable (Short et al., 2019). Beavers have been posited as a possible natural flood management option (Environment Agency, 2014). However, with a few exceptions (e.g., de Visscher et al., 2014; Nyssen et al., 2011) the existing hydrological research into the impacts of beaver has been undertaken in North America in extensively managed landscapes (Burns & McDonnell, 1998; Green & Westbrook, 2009). Previous work on a small, first-order stream in England demonstrated the ability of beavers to transform a single channel into a series of ponds (Puttock et al., 2015), store large volumes of water, attenuate flow regimes leading to reduced peak and total flows downstream during storm events (Puttock et al., 2017) and also trap sediment and nutrients (Puttock et al., 2018). On a 2nd order stream in a forest mountain catchment in Belgium, beaver dams were shown to result in flow attenuation by reduced flood peaks and increased low flows (Nyssen et al., 2011). Modelling on Bavarian river systems (Neumayer et al., 2020) showed alternation to flow regimes and flow attenuation. Whilst these studies illustrate the potential of beaver dams to attenuate flooding, there is little empirical understanding into the impact of beaver upon hydrological functioning across the range of scales where damming may occur (Graham et al., 2020) in intensively managed landscapes representative of large areas of northern Europe.

Most European catchments have become a product of human activity with associated problems including hydrological extremes, diffuse pollution and soil erosion (Hewett et al., 2020). In such landscapes it has been suggested that beaver previously exerted a large influence on riverine structure and function (Brown et al., 2018). Hunted to near extinction, the Eurasian beaver (*Castor fiber*) has now been reintroduced to much of its former range (Halley et al., 2012), with recent reviews estimating populations at 1.5 million (Halley et al., 2020). In Great Britain (GB), where beavers were extirpated and thus absent by the 16th Century (Conroy & Kitchener, 1996), there are now an increasing number of controlled release sites and expanding wild populations (Brazier, Puttock, et al., 2020; Campbell-Palmer et al., 2018). Such population increases add urgency to the need for increased understanding of beaver impacts to inform catchment management strategies, to maximize opportunities but also mitigate conflict (Auster et al., 2019, 2020; Campbell-Palmer et al., 2016). Key examples of conflicts recorded GB landscapes include agricultural crop feeding, burrowing and damming that puts agriculture or critical infrastructure at risk (Campbell-Palmer et al., 2020).

Working across spatial scales represented by differences in drainage density at the small catchment size (with second to fourth order channels) and catchments dominated by both lowland agriculture and forestry, this study applied a standardized suite of hydrological analyses to address the following hypotheses:

H1. Hydrological event peak flows and flashiness are reduced following beaver modification.

H2. Peak flow attenuation can be attributed beaver engineering, particularly the construction of dams.

2 | METHODS

2.1 | Study sites

Hydrological monitoring was undertaken across four sites (Locations in Figure 1 with additional aerial imagery of sites in SI.6) in England adopting a multi-site before-after beaver experimental design, that is, monitoring downstream of beaver reintroduction sites was undertaken prior to release, then continued post-release to understand impacts upon hydrological functioning, relative to rainfall. At one site (Budleigh Brook) where beavers established a territory, a suitable control site was fortunately available allowing for a full Before-After-Control-Impact (BACI) experimental design (Bilotta et al., 2016). Two of the beaver impacted sites (Woodland Valley and Budleigh Brook) had agriculturally dominated catchments (both intensive and extensive grassland and some arable), whilst the other two beaver impacted sites (Forest of Dean and Yorkshire) were forestry dominated. Beaver dam modelling presented in Graham et al. (2020) showed all sites to have high capacities for supporting dam sequences, indicating that they were suitably representative of where beaver dam sequences may be expected. The authors were not responsible for the release of beavers, the timing and location of releases or, in the case of Budleigh Brook, natural colonization could not be prescribed. Therefore, the

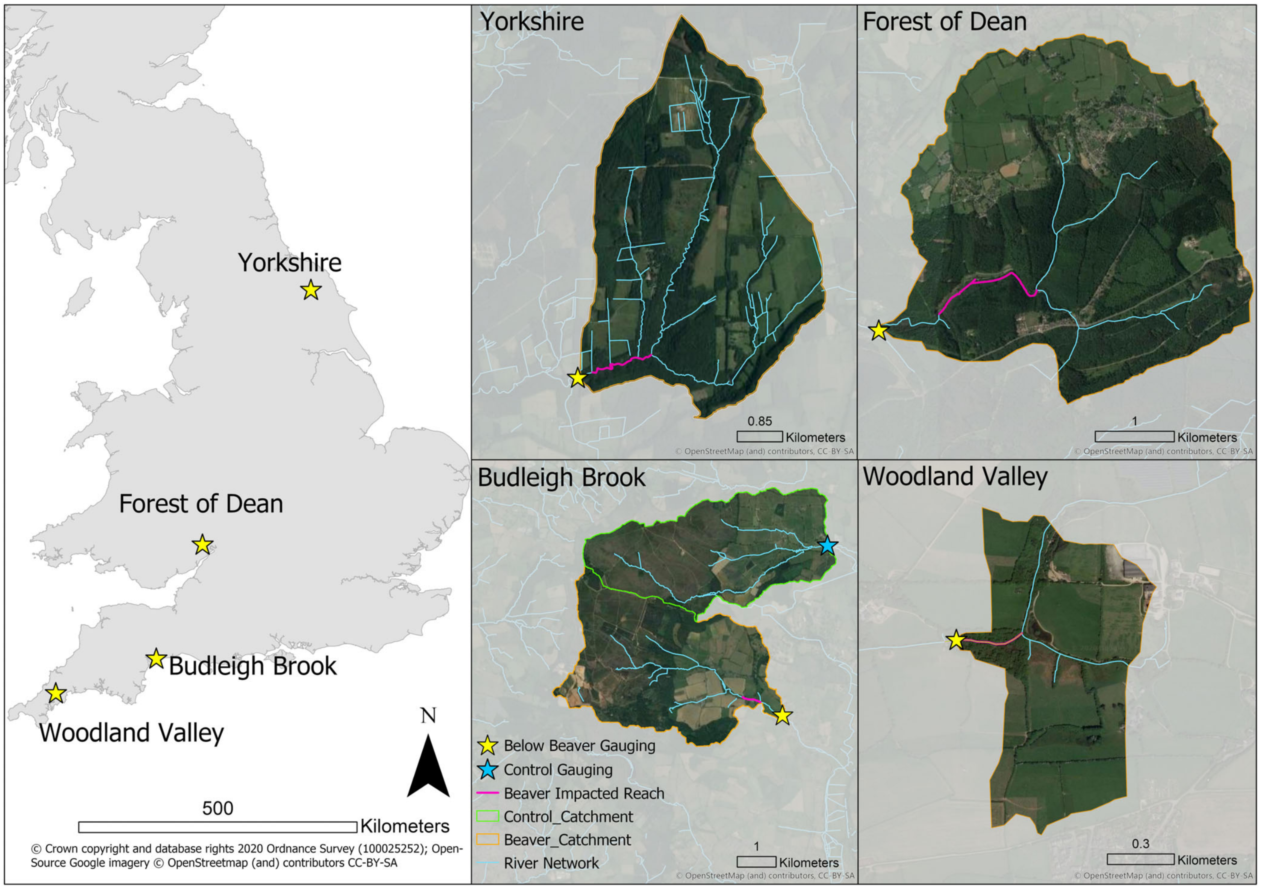


FIGURE 1 Left: Study site locations within England. Right: Catchment areas for the four study sites indicating the location of beaver complexes and flow gauging

duration of monitoring and therefore the number of hydrological events analysed varies between sites and before/after beaver colonization. We have therefore adopted statistical approaches that can accommodate such an experimental design but acknowledge that the power of derived statistical models will vary between sites as a consequence.

2.1.1 | Woodland valley

Woodland Valley (WV) hosts the Cornwall beaver project and is situated on a 2nd order stream. The site experiences a temperate climate with an annual mean maximum temperature of 13.5°C and mean annual rainfall of 1017.4 mm (Met Office, 2020). In June 2017, a pair of beavers were introduced to a 1.5 ha enclosure, dominated by willow and birch woodland, in addition to gorse scrub. The site has a 134 ha contributing area dominated by grazed grassland (~70%) and some arable that didn't change through the monitoring period. Beavers created 7+ dams in addition to damming and raising the water level in a pre-existing pond. Further information on the project and partnership involved can be found at: https://www.cornwallwildlifetrust.org.uk/what-we-do/our-conservation-work/on-land/cornwall-beaver-project.

Flow in and out of the site was monitored to create a continuous record of discharge from November 2015 to March 2019. A smooth lined culvert on the channel leaving the enclosed site was instrumented with an in-situ submersible pressure transducer (IMSL–GO100, Impress, United Kingdom) situated in a stilling well. Water level was recorded on a 15 min time step. Water level was converted to discharge using Manning's equation with a surface roughness value of 0.015 =:

$$Q = \frac{KAR^{0.667}S^{0.5}}{n}$$

Q = flow rate; A = cross sectional area of flow; R = hydraulic radius (cross sectional area divided by wetted perimeter); S = slope of channel (rise) n = Manning's surface roughness value. K = constant (1 for metric measurements).

2.1.2 | Budleigh Brook and control site

A free-living beaver group established themselves on the 3rd order Budleigh Brook in the River Otter catchment, Devon. The population has been present since January 2017. The occupied section of channel is ~1 km long and has contained up to 6 dams. It has a 6.3 km^2 contributing catchment area of mixed landuse, (intensively managed grassland, pig farming, arable, heath and woodland). The site experiences a temperate climate with an annual mean maximum temperature of 12.6°C and mean annual rainfall of 1065.3 mm (Met Office, 2020). Further information about the trial can be found at: https://www.devonwildlifetrust.org/what-we-do/our-projects/river-otter-beaver-trial.

An Environment Agency (EA) gauging station is located 700 m downstream of the lowest beaver dam. No substantial hydrological inputs occur between the site and the gauge. The gauge measures water depth, at 15 min intervals, within a stilling pond, upstream of a trapezoidal weir with low flow trapezoidal notch. The weir was rated with an area-velocity flow meter (NivuFlow Mobile 750, Nivus, Germany) for two months. A flow rating equation (data repository in Data S1) was generated between flow and depth using piecewise spline regression as described in Fenton (2018); undertaken using the splines package (R core team, 2020). The period of monitoring extends from July 2009 – March 2020.

The neighbouring catchment is Colaton Brook a 3rd order stream with a contributing catchment area of 5.5 km^2. The landuse is mixed, comprising heathland, managed grassland, arable, and woodland. No beavers have been observed in the catchment. A downstream EA gauging station provides 15 min interval flow measurements. The comparable size and locale of this catchment makes it a highly suitable control catchment, which can be used to evaluate the effect of beavers on Budleigh Brook in a BACI framework.

2.1.3 | Forest of Dean

The Forest of Dean beaver project is situated on the 3rd order Greathough Brook, Gloucestershire. The site experiences an annual mean maximum temperature of 14.4°C and mean annual rainfall of 733.5 mm (Met Office, 2020). In July 2018, a pair of beavers was introduced to a 6 ha enclosure, dominated by mixed broad-leaf woodland. The site has a 410 ha contributing area dominated by mixed broad leaf woodland and some roads/ urban areas. Since release, beaver have created 3 dams. Further information on the project can be found at: https://www.forestryengland.uk/beavers-greathough-brook-forest-dean.

The site was from October 2017 to May 2019 at which point beavers were temporarily removed from the site for a project pause (the monitoring time series used included 9 months of pre-beaver baseline data and 10 months of post-beaver data). A monitoring station on a culvert leaving the site was instrumented with an in-situ submersible pressure transducer (MX2001, HOBO ONSET, USA) recording on a 15 min time step. Water level through the culvert was converted to discharge using Manning's equation using a roughness coefficient of 0.015 for a smooth lined culvert [Equation (2)].

2.1.4 | Yorkshire

On 17 April 2019, a beaver pair were released into a 16 ha enclosure in Cropton Forest, North Yorkshire, on a 4th order stream (Sutherland Beck) as part of a five-year scientific trial. The site has a 747 ha catchment upstream and the landuse is a mixture of widely spaced beech and pine with a rhododendron understorey, plantations of Norway Spruce, Scots Pine, Douglas fir and stands of Silver Birch (Forestry England, 2020). The site experiences an annual mean maximum temperature of 11°C and mean annual rainfall of 978.9 mm (Met Office, 2020). The site was part of a project focusing on natural measures to alleviate flooding downstream. Information on the Slowing the Flow project in the River Seven and Pickering Beck catchments, can be found at: https://www.forestresearch.gov.uk/research/slowing-the-flow-at-pickering/slowing-the-flow-at-pickering-about-the-project/. As part of this initiative multiple timber bunds are in place across the channel. However, they have not changed post-beaver reintroduction and, during the analysis, there was no interaction recorded between beavers and these structures so they were treated as a constant and not explicitly considered in analysis. Further information on the project can be found at: https://www.forestryengland.uk/beaver-trial-cropton-forest.

The site was monitored to create a continuous record of discharge from December 2018 to March 2020 (this monitoring included 5 months of pre-beaver baseline data and 11 months of post-beaver data). A monitoring station on the channel leaving the site was instrumented with an area-velocity flow meter (NivuFlow Mobile 750, Nivus, Germany) and an in-situ pressure transducer (MX2001, HOBO ONSET, USA), recording on a 15 min time step. Discharge from the area-velocity flow meter was checked against level data from the pressure sensor.

2.2 | Data analysis

Links to full data analysis repositories are included in Data S1.

2.2.1 | Rainfall data collection

Whilst sites were equipped with a tipping bucket rain gauge (RG3M, HOBO ONSET, USA), rainfall is spatially variable and data from a single rain gauge can be non-representative, particularly in forested catchments (Younger et al., 2009; Zeng et al., 2018). Therefore, rainfall radar data, derived from the NIMROD system (Met Office, 2003), was used across sites. NIMROD data are provided as gridded total rainfall with resolutions of 1 km and 5 min, respectively. Total rainfall for each time step was extracted for each site's contributing catchment area and converted to mean rainfall rate, before aggregating to 15 min to align with the temporal resolution of flow data. Data download and conversion (Data S1) was conducted using Python 3 and raster statistics were extracted with R using the exactextractr package (Bastion, 2020).

2.2.2 | Data preparation and storm event extraction

The systematic extraction of rainfall-runoff events and corresponding metrics was undertaken using a semi-automated rules-based approach for the identification and pairing of rainfall and flow geometries from sub-hourly observations (Ashe et al., 2019; Deasy et al., 2009; Glendell et al., 2014; Ladson et al., 2013; Luscombe, 2014; Puttock et al., 2017) summarized in Figure 2. Data were sub-sampled at 15 min intervals and pre-processed for quality control (Ashe et al., 2019). The automated systematic approach for flow event extraction is sensitive to low flow variability in the discharge time series. Therefore, we used an automated cleaning strategy. This approach calculates rolling quantiles for a specified time window (12.5 h) at the 25th and 75th percentile, (Q25th and Q75th respectively). A rolling quantile for the 70th percentile for a one month period is also calculated (MQ70). Where (Q75th - Q25th) > MQ70, the flow is considered to be elevated and any fluctuation in flow is driven by precipitation; therefore measured Q is used. Where (Q75th - Q25th) < MQ70, the flow is considered to be low and not responding to a flow event; we therefore used a 7.5 h rolling mean for Q in place of measured Q to smooth out sensor noise during low flows. No cleaning was applied to flow event peaks and thus did not alter the observed results derived from the event extraction process. Slow flow (equivalent to base flow) and quick flow (equivalent to stormflow) was estimated by implementing flow separation on the time series after Ladson et al. (2013). Analysis was done in R 3.6.3. (R Core Team, 2020). Event extraction time series for each site are included in data repository with an example in Figure S1. Event metrics were calculated for each event (Data S1). Misidentified events were located through visual inspection and removed from analysis.

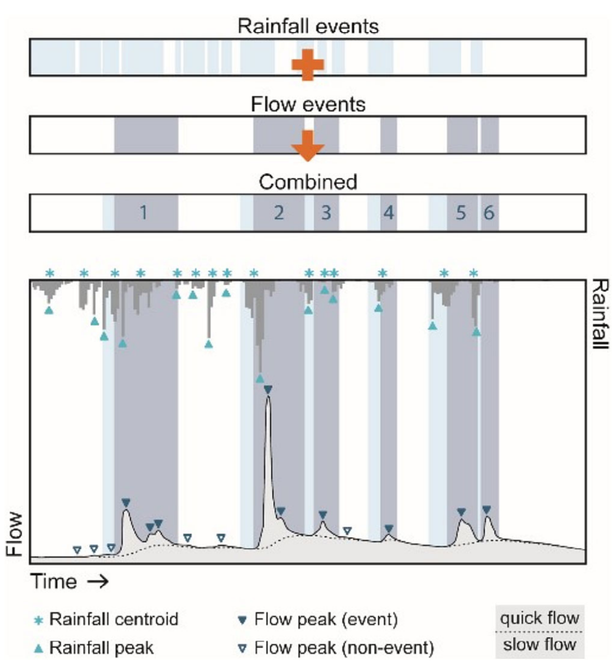


FIGURE 2 A conceptual figure depicting the event extraction methodology. Periods of continuous rainfall are identified alongside corresponding flow events where quick flow exceeds slow flow. The durations of both rainfall and elevated flow are combined to create an event window which is used to extract hydrological information for a given storm event

2.2.3 | Statistical design and analysis

The statistical design used in this study focusses on the before-after (BA) intervention comparison as used previously in hydrological studies including beaver (Hill & Duval, 2009; Nyssen et al., 2011) and related river or restoration studies (Grayson et al., 2010; Sear et al., 2006). The lack of control monitoring increases uncertainty that another, unmeasured, factor could cause change (Downes et al., 2002). However, to our knowledge there were no major land use changes or known confounding factors during the monitoring period. The monitoring of four different sites further strengthens the robustness of findings where common trends are observed across sites. Additionally, at one site (Budleigh Brook), beavers colonized an area with suitable control monitoring, allowing the opportunistic adoption of full Before-After-Control-Impact (BACI) experimental design as outlined in (Bilotta et al., 2016). BACI analysis was not possible across all sites because no suitable control catchments were available. Whilst selection of controls at the catchment scale is complex, due to the probability of confounding processes (Lane, 2017), it is recognized as a stronger analytical approach (Shuttleworth et al., 2019). Therefore, we adopted a mixed experimental design with a BA design across four sites and a repeated analysis of one of these sites, using a BACI design (as in Bilotta et al., 2016). Should results from the BACI site align with those from the BA sites, greater confidence can be held in the findings from BA sites.

Hydrological data from storm events is non-normally distributed and as such all statistical analysis was undertaken using appropriate tests; either non-parametric (as in Table 2) or generalized linear models (GLM). Additionally, the experimental design did not give us control over when beavers were released into or impacted upon sites or when and how many rainstorm events occurred during the monitoring period. As such, an unbalanced dataset, both between sites and between Before-After periods was inevitable. This imbalance is often an unavoidable issue for field researchers with access to limited, or in this case pre-determined, field sites (Warton et al., 2016). Rather than exclude data from analysis which risks incurring bias, loss of precision or obscuring key information on system function (Shaw & Mitchell-Olds, 1993), statistical approaches were carefully selected that could handle unbalanced datasets to support robust conclusions.

Statistical analysis was undertaken in R 3.6.3. (R Core Team, 2020) with data manipulation, summary statistics and plotting undertaken using the tidyverse (Wickham et al., 2019). Q5:Q95 ratio was used as a simple flashiness index (Jordan et al., 2005). The statistical significance for differences between pre- and post-beaver groups for

TABLE 1 Beaver impacted study site characteristics

	Site and catchment characteristics						Monitoring period		
Site	Site size (ha)	Catchment size (ha)	Stream order	Mean annual rainfall (mm)	Dominant landuse	Dam numbers[a]	Beaver impact	Pre beaver (months)	Post beaver (months)
Woodland Valley	2	134	2	1017	Agricultural grassland	1–7	June 2017	19	21
Budleigh Brook	3	630	3	1065	Agricultural grassland	1–6	January 2017	84	38
Forest of Dean	6	410	3	734	Mixed Woodland	1–3	July 2018	9	10
Yorkshire	16	747	4	979	Mixed Woodland	1–3	April 2019	5	11

Note: Mean annual rainfall (Met Office, 2015).
[a]Dam number is given as a range, as this has varied throughout the monitoring period and is highly dynamic. Beaver impact – denotes the point at which beavers began to engineer the sites. Pre- and post-monitoring periods denote in months the length of the time series used for event separation and subsequent analysis.

TABLE 2 Summary statistics for all events across all beaver impacted sites

All data	Beaver	Woodland valley	Budleigh Brook	Yorkshire	Forest of Dean
Event n	No	78	418	29	57
	Yes	205	207	73	86
ER - median (IQR)	No	7.62 (7.47)	8.84 (9.79)	2.74 (8.32)	5.96 (10.53)
	Yes	6.65 (9.07)	8.37 (9.69)	7.17 (10.33)	4.32 (6.33)
	p value	*0.902*	*0.951*	*0.004**	*0.301*
Total stormflow Q - Median (IQR)	No	5839 (19097)	12 099 (11789)	12 782 (50341)	58 344 (49968)
	Yes	5997 (7963)	9745 (6401)	16 254 (23597)	32 699 (25844)
	p value	*0.012**	*0.000**	*0.607*	*0.000**
Peak Q - median (IQR)	No	0.15 (0.42)	0.15 (0.54)	0.32()	0.89 (0.38)
	Yes	0.15 (0.18)	0.13 (0.13)	0.21()	0.55 (0.22)
	p value	*0.027**	*0.000**	*0.063*	*0.000**
Lag peak to peak - median (IQR)	No	1.75 (3.25)	2.5 (2.75)	7.5 (13.50)	6.5 (8.25)
	Yes	2.75 (4.63)	3.75 (2.75)	5.6 (4.81)	8.4 (13.19)
	p value	*0.005**	*0.000**	*0.318*	*0.230*
Q5:Q95 ratio	No	11.15	2.73	42.37	4.97
	Yes	6.73	2.04	35.72	3.93

Note: Event n, total number of events extracted from the time series dataset at each site; ER, total event rainfall (mm); Total Stormflow Q, total stormflow discharge during storm event determined via event separation (m^3); Peak Q, event maximum flow recorded during storm event ($m^3 s^{-1}$); Lag peak to peak, the time between peak rainfall and peak discharge in a storm event (hours). For each metric the median value is presented along with the interquartile range and p value from Man–Whitney U tests (with statistical significance at the $p < 0.05$ level indicated by*). Q5:Q95 = flashiness index results showing ratio between high and low flow metric an increase in Q5:Q95 indicates increased flashiness and a reduction indicates a more attenuated flow regime.

summary statistics were determined using the non-parametric Mann–Whitney *U* test.

Direct comparison of hydrological metrics pre- and post-beaver, provides an indication of beaver impact. However, this does not consider the amount of rainfall. We therefore used GLMs, with a Gamma error distribution and identity link functions, where event rainfall is the control variable, event peak Q is the response variable and beaver presence is considered as an additive explanatory variable.

The model form is shown below:

Q peak ~ Total Rainfall + Beaver Presence.

This allows for testing the effect of beaver on peak flows, relative to contributing event rainfall. GLMs were chosen over linear regression, due to their ability to cope with non-normally distributed response variables (Dunn & Smyth, 2018). As smaller flow events are more common than large events the error distribution of event peak flows for all sites has a Gamma distribution. Unique regression models were designed for each site, negating issues of sample size imbalance between sites. Analysis was undertaken using the glm2 R package (Marschner, 2011). Critically, this approach can also handle unbalanced sample size (i.e., unequal factor levels) as General Linear Models do not require equal group sizes (Dunn & Smyth 2018; Venables & Ripley, 2002; Warton et al., 2016). Unequal group sizes can have two important effects relevant here: (i) the power of the model is limited by the size of the smallest group (Shaw & Mitchell-Olds, 1993) and

(ii) Care should be taken when selecting a model and interpreting its results from an unbalanced design to ensure the hypothesis may be addressed (Hector et al., 2010; Warton et al., 2016). In addressing the first point; we acknowledge the difference in statistical power across our different sites. Regarding point ii; imbalance is a greater problem with sample sizes smaller than those presented in this paper (Warton et al., 2016) and any issues can be identified during model evaluation with visual diagnostic plots. This was carried out using the "performance" package in R (Lüdecke et al., 2020).

Large storms are of most interest for catchment management and flood risk (Puttock et al., 2017). As with most empirical hydrological monitoring projects, the long-term time series data required to calculate robust storm recurrence intervals was not available and there are significant limitations in trying to predict return periods from limited time series (Pomeroy et al., 2016). Therefore, exceedance limits were used to evaluate the effect of beaver on peak flows. At each site, a subset of events was created where peak flows exceeded the Q5 flow exceedance value. The GLM analysis was repeated for this high-flow subset to test if there was significant difference between pre- and post-beaver periods for events where flow percentage exceedance values were greater than 95th percentile. Q5 was chosen as a recognized high flow metric (Jordan et al., 2005; Kamamia et al., 2019).

To investigate how impact varied over different hydrological seasons, GLMs were produced for the full dataset across all sites including hydrological year as an interactive covariate which, in Great Britain, is widely recognized as starting on the 1st of October (NRFA, 2018). It has been shown that heaviest rain events typically occur in the winter or wet half of the hydrological year between October and March and this is a key driver over extreme flood events (Lavers et al., 2011). In line with previous research (Lavers et al., 2011, 2013; Puttock et al., 2017) the "wet season" was defined as the period between 1st October and 1st April with the other half of the year defined as the "dry season". The model form is described below.

*Q peak ~ Total Rainfall + Beaver Presence * Hydrological Season*.

For the Budleigh Brook site, a suitable control site was monitored in the neighbouring Colaton Brook catchment (Figure 1). Therefore the GLM analysis described above was repeated to investigate the impact of a beaver dam complex on: (i) all measured peak flows, (ii) peak flows >Q5 exceedance levels and (iii) with hydrological season as a covariate. However, for all of these GLMs, the models were also run with the control site data included, with site used as an additional interactive covariate, in line with BACI sampling designs (Bilotta et al., 2016). The formulations of the models are:

*Q peak ~ Total Rainfall + Beaver Presence * Site*.

*Q peak ~ Total Rainfall + Beaver Presence * Hydrological Season * Site*.

The inclusion of a control site allows for a greater degree of confidence in the observed response reported in the GLMs. If a significant difference in flows can be attributed to beaver, then this will be reflected in the interaction between site and beaver presence.

Estimated marginal means (i.e., adjusted or least-squares means), along with associated standard errors, were calculated using the emmeans R package (Length, 2020) for all GLMs to compare differences in mean peak flows before and after beaver, over different hydrological seasons and, where the control is used, between control and impacted sites. Estimated marginal means (emmeans) are useful for interpreting the outputs of regression analysis where the difference between, and or the effect of, factor levels is of interest (Castorani et al., 2018; Piepho & Edmondson, 2018). Furthermore, emmeans are designed to handle factor levels of different sizes by adding equal weight to each cell (or group). This eases the interpretation of model predictions in this unbalanced case (Length, 2020).

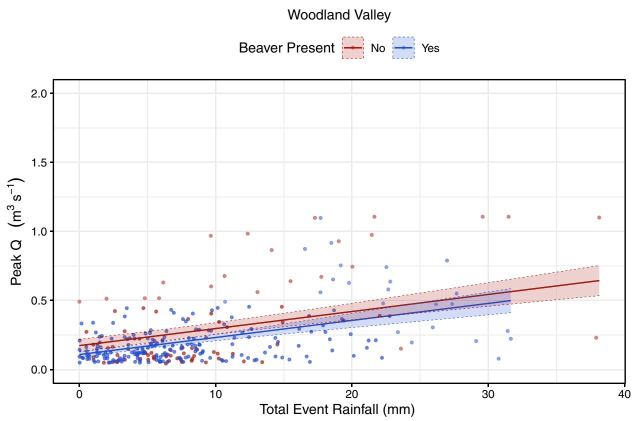
3 | RESULTS

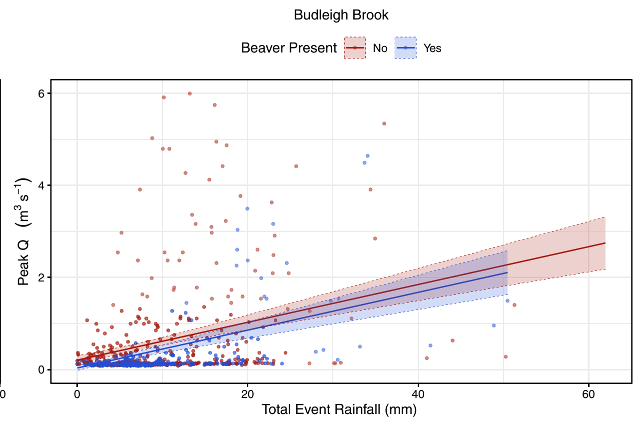
3.1 | Hydrological response across four sites before and after beaver

Summary results from all events before and after beaver are illustrated in Table 2. In total across the four sites, 1153 events were extracted with 582 occurring before beaver and 571 following beaver reintroduction. Across all sites, there was a trend of total stormflow and the peak flow reduction following beaver impact (Figure S2). Results from Mann–Whitney *U* tests (Table 2) show before after differences to be significant ($p < 0.05$) at all sites apart from Yorkshire which, in addition to having the shortest monitoring period, was the only site to have a significant difference in event rainfall (Figure S3), with storms having greater median rainfall ($p < 0.05$) in the post beaver period. The time between peak rainfall and peak discharge in a storm event (lag time) was shown to increase across all sites apart from Yorkshire, with the increase being significant ($p < 0.05$) at Woodland Valley and Budleigh Brook.

Additionally, Q5:Q95 ratios were calculated as a flashiness index from the whole time series across the sites, before and after beaver impact. All sites showed a reduction in Q5:Q95 after beaver impact (Table 2). This indicates that overall flow regimes were less "flashy" or more attenuated with less difference between high (Q5) and low (Q95) flow periods when beaver were present. In addressing hypothesis 1, results indicate that across the four sites there had been a change in flow regimes following beaver reintroduction. Although it must be recognized that summary statistics presented in Table 2 do not in isolation prove a causal link between change and beaver engineering as they do not account for variability in rainfall. Therefore, the following sections address hypothesis 2, to understand whether changes to observed peak flows can be attributed to beaver activity.

GLM analysis was undertaken for all event data across the sites with beaver presence/absence as an additive variable (results and summary test statistics in Figure 3). As shown by marginal means, peak flow showed a reduced response to rainfall across all sites. In regression summary tables for each site, the estimate value gives the modelled magnitude of change in peak flow (m^3 s^{-1}), and also the direction (increase or reduction) for every unit of total event rainfall (mm). Models showed beaver impact to result in a statistically significant ($p < 0.05$) reduction in peak flow. The estimate value for these reductions range from -0.359 m^3 s^{-1} at the Forest of Dean to -0.065 m^3 s^{-1} at Woodland Valley.





Woodland Valley Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.173	0.024	7.373	< 0.001 **
Beaver	-0.065	0.023	-2.832	0.005 *
Total Rainfall	0.012	0.002	7.537	< 0.001 **

Marginal Means

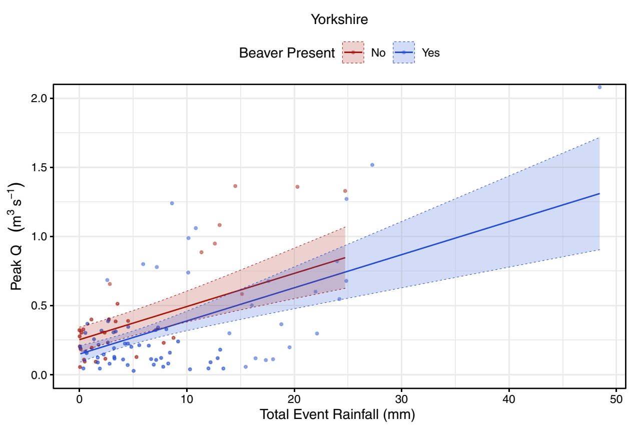
Beaver	estimate	std.error
No	0.288	0.021
Yes	0.223	0.011

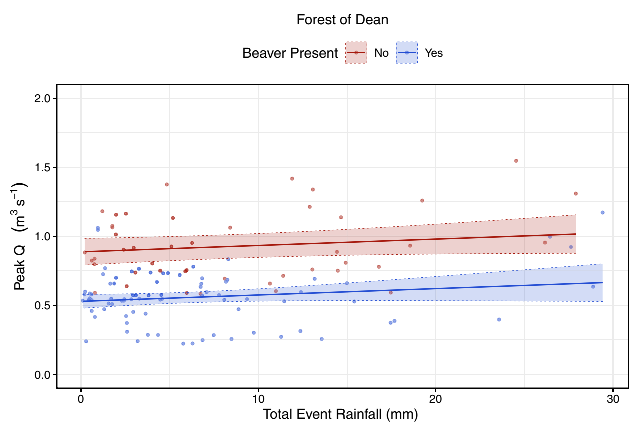
Budleigh Brook Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.204	0.048	4.251	< 0.001 **
Beaver	-0.170	0.047	-3.609	< 0.001 **
Total Rainfall	0.041	0.005	8.048	< 0.001 **

Marginal Means

Beaver	estimate	std.error
No	0.66	0.047
Yes	0.49	0.048





Yorkshire Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.253	0.046	5.470	< 0.001 **
Beaver	-0.104	0.051	-2.023	0.046 *
Total Rainfall	0.024	0.005	5.151	< 0.001 **

Marginal Means

Beaver	estimate	std.error
No	0.460	0.053
Yes	0.356	0.032

Forest of Dean Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.888	0.050	17.908	< 0.001 **
Beaver	-0.359	0.048	-7.401	< 0.001 **
Total Rainfall	0.005	0.003	1.627	0.106

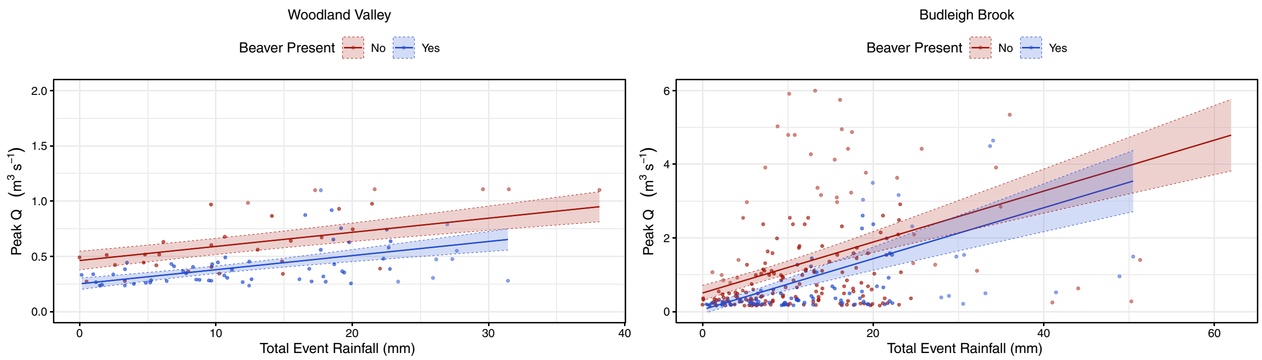
Marginal Means

Beaver	estimate	std.error
No	0.921	0.044
Yes	0.563	0.020

FIGURE 3 GLM model results between peak Q and total event rainfall, before and after beaver impact across all sites for all recorded storm events. Top: model output plots; Bottom: model summary and marginal mean values for each site

To investigate whether flow attenuation persisted for large events, identical analysis was undertaken on a > Q5 subset of events (Figure 4). Emmeans and estimates showed even for this subset of the largest events monitored, there was still a reduction in peak flow across all sites. Notably, estimated reduction effects of beaver upon peak flow per unit rainfall during large events increased at the two more established beaver impacted sites with agriculturally dominated catchments (Woodland Valley −0.065 to −0.211 m^3 s^{-1} and Budleigh Brook −0.170 to −0.452 m^3 s^{-1}), but reduced at the less established sites with fewer dams and woodland dominated catchments (Yorkshire −0.104 to −0.050 m^3 s^{-1} and Forest of Dean −0.359 to −0.153 m^3 s^{-1}).

To determine if seasonality affected the impact of beaver upon peak flows, hydrological year was included as an interactive covariate in GLM analysis (Figure 5). Model summary statistics (Figure 5) show that, for all sites, season has a significant effect (p < 0.05), with an increased peak flow response to rainfall during the wet season. Results across all sites apart from the Forest of Dean also show the interactive effect between the presence of beaver and wet season to be negative (i.e., beaver activity leads to a reduction in peak flow) and that the impact of beaver presence upon peak flow is greatest during the wet season of the year. This effect is statistically significant at both Woodland Valley and Budleigh Brook, sites with agriculturally



Woodland Valley Q5 Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.462	0.043	10.766	< 0.001 **
Total Rainfall	-0.211	0.041	-5.118	< 0.001 **
Beaver	0.013	0.002	6.092	< 0.001 **

Marginal Means

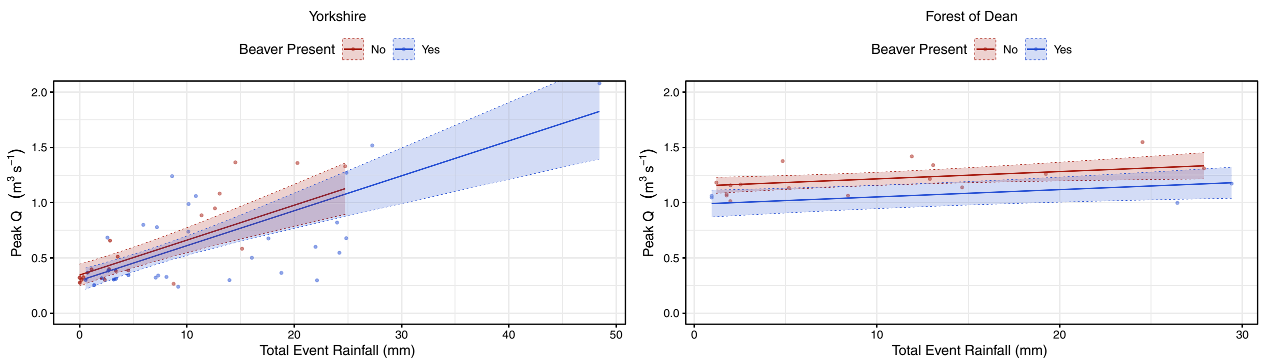
Beaver	estimate	std.error
No	0.633	0.038
Yes	0.422	0.019

Budleigh Brook Q5 Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.505	0.106	4.749	< 0.001 **
Beaver	-0.452	0.108	-4.167	< 0.001 **
Total Rainfall	0.069	0.009	7.800	< 0.001 **

Marginal Means

Beaver	estimate	std.error
No	1.505	0.110
Yes	1.053	0.115



Yorkshire Q5 Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.345	0.050	6.865	< 0.001 **
Beaver	-0.050	0.063	-0.789	0.434
Total Rainfall	0.032	0.005	6.204	< 0.001 **

Marginal Means

Beaver	estimate	std.error
No	0.70	0.062
Yes	0.65	0.048

Forest of Dean Q5 Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	1.149	0.039	29.418	< 0.001 **
Beaver	-0.163	0.062	-2.619	0.018 *
Total Rainfall	0.007	0.003	2.393	0.029 *

Marginal Means

Beaver	estimate	std.error
No	1.219	0.031
Yes	1.056	0.054

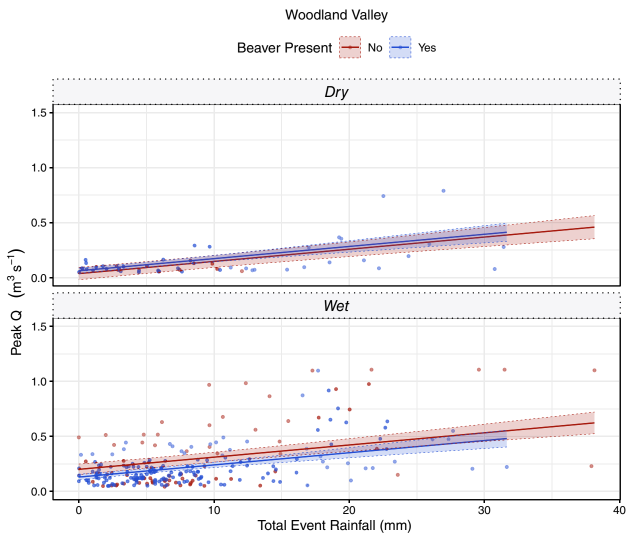
FIGURE 4 GLM model results between peak Q and total event rainfall, before and after beaver impact across all sites for events larger than the Q5 exceedance level. Top: model output plots; Bottom: model summary and marginal mean values for each site

dominated catchments and where most events were monitored (908 total).

Observed differences in impact of beaver upon the response of peak flow to rainfall, between seasons, is further illustrated in the tables of emmeans from model outputs (Figure 5). Across all sites, emmeans estimates from the models are higher during the wet season again illustrating that, during the wet half of the year, a greater peak flow response to rainfall will be predicted. Emmeans values show a general trend of reduced peak flow values after beaver reintroduction. However, as illustrated most clearly for Woodland Valley and Budleigh Brook, this reduction in peak flow impact of beaver is greater during the wet season. For example, at Woodland Valley, after beaver reintroduction there was actually a small (0.025 m^3 s^{-1}) increase during the dry season, but a reduction of 0.071 m^3 s^{-1} (23%) during the wet season. At Budleigh Brook there was a reduction of 0.041 m^3 s^{-1} (10%) during the dry season and a reduction of 0.414 m^3 s^{-1} (50%) during the wet season. At the two forested sites there was less of a clear seasonal differentiation with Yorkshire showing a 22% reduction during the dry season and an 11% reduction during the wet season and Forest of Dean showing a 48% reduction after beaver during the dry season and a 36% reduction during the wet season.

3.2 | Hydrological response at a site before and after beaver compared to a control site

To investigate hypothesis 2 further, at Budleigh Brook a suitable control site, with a comparable data record (634 events over the same time period), was available. Therefore, adopting a full BACI approach,



Woodland Valley Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.037	0.029	1.285	0.200
Total Rainfall	0.011	0.001	7.688	< 0.001 **
Wet Season	0.164	0.035	4.623	< 0.001 **
Beaver	0.025	0.030	0.847	0.398
Beaver:Wet Season	-0.096	0.039	-2.470	0.014 *

Marginal Means

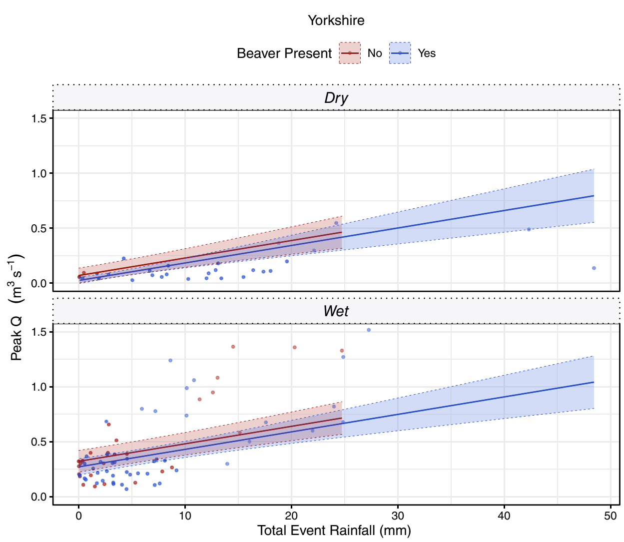
Beaver	HydYear	estimate	std.error
No	Dry	0.140	0.028
Yes	Dry	0.165	0.014
No	Wet	0.304	0.023
Yes	Wet	0.233	0.012

Budleigh Brook Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.055	0.036	1.558	0.120
Total Rainfall	0.032	0.004	8.096	< 0.001 **
Wet Season	0.409	0.072	5.716	< 0.001 **
Beaver	-0.041	0.047	-0.869	0.385
Beaver:Wet Season	-0.373	0.084	-4.440	< 0.001 **

Marginal Means

Beaver	HydYear	estimate	std.error
No	Dry	0.416	0.040
Yes	Dry	0.375	0.046
No	Wet	0.825	0.066
Yes	Wet	0.411	0.039



Yorkshire Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.069	0.034	2.004	0.048 *
Total Rainfall	0.016	0.003	5.891	< 0.001 **
Wet Season	0.253	0.061	4.149	< 0.001 **
Beaver	-0.045	0.037	-1.208	0.230
Beaver:Wet Season	-0.005	0.071	-0.073	0.942

Marginal Means

Beaver	HydYear	estimate	std.error
No	Dry	0.206	0.041
Yes	Dry	0.161	0.020
No	Wet	0.459	0.051
Yes	Wet	0.409	0.037

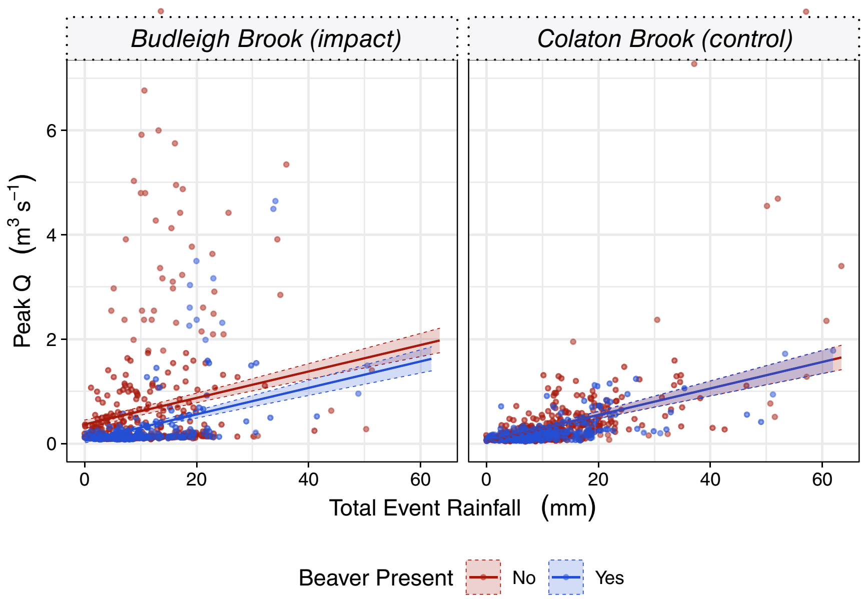
Forest of Dean Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.743	0.067	11.041	< 0.001 **
Total Rainfall	0.007	0.003	2.529	0.013 *
Wet Season	0.185	0.082	2.265	0.025 *
Beaver	-0.386	0.068	-5.666	< 0.001 **
Beaver:Wet Season	0.036	0.089	0.404	0.687

Marginal Means

Beaver	HydYear	estimate	std.error
No	Dry	0.791	0.063
Yes	Dry	0.405	0.025
No	Wet	0.976	0.052
Yes	Wet	0.626	0.024

FIGURE 5 GLM model results between peak Q and total event rainfall, before and after beaver impact across all sites with the addition of season as an effect. Top: model output plots; Bottom: model summary and marginal mean values for each site



Budleigh:Colaton Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.042	0.016	2.641	0.008 *
Total Rainfall	0.025	0.002	12.567	< 0.001 **
Beaver	0.000	0.021	0.016	0.987
Budleigh Brook	0.326	0.042	7.766	< 0.001 **
Beaver:Budleigh Brook	-0.315	0.049	-6.418	< 0.001 **

Marginal Means

Beaver	Site	estimate	std.error
No	Colaton Brook (control)	0.336	0.019
Yes	Colaton Brook (control)	0.336	0.023
No	Budleigh Brook (impact)	0.662	0.040
Yes	Budleigh Brook (impact)	0.347	0.024

FIGURE 6 GLM model results between peak Q and total event rainfall, before and after beaver impact at Budleigh Brook and compared to a control site (Colaton Brook). Top: model output plots; Bottom: model summary and marginal mean values for each site

GLM analysis was run, incorporating site as an interactive effect with results illustrated in Figure 6. BACI results for Budleigh Brook add further weight to support the acceptance of Hypothesis 2 with the combined effect of site and beaver presence shown to result in a significant reduction in peak flows ($p < 0.01$). This effect is most clearly shown in the marginal means; at the control site (Colaton Brook), the modelled effect of rainfall was 0.33 m^3 s^{-1} both before and after the period where beaver colonized Budleigh Brook. In contrast, at Budleigh Brook there was a reduction in mean peak flow from 0.66 to 0.35 m^3 s^{-1} (47%) after beaver reintroduction.

Identical analysis was undertaken on a data subset with flows greater than Q5 (Figure S4). Results showed the attenuation effect of beavers, at the occupied Budleigh Brook site, persisted for large events with a significant reduction in peak flows ($p < 0.01$) in contrast to the control. Marginal mean values from GLM analysis (Figure S4) show a mean peak flow of 0.50 m^3 s^{-1} before and 0.48 m^3 s^{-1} after at the control site. In contrast Budleigh Brook, the beaver impacted site, showed a reduction from 1.53 to 0.65 m^3 s^{-1} for Q5 events after beaver were reintroduced (57% reduction).

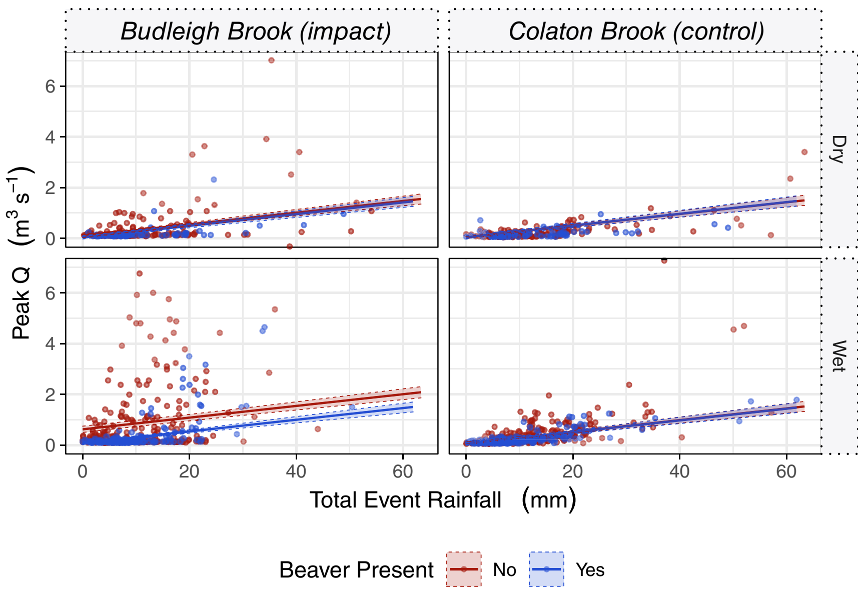
Analysis was also undertaken for Budleigh Brook incorporating both season and control data (Figure 7). Results showed the combined effect of beaver presence, site and season to be statistically significant. Marginal means allow further interpretation of this multi-parameter analysis (Figure 7), effectively showing no change at the control throughout seasons and the period of beaver impact (all have an effect of ca 0.3 m^3 s^{-1}). In contrast the beaver impacted site showed a reduction from 0.36 to 0.30 m^3 s^{-1} (17%) after beaver reintroduction in the dry season, but a greater reduction from 0.87 to 0.34 m^3 s^{-1} (62%) during the wet season.

4 | DISCUSSION

4.1 | Alteration of flow regimes by beaver dams

Analysis of storm events, across four sites, demonstrated that flow regimes were altered after the construction of beaver dam complexes, with an overall trend of reduced peak flows, reduced total stormflow, and increased lag times. Additionally, the overall "flashiness" of flow regimes was reduced. Results support the acceptance of Hypothesis 1 that there was a change in flow regime and hydrological response to storm events following beaver modification. Furthermore, before-after analysis across four sites and full BACI analysis at one site significantly attributes changes in peak flows to beaver impact, supporting the acceptance of Hypothesis 2.

Results support previous research showing beaver impact can alter flood hydrographs, reduce the peak discharge of floods and increase lag times (Burns & McDonnell, 1998; Green & Westbrook,



Budleigh:Colaton Regression Summary

term	estimate	std.error	T.statistic	p.value
Intercept	0.036	0.021	1.709	0.088 .
Total Rainfall	0.023	0.002	13.495	< 0.001 **
Wet Season	0.024	0.024	1.002	0.317
Beaver	0.009	0.035	0.258	0.796
Budleigh Brook	0.053	0.032	1.646	0.100
Beaver:Wet Season	-0.022	0.042	-0.512	0.608
Wet Season:Budleigh Brook (impact)	0.505	0.071	7.077	< 0.001 **
Beaver:Budleigh Brook	-0.068	0.051	-1.331	0.183
Wet Season:Beaver:Budleigh Brook	-0.464	0.086	-5.370	< 0.001 **

Marginal Means

Beaver	Hydro.Seas	Site	estimate	std.error
No	Dry	Colaton Brook (control)	0.303	0.022
Yes	Dry	Colaton Brook (control)	0.312	0.032
No	Wet	Colaton Brook (control)	0.328	0.019
Yes	Wet	Colaton Brook (control)	0.315	0.022
No	Dry	Budleigh Brook (impact)	0.356	0.028
Yes	Dry	Budleigh Brook (impact)	0.297	0.030
No	Wet	Budleigh Brook (impact)	0.886	0.062
Yes	Wet	Budleigh Brook (impact)	0.341	0.024

FIGURE 7 GLM model results between peak Q and total event rainfall, before and after beaver impact at Budleigh Brook and compared to a control site (Colaton Brook) with the addition of season as a fixed effect. Top: model output plots; Bottom: model summary and marginal mean values for each site

2009; Nyssen et al., 2011; Puttock et al., 2017). The attribution of flow attenuation to beaver supports research highlighting the need to acknowledge the influence of biotic factors upon river form and process (Johnson et al., 2019). More specifically, multiple previous studies have identified beaver modified landscapes, as a potential cause of flow attenuation (Green & Westbrook, 2009; Gurnell, 1998; Pollock et al., 2007). When presenting the reductions in peak flows and total stormflows it is important to understand that water is not disappearing, but is instead being released downstream more slowly. The attenuation impact of beavers has been ascribed primarily to increased water storage in beaver pond sequences (Westbrook et al., 2020). That is, at the Budleigh site >1000 m^2 of ponded area was created (Brazier, Elliott, et al., 2020) whilst recent estimates at the Woodland Valley site indicate >2000 m^2. A previous study at a smaller site (Puttock et al., 2017) showed >1000 m^2 of ponded area to result in over a million litres of water storage in 13 beaver ponds. Attenuation is also attributed to increased hydrological roughness from dams and surrounding floodplain wetlands (Puttock et al., 2017), increasing lateral connectivity (Macfarlane et al., 2015), diverting water sideways into ponds, soil and also ground water (Feiner & Lowry, 2015; Westbrook et al., 2006). Increased water storage also lengthens water retention times (Grygoruk & Nowak, 2014; Gurnell, 1998; Woo & Waddington, 1990), leading to slower downstream release; for example, Green and Westbrook (2009), showed the removal of a beaver dam sequence can lead to substantial (81%) increases in flow velocity. The increased surface area of water could also lead to greater evapotranspiration. Though evaporative fluxes were not measured in this study, previous research (albeit in a dryland environment as opposed to the temperate sites herein) has shown evapotranspiration to be 50–150% higher in riparian areas with beaver damming (Fairfax & Small, 2018).

Whilst there is a body of research attributing flow attenuation to beaver activity, this is the first empirical research to analyse hundreds of events, before and after beaver reintroduction, across multiple sites, using a standardized approach. The study thus adds considerable weight to previous research which demonstrates flow attenuation at small or individual sites (Law et al., 2016; Nyssen et al., 2011; Puttock et al., 2017), individual large storm events (Westbrook et al., 2020) or modelled simulations (Neumayer et al., 2020) and quantifies the peak flow and flashiness changes that beaver impacts can deliver across different stream orders and land uses.

This study focuses on high flow periods, but it is worth noting that reduced flashiness observed supports research indicating the slowed release of water from leaky dams may maintain or elevate stream baseflows (Nyssen et al., 2011) during dry periods (Majerova et al., 2015; Puttock et al., 2017; Woo & Waddington, 1990). There is a need for further research into baseflow maintenance, with an increase in hydrological extremes predicted globally (Dadson et al., 2017; Larsen et al., 2009; Romanowicz et al., 2016) both attenuating stormflow *and* maintaining flow and wetness during drought periods (Fairfax & Small, 2018; Gibson et al., 2015) or even fire episodes (Fairfax & Whittle, 2020) which could have major ecological and societal benefits.

4.2 | Spatial and temporal variation

The overall finding of this study is that beaver impacts result in flow attenuation. However, it is also important to acknowledge that results show variation spatially across sites and temporally, both seasonally and between events.

4.2.1 | Variability between sites

Beaver engineering is highly site specific and depends on the existing habitat, building material availability and channel characteristics (Collen & Gibson, 2000; Graham et al., 2020; Woo & Waddington, 1990). It is difficult to define a "typical" dam, although Woo and Waddington (1990) identified some of the multiple ways in which dam structure can influence flow pathways, that is, stream flow can overtop or funnel through gaps in the dams, leak from the bottom of the dams or seep through the entire structure. The impact upon flow velocity will consequently differ (Hering et al., 2001; Woo & Waddington, 1990). It is also important to note the number of dams and density could influence hydrological function. Existing work has discussed the importance of the number of dams in a reach, with beaver dams having the greatest impact on hydrology when they occur in a series (Beedle, 1991; Gurnell, 1998; Nyssen et al., 2011). Ponds located in series provide greater storage and greater roughness (Puttock et al., 2018), resulting in a greater reduction in flow velocities (Green & Westbrook, 2009). Pond sequences have also been shown to reduce the peak flows of 2-year return floods by 14% whereas individual dams reduced flood peaks of similar events by 5.3% (Beedle, 1991).

Whilst not examined herein in detail, beaver dam numbers and the level of site impact varied throughout the monitoring period and between sites (Table 1). At Woodland Valley (max observed dams = 7) and Budleigh Brook (max observed dams = 6), the longer data record available covered the transformation of each site into a complex beaver engineered wetland, with extensive damming pushing water sideways, connecting the channel and riparian zone. For example, at Budleigh Brook the largest dam extended 60 m across the floodplain (Brazier, Elliott, et al., 2020; Brazier, Puttock, et al., 2020). In contrast, monitoring at the two forested sites, covered the initial period of beaver engineering following release. For example, dams at the Forest of Dean (max observed dams = 3) were still contained within the channel, holding back water in the incised channel to a bankfull height, but not yet pushing water sideways onto the floodplain. Such differences in level of site impact can be seen in the aerial images (Figure S5) and ground images contrasting the impacts of dams during the monitoring period at Woodland Valley and the Forest of Dean (Figure S6). Such differences may explain some of the variation in results observed, that is, the greater reduction in peak flows at the more established sites, with a higher number of dams during large events and the wet season. Whilst research has illustrated that dam sequences have a higher impact than individual dams (Beedle, 1991; Green & Westbrook, 2009), recent research has also show that the configuration of beaver dam analogues also exerts an influence (Munir & Westbrook, 2020) something that must be considered for actual beaver dams too.

Monitoring of these dam sequences as they mature will continue and may elucidate how hydrological response varies with magnitude or spatial configuration of beaver impact or how long it takes for stable and consistent flow attenuation to occur through a beaver impacted wetland.

4.2.2 | Flow attenuation during large events

For flood management there is a focus on the performance of different management approaches during large storms, where there is the greatest volume of water and therefore greatest flood risk. As identified by Westbrook et al. (2020) there has been a commonly held misconception that, due to their relatively small water storage capacity and potential to fail, beaver dams will cause limited attenuation during large rainstorms. To address this question Westbrook et al. (2020) monitored a large flood (200–350 mm over 4 days), concluding that beaver dam sequences can provide attenuation even in large storms. The authors attribute this to the persistence of the majority of dams and the transient storage of flood water in ponds. Data analysed herein did not include events of the magnitude of that recorded by Westbrook et al. (2020), with the largest rainfall event recorded in the 3+ years of post-beaver monitoring being a 50.5 mm event at Budleigh Brook. However, continuous monitoring at sites resulted in >400 events for the Q5 event subset, demonstrating that the flow attenuation impact persisted for larger events. Due to their leaky nature, water storage in beaver dams is temporally variable (Karran et al., 2016; Puttock et al., 2017) and therefore capacity for attenuation is transient rather than finite during and between storm events.

At the more established sites (Woodland Valley and Budleigh Brook), reductions in peak flow increased during larger events. This supports Nyssen et al. (2011) who showed that, in a mountainous stream in Belgium with a sequence of six dams, peak flow attenuation for the highest discharges was greater than for smaller events. Therefore, in agreement with Butler and Malanson (2005) and Puttock et al.

(2017) it is proposed that increased water storage and the slowed release of water through dams, can deliver flow attenuation for large storm events across multiple scales.

4.2.3 | Seasonal variation

A somewhat unexpected finding from this study was that, not only did flow attenuation persist and at two sites increase during large flood events, but at the same sites (Woodland Valley and Budleigh Brook) greater flood flow attenuation was observed during the wet season. Water levels in beaver ponds vary significantly as a result of meteorological conditions (Puttock et al., 2017; Westbrook et al., 2020), particularly in areas with large seasonal variations in flow, for example, due to snowmelt (Majerova et al., 2015) or ephemeral drylands. However, given the consensus that flow attenuation is primarily due to water storage, greater attenuation during wet periods is surprising in a temperate climate. It might be expected that, in the wet season, an increase in the magnitude and frequency of rainfall events, combined with reduced vegetation cover, reduced evapotranspiration losses and an increase in saturated soils and runoff would result in the opposite effect. A possible explanation is that, during drier periods; (i) as observed by Nyssen et al., 2011 and others, beaver activity results in increased flows and (ii) the overall smaller storm events typically experienced during the dry seasons can flow through the leaky dams (conceptualized by Neumayer et al. (2020) as a series of pipes through a barrier by which water can flow), whilst the more intense storm flows experienced during winter, back up against dams, which maintain enough "leakiness" and consequent "freeboard" to ensure storage is transient enough to provide ongoing attenuation capacity, but enough of a barrier to significantly reduce the flood peak flows experienced during wet seasons.

It must be acknowledged that this seasonal variation was not observed at the other less mature sites (Forest of Dean and Yorkshire). Although, whether this inconsistency was due to forest landscapes showing less seasonal variation or whether it was because these two sites were younger and less beaver impacted is not clear. What is clear is that a greater understanding of the mechanisms by which beaver dam sequences and associated wetlands alter flow regimes through a range of flow and seasonal conditions is still required.

4.3 | Implications for catchment and natural flood management

Recent years have seen a growing interest in natural catchment management strategies (Dadson et al., 2017). For instance, in England, "Working With Natural Processes" (WWNP) and Natural Flood Management (NFM) is now incorporated into government policy (Environment Agency, 2017). It has been suggested that wetland re-creation, woody debris dams and floodplain reconnection, can all play a significant role in reducing downstream flooding (Lane et al., 2004; Ockenden et al., 2012; Pettorelli et al., 2018.; Wharton & Gilvear, 2007; Wilkinson et al., 2010).

There is growing understanding of where beavers can dam (Graham et al., 2020; Macfarlane et al., 2015) and how beavers will utilize catchments (Brazier, Elliott, et al., 2020; Brazier, Puttock, et al., 2020; Campbell-Palmer et al., 2018; Halley et al., 2020). However, European catchments have become dominated by human activity (Brown et al., 2018; Hewett et al., 2020) and, as a truly nature based approach, it must be recognized and reconciled that managers will not have the level of control over beaver engineering they do over human engineering (as indeed, we as researchers did not). Beavers will bring unique but manageable issues (Campbell-Palmer et al., 2016); stakeholder and public engagement will therefore be required to mitigate the risk of conflict (Auster et al., 2019).

NFM now covers a range of approaches from those that are engineered in line with precise flood risk mitigation specifications to those that are more akin to "rewilding" giving space to allow the reinstatement of natural processes (Lawton et al., 2010). Beavers may sit uncomfortably with approaches towards the engineered end of the spectrum, that is, the catchment systems engineering approach proposed by Hewett et al. (2020) which advocates a combination of hard engineering with catchment interventions that mimic natural processes. Within such approaches, the highly dynamic nature of beaver engineering may be deemed risky. In contrast, beaver engineering sits more comfortably within restoration approaches that advocate restoring natural structure and function to catchments including biomic river restoration or Stage 0 approaches (Cluer & Thorne, 2014; Johnson et al., 2019) or proposals to return our riverine ecosystems to pre-Anthropocene dynamic equilibrium (Brown et al., 2018). Such approaches could embrace the dynamic nature of beaver, whilst conflicts could be minimized and a host of other ecosystem service benefits provided (Dalbeck et al., 2020; Law et al., 2016, 2017). Perhaps the most pragmatic way forward is an open-minded holistic assessment on catchment scales to determine where more tightly constrained engineering approaches are required and where more natural multi-benefit approaches could be encouraged.

This study supports the conclusion of Westbrook et al. (2020) (albeit from research in a very different Canadian landscape) that, while beaver dam sequences are unlikely to provide 100% downstream flood protection, they can transiently store water and attenuate flood flows. It is thus argued, that the results provided herein, and research they build upon, that is, (Law et al., 2016; Nyssen et al., 2011; Puttock et al., 2017), support the incorporation of beavers into multiple-benefit catchment management strategies that embrace natural flood management objectives. However, to maximize the effectiveness of beavers a greater understanding of the density and distribution of beaver dams needed to mitigate downstream flooding effectively, is required. Further research, should incorporate both empirical studies to gain a greater mechanistic understanding of beaver dam sequences and wetlands, combined with development of modelling approaches to upscale robustly such understanding and facilitate adoption by the flood management community.

5 | CONCLUSION

Results demonstrate that the dams and associated complex wetlands that beaver engineering creates, can alter flood flow regimes. Statistical analysis, across the multiple sites in England presented herein adds significant confidence to the assertion that beaver engineered landscapes can result in significant flood flow attenuation following rain storm events. Critically, results quantitatively demonstrate that the peak flow reductions, observed after beaver dam complex construction, persist during both the wet times of the year and during large events when the societal, economic and environmental risks of flooding are greatest.

Results also showed that, across all sites, the overall "flashiness" of flow regimes was reduced. This suggests that the increased water storage resulting from the creation of beaver ponds and wetlands could also play a base flow maintenance role during dry, low flow periods, creating a valuable ecological refuge and potentially increasing the sustainability of water supplies. The hydrological behaviour of beaver-impacted systems during drought periods is a promising avenue for further research to quantify whether beaver engineering has significant benefits during both hydrological extremes, that is, floods and droughts.

The exact impact of beaver will be site specific to an extent, depending on the level of engineering and the structure of the ecosystem. Further research should aim to contribute greater mechanistic understanding of how dams and dam sequences drive the flow attenuation impact observed herein. Results demonstrated the strength of BACI analysis for empirical hydrological analysis and we advocate the wider use of this analysis in related studies. A mechanistic understanding of beaver systems across different environments and climatic zones would also be beneficial. Combined with modelling approaches, this increase in empirical understanding could enable prediction of the catchment outlet effects of cumulative dam complexes across a range of beaver impact scenarios, up to the impact from a widespread return of beaver to all headwater streams. Alongside the well documented biodiversity benefits of beaver, results presented demonstrate that beaver could, with appropriate management, provide a valuable component of more natural catchment management approaches, increasing the resilience of landscapes to extreme climatic events.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Github at https://github.com/exeter-creww. Full details of repositories for each section of data analysis are provided in S.I.1. This is publically available under a GNU General Public Licence (GPL-3.0 License).

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SUPPORTING INFORMATION

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

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Appendix 5. Using field sign surveys to estimate spatial distribution and territory dynamics following reintroduction of the Eurasian beaver to British river catchments

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RESEARCH ARTICLE

WILEY

Using field sign surveys to estimate spatial distribution and territory dynamics following reintroduction of the Eurasian beaver to British river catchments

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Abstract
Eurasian beavers, keystone species, have returned to inhabit much of its former range following near extinction. Evidence repeatedly demonstrates that beavers can provide important riparian biotic and abiotic ecosystem services. These abilities to modify their surroundings can cause conflict, especially in prime agricultural landscapes. Understanding how beavers are utilizing and expanding in European catchments is therefore essential. This paper presents a methodology by which the spatial extent and environmental impact of beavers can be quantified via distinctive field signs. This has widespread application in understanding their distribution, expansion, and any management implications. Its application is tested within two diverse case studies, the Tayside catchment, Scotland, and the Wye catchment, Wales/England, collectively covering >10,000 km^2 of catchment area. A minimum of 114 active territories were identified in Tayside and a small number of free-roaming beavers with no strong evidence of breeding territories were recorded on the River Wye. This study demonstrates that a detailed, time and cost efficient but also easily replicable, field survey method can allow estimates of beaver territorial zones when combined with geospatial analysis and expert assessment. As populations of Eurasian beavers continue to expand and be actively reintroduced across Europe, this survey-based approach can be utilized to increase understanding of their distribution, population dynamics, and territorial behavior, as well as informing management strategies and identifying areas of potential benefit and/or conflict.

KEYWORDS
Castor fiber, density models, Eurasian beaver, field survey method, management, population dynamics, reintroduction

1 | INTRODUCTION

1.1 | The restoration of beavers in Europe

Since the 1900s, following near extinction, Eurasian beaver numbers have recovered (up to ~1.5 million) throughout much of their former range via protected natural recolonization along with active reintroductions (~25 European countries) (Halley, Rosell, & Saveljev, 2020). The majority of these restoration projects have been officially sanctioned, though unofficial releases have seen large populations establish that is, in Belgium (Verbeylen, 2003) and Scotland (Gaywood, 2018). As beavers return to these now densely human-populated and intensively managed European landscapes, detailed understanding of these populations is required to inform any future catchment management strategies.

Beavers became generally extinct in Britain by the 16th century, though small numbers may have existed up until the early 18th century (Kitchener & Conroy, 1997; Coles, 2006). In 2009 a government approved, scientific trial reintroduction project was undertaken in Knapdale forest, mid-Argyll & Kintyre, West Scotland (Scottish Beaver Trial, SBT, https://www.scottishbeavers.org.uk). Outside this official process, beavers were increasingly recorded in parts of the Tayside catchment, following unlicensed releases (Gaywood, 2015). Beavers are also present in other parts of Britain for example, the River Otter, Devon, leading to a licensed trial in England (Brazier et al., 2020a), whilst other unlicensed populations have been reported.

1.2 | Ecosystem engineers

Beavers are renowned for their ability to create, modify, and maintain habitats on a catchment scale, resulting in significant geomorphic change to rivers, increasing lateral connectivity with the flood plain and overall channel dynamism (Gorczyca, Krzemień, Sobucki, & Jarzyna, 2018; Pollock et al., 2014). Unique processes, such as damming waterways and selectively felling trees, transform degraded habitats, and boost habitat heterogeneity. Numerous studies document an overall positive effect on biodiversity and biomass across a wide range of species (Rosell, Bozser, Collen, & Parker, 2005; Stringer & Gaywood, 2016), compared to areas uninhabited by beavers (Rosell et al., 2005). Riparian habitat has experienced widespread and prolonged biodiversity loss across Europe. Declines of 83% in freshwater species have been documented in the last 50 years—higher than terrestrial or marine species (WWF, 2018). Beaver's unique ability to increase habitat heterogeneity; influencing key abiotic factors at a landscape level has resulted in their increasing role as a component in ecological restoration projects (Hood & Larson, 2015; Johnston et al., 2017; Law, Gaywood, Jones, Ramsay, & Willby, 2017; Willby, Law, Levanoni, Foster, & Ecke, 2018). Furthermore, there is interest in additional ecosystem services beaver may provide, that is, flow attenuation and downstream water quality improvements due to trapping of sediment and associated nutrient storage (Westbrook et al., 2017; Puttock, Graham, Cunliffe, Elliott, & Brazier, 2017; Puttock, Graham, Carless, & Brazier, 2018; Brazier et al., 2020).

1.3 | Conflict and management

Beavers are not confined to wild landscapes. They can readily adapt to urban and agricultural landscapes where suitable freshwater and vegetation are available. In parts of Europe, beavers have returned to heavily populated and intensively managed river catchments, leading to human–beaver conflict and management issues (Auster, Puttock, & Brazier, 2019; Campbell-Palmer et al., 2016). Beaver activities can conflict with human interest and land use, imposing a cost (time and financial). This includes parts of Tayside, where lethal control licenses have been legally issued by Scottish Natural Heritage (SNH) despite their newly European Protected Species status (SNH, 2020), resulting in the culling of 87 animals in 2019 (SNH, 2020).

Therefore, there is a need to understand how beavers are colonizing river catchments, particularly in areas where they have been extirpated for decades, even centuries and where, in the meantime, human activities have led to significant changes (Brown et al., 2018; Hewett, Wilkinson, Jonczyk, & Quinn, 2020). A time/cost efficient and replicable survey method across diverse landscapes, which can form the foundation for further environmental and socio-economic research, is required. Perhaps more critically, a survey method is also needed to inform policy and management of catchments containing beaver to allow maximization of any benefits they may bring and pre-empt and minimize any conflicts.

1.4 | Beaver group behavior and territories

Beavers live in family units, typically made up of an adult breeding pair with any offspring from that and the previous year, ranging, on average, from two to seven individuals in total (Wilsson, 1971). When determining population numbers, an active territory is usually assumed to represent one family group, though it is possible that a singleton or newly formed pair are also present (non-breeding territories). Therefore, "counting" beavers can be problematic and the number of beavers present can be difficult and time consuming to determine. Population size is, therefore, typically expressed by the number of active territories (Rosell, Parker, & Steifetten, 2006). As beaver family groups will utilize a number of burrows and/or lodges within their territory, the number of burrows and lodges should not be used as a measure of group size. Group size in beavers is generally assessed through one of three methods: removal trapping/culling, mark and release, or observational censuses. The size of an average beaver family, derived from a review of 13 studies in Europe and observations of beavers living at high densities in Norway, has been estimated at 3.8 ± 1.0 individuals, with a range of 2.4–5.5 (Rosell et al., 2006; Rosell & Parker, 1995). Actual numbers of beaver within a territory is less relevant from a management point of view, whereas number of territories, their location, and distribution are more important factors (Campbell-Palmer et al., 2018).

Territory and group size vary greatly within beaver populations (Herr & Rosell, 2004; Nolet & Rosell, 1994; Wilsson, 1971). Territory size is not necessarily correlated with group size or reproductive rate (Campbell, Rosell, Nolet, & Dijkstra, 2005). Territories have been defined previously using: scent mound mapping as indicators of territory borders (Campbell et al., 2005); biologging individuals (Campbell et al., 2005; Graf, Mayer, Zedrosser, Hackländer, & Rosell, 2016); riverbank length with minimum convex polygons or kernel methods (Herr & Rosell, 2004); or patterns of beaver field sign density (Fustec, Lode, Le Jacques, & Cormier, 2001; McClanahan, Rosell, & Mayer, 2020).

Beavers tend to colonize suitable habitat in a linear manner (i.e., dispersal predominately follows water courses) although they can travel over land between catchments (Halley, Rosell, & Saveljev, 2012; Simunková & Vorel, 2015). Dispersal distances can range from a few kilometers to tens of kilometers, depending on a range of factors including population density and habitat, quality, and availability (Fustec et al., 2001; Zurowski & Kasperczyk, 1990). Most dispersing beavers will attempt to establish new territories within 5–10 km of their natal area, with no real sex differences, though greater distances (25–80 km+) have been recorded (Mayer, Zedrosser, & Rosell, 2017; Saveljev, Stubbe, Stubbe, Unzhakov, & Kononov, 2002). Territories range from 0.5 to 20 km, with Graf et al., 2016 reporting a mean of average 3.6 ± 1.6 km of shore or riverbank (Campbell et al., 2005; Herr & Rosell, 2004; Macdonald, Tattersall, Brown, & Balharry, 1995), and are aggressively defended. The size and numbers of territories depend on a multitude of factors including the density of populations, habitat quality, and settlement pattern (Campbell et al., 2005).

1.5 | Research objectives

This study sought to address the following objectives:

1. Develop a standardized field-sign survey method, designed to be time/cost efficient, replicable and deployable across diverse landscapes.
2. Apply the described survey method to demonstrate its ability to determine the spatial distribution of beaver and number of active territories for two case studies in Britain.

2 | METHODS

2.1 | Field survey methods

Surveys were conducted through a combination walking and canoeing, according to accessibility. Beavers display distinct field signs. Mapping field signs (see Figure 1 for example images and SI 1.4 for description of typical beaver field signs) can identify distribution, and estimate the number of active territories present within an area. Additionally, this protocol enables comparable datasets to be produced against previous surveys (Campbell, Harrington, Ross, & Harrington, 2012), in order to build longitudinal understanding of change. Full, step-by-step field survey, data analysis, and territory determination methods are provided in SI 1.1–1.3, to facilitate replication.

Field signs were logged during low growth seasons (i.e., autumn-early spring) using handheld GPS devices (Garmin Garmin eTrex or |Trimble Geo7x), with an XY resolution of 10 m. This approach allowed the classification of large stretches (up to hundreds of meters) of continuous beaver activity of the same feeding intensity (low, medium, high) efficiently. Point data were also collected, specifically the location of features such as lodges, dams, and burrows (when seen). Water courses were surveyed for field signs at least 2 km from the last recorded beaver field signs or until suitable habitat ended, for example, at steep waterfalls or on open moorland.

Additional information, recorded for each point feature, is detailed in Table 1 (full description of survey techniques and data collection methods in SI 1.1). Beavers leave a range of visible signs that are indicative of their behavior and at each data point the beaver sign/activity type was recorded (SI 1.4). Mapping and analysis were undertaken in ArcGIS 10.2. In addition to primary data, previous survey data and associated datasets held by SNH were supplied.

2.2 | Determination of territories from survey data

Gaps in field sign activity may relate to a lack of suitable habitat as opposed to an indication of beaver absence. Survey information was therefore used to help delineate beaver territories based upon expert judgment. As described in Campbell-Palmer et al. (2018), gaps in beaver activity were also cross-referenced with habitat suitability modeling (Graham et al., 2020; Stringer, Blake, & Gaywood, 2015) and aerial images (Google Maps), to refine delineation of territory boundaries (Campbell-Palmer et al., 2018) .

Kernel density analysis was undertaken and then combined with expert knowledge of the survey area to estimate territorial zones. Kernel density describes the magnitude per unit area of point features using a kernel function to fit a smoothly tapered surface to each point. Kernel density maps or "heat maps," with a search radius of 1 km^2 were used to infer the spatial distribution of beaver activity and territories, which were considered to be spatially explicit clusters of activity.

For Scotland, the model was run on 2012 dataset Campbell et al. (2012), to compare territory numbers and determine change over the intervening 6-year period. Figure 2 provides a summary of data analysis undertaken for the Tayside case study (see SI material for full information).

2.3 | Territory refinement

It was recognized that some known territories may not be captured by the modeling approach due to: (a) difficulties determining between continuous/high density areas of activity; (b) access constraints preventing full survey, resulting in reduced recording of field signs; (c) visibility of field signs. Therefore, modeled results were interpreted using expert judgment and local knowledge to refine and fill in known gaps, and to identify territories. These included assessments of water body type, knowledge of known breeding lodge/natal burrows, or presence of scent marking.

3 | CASE STUDY 1. TAYSIDE CATCHMENT, PERTHSHIRE, SCOTLAND

3.1 | Background and study area

The Tayside catchment is the seventh largest in Great Britain (Figure 3), draining an area of ~5,000 km^2. Predominant land use is

FIGURE 1 Example of commonly observed typical beaver field signs recorded during the surveys: (a) beaver dam, (b) lodge, (c) bankside burrow, (d) scent mound, (e) woody feeding/felling, (f) canal leading to a woody feeding site, a less developed version of this is also common consisting of a clear feeding trail [Colour figure can be viewed at wileyonlinelibrary.com]

agricultural with ~2,000 km^2 of arable farmland (TLBAP, 2016). Urban areas lie in the lowlands, with significant stretches of the riparian corridor used for recreation including fishing. Further up catchment, land-use is a mosaic of mixed agriculture, commercial plantations, and woodlands, with a range of standing water bodies. Neighboring catchments to the north (South Esk) and south (Forth) were also surveyed.

Scottish Government commissioned a survey in 2012, which estimated that there were 38–39 active groups of beaver present (Campbell et al., 2012). This study replicated the methods of (Campbell et al., 2012), allowing comparison to the two datasets. Field sign mapping in Tayside took place during low vegetation growth periods between April 2017 and January 2018, ensuring field signs were visible (i.e., not during summer when vegetation cover greatest). Survey area included all water courses with suitable habitat. In addition, OS maps, SNH beaver woodland maps, and GIS suitability layers (Stringer et al., 2015) were consulted.

TABLE 1 Data recorded at each survey point

N	Recorded information
1	Beaver sign/activity type
2	Ordnance Survey (OS) grid reference
3	Photo No (if appropriate)
4	Estimated age (fresh, old or mix of both)
5	Distance from water (m)
6	Area affected (m)
7	River width and approximate depth (m)
8	Land use (along water course and surrounding area)
9	Effort expended into the activity by beaver (low, medium or high)
10	Management impact (low, medium or high)
11	Any other comments

3.2 | Results

3.2.1 | Observed beaver signs

Surveys resulted in 29,036 data points being recorded (Figure 4), with the most dominant field sign being woody felling. A total of 72 beaver lodges were recorded. The majority (64%, *N* = 46) were in active use. Beaver territories contained 1–4 lodges, with active lodges recorded within 41 territories. Where terrain was suitable, numerous burrows were also present. Therefore, the absence of a lodge does not signify beavers are not within a given area. A total of 339 beaver burrows were found across 75 territories. As burrow entrances are often submerged, this was not treated as a full count. Eighty-six beaver dams or recently removed dams were recorded.

Signs at a site could vary in their age classification (old, new, or a mixture of both). Most sites of beaver activity (*N* = 15,575, 68%) consisted of a mixture of both new and old field signs. A total of 25% (*N* = 5,833) of all activity was classed as old and the remaining 7% (*N* = 1,682) was new beaver activity. The majority (55%, *N* = 13,103) of land use with recorded beaver activity were riparian deciduous

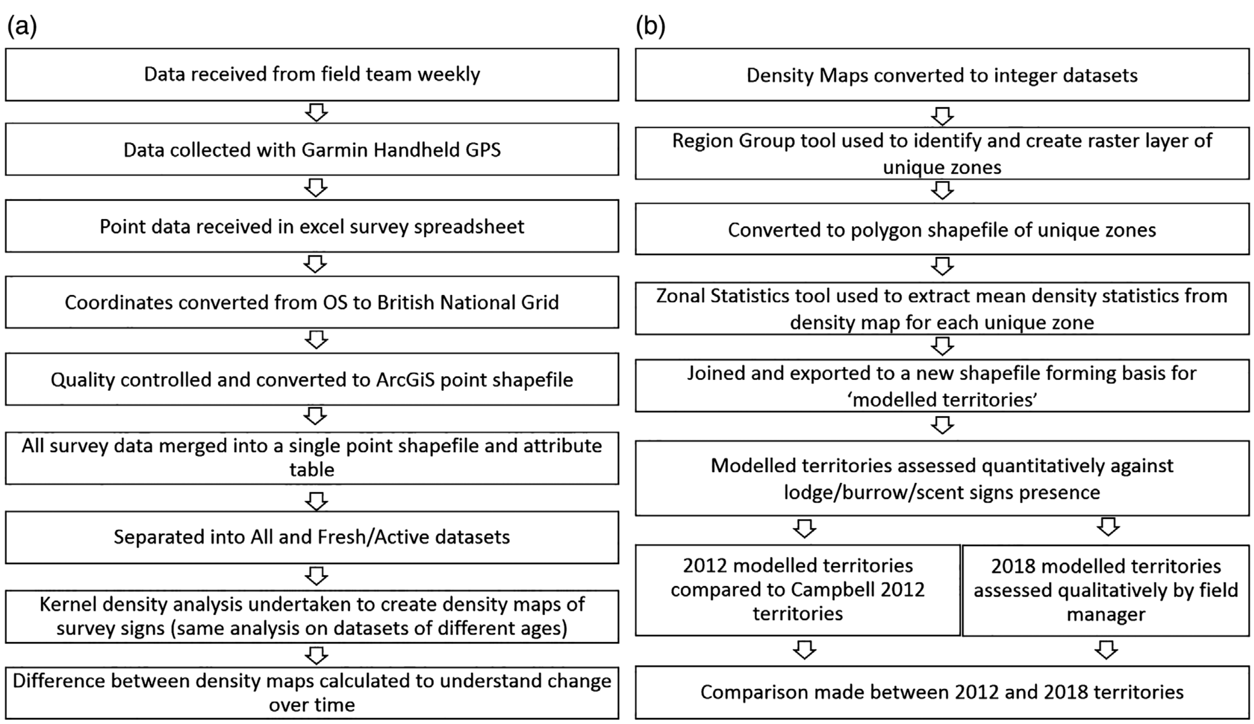


FIGURE 2 Flow charts illustrating Tayside data processing and analysis example. Left: data processing and analysis workflow used. Right: process of modeling zones of territory based upon density of survey points and subsequent interpretation. All initial data collection and processing on the Wye were the same but due to the lack of any indication of beaver territory presence or previous record for comparison, the more advanced data analysis was not undertaken

FIGURE 3 Location of two study catchments in Europe

woodland. Agriculture was the second most common landuse (37%, *N* = 8,798).

3.2.2 | Beaver territories and current habitat

Analysis indicated that the study area contained a minimum number of 114 active and spatially distinct territories (Figure 5). Out of the 114 beaver territories defined, 100% were contained within the areas identified as "Potential Beaver Woodland" (Stringer et al., 2015), supporting the key role suitable vegetation plays in determining the spatial extent of beaver (Graham et al., 2020), and understanding possible future population dynamics. Examples of territories are included in Figure 6, with further discussion of these examples provided in SI 2.

3.2.3 | Impacts and recorded signs of potential management concern

Results showed areas of both population increase and decrease since 2012, due to both expansion and culling (Figure 7). The potential impact of beaver activity on land management varied greatly, from negligible to significant. Measuring this impact involves a level of subjectivity, so the perceived impact was recorded by surveyors using a simple score of "low," "medium," or "high." This did not include consultation of landowner/manager views, which are likely to vary and be open to perception of the species. A total of 159 potential management issues (across at least 21 identified territories) were logged, with majority (61%) occurring on agricultural land. Remaining issues were recorded on deciduous woodland (25%), residential/urban/garden (10%), fishing/recreation/amenity (3%), and wetland/marsh (1%). Three main types of potential management issues were identified; damming and flooding in unwanted areas (27%); active management/removal of beavers (24%); and burrowing (21%). Agricultural crop raiding accounted for 12% of issues, in addition to residential/urban/garden and fishing/recreation/amenity (8%) and road/rail infrastructure conflicts (8%). Recorded conflicts occurred an average of 3.6 m from the riverbank with a minimum of 0 m for in channel conflict issues such as damming and a maximum of 15 m for disturbance in fields.

4 | CASE STUDY 2. RIVER WYE

4.1 | Background

Unlike the Tay catchment, the River Wye has little documented beaver presence. Sporadic reports of beavers have occurred in recent years including dead animals, feeding signs and footage of swimming beavers. No surveys have previously been conducted to validate these reports. Previous experience in Britain suggests that beavers have regularly escaped from captive collections and/or assisted releases outside official processes have occurred to speed their establishment. Such reasons may explain the sporadic reports of beavers on the Wye, though their exact distribution and population status was unknown prior to this survey.

4.2 | Study area

The River Wye (*Afon Gwy*) is approx. 250 km long and the catchment covers approximately 4,200 km^2, Britain's fifth longest river. Its source is located on Plynlimon in the Cambrian Mountains and mouth at the Severn Estuary, passing from Wales into England and back again (Figure 3). The entire river is designated an SSSI and SAC.

The upper Wye is characterized by fast flowing water, including rapids, steep-sided valleys, and vegetation dominated by open moorland, with conifer plantations. The Elan valley is one of the main tributaries joining the Wye in this section, the lower section of which was included in the survey, whilst upper sections are controlled by extensive artificial dams and therefore were excluded from the survey. The middle Wye is highly sinuous with numerous major adjoining tributaries. Vegetation cover is largely deciduous (dominated by Ash, Beech, and Oak woodland); forestry and agriculture are the dominant land uses. The lower Wye is characterized by slow flowing, broad river that cuts through two gorges before becoming tidal and entering the Severn Estuary.

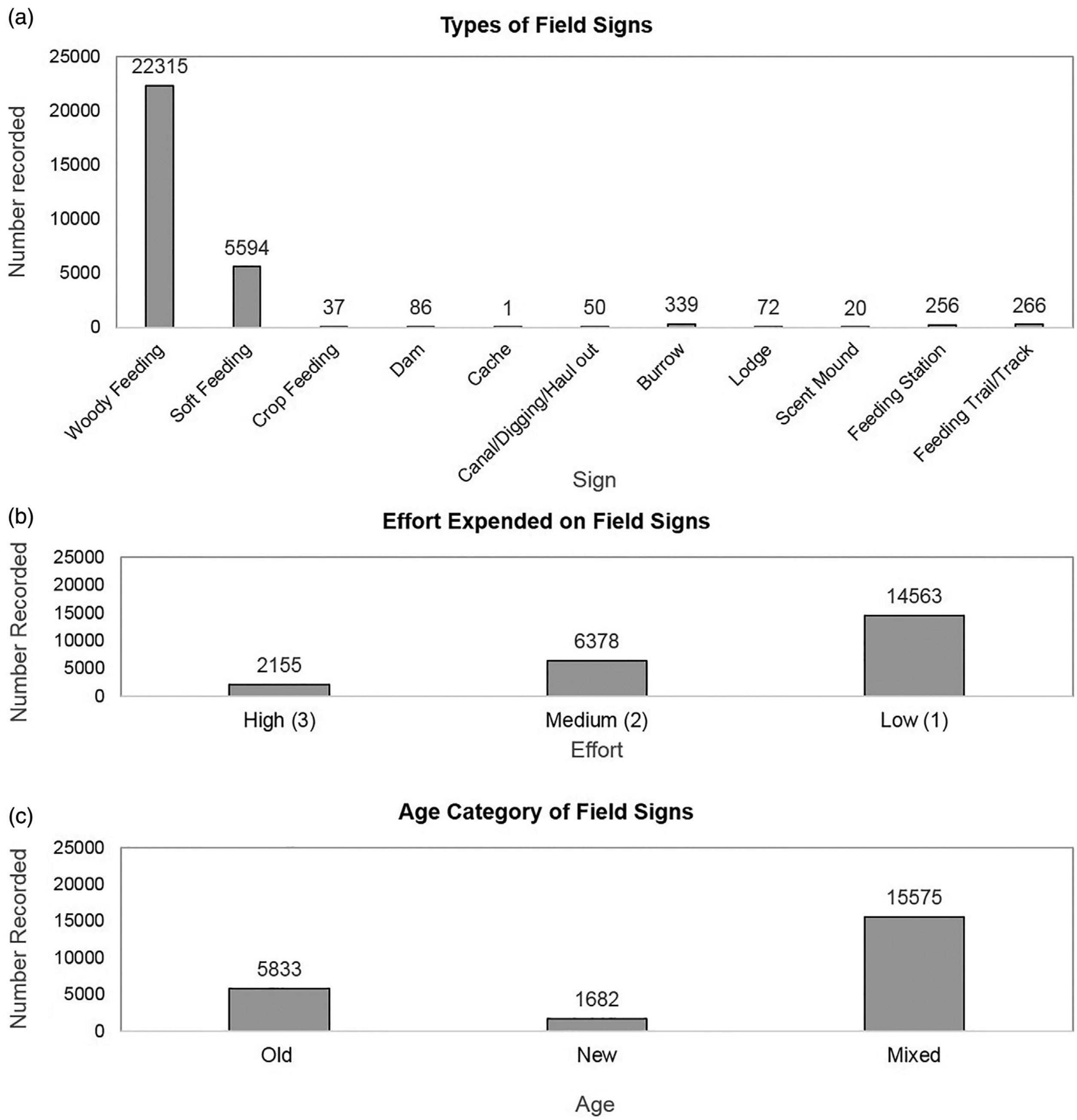


FIGURE 4 (a) Types of beaver signs recorded. (b) Number of beaver field signs requiring high, medium, or low effort to be expended into the activity. (c) Number of beaver field signs recorded in each age category (old, new, or a mix of old/new)

All field sign mapping in the Wye catchment took place during low vegetation growth periods between late January 2019 and March 2019. A continuous stretch of 198 km of the Wye was surveyed using canoe whilst additionally, 127 spot surveys were undertaken on foot. These areas were selected according to previous beaver activity reports, accessibility, and habitat suitability. At each spot check, the shoreline was walked to search for field signs for a minimum of 200 m and up to 1 km of bank. Spot checks in areas of previously recorded beaver activity, which were not canoed, involved walking 2 km above and below the location and also, where possible, further discussion with those reporting the activity to gather additional information to confirm extent of beaver activity.

There have been rumors of signs being intentionally created or faked in the Wye to exaggerate beaver activity, though additionally other animals such as sheep have been reported resembling beaver feeding activity. With this in mind, an additional "confidence" rating was given to each sign during surveys. "Confirmed" indicates a sign definitely believed to be beaver; "unconfirmed"

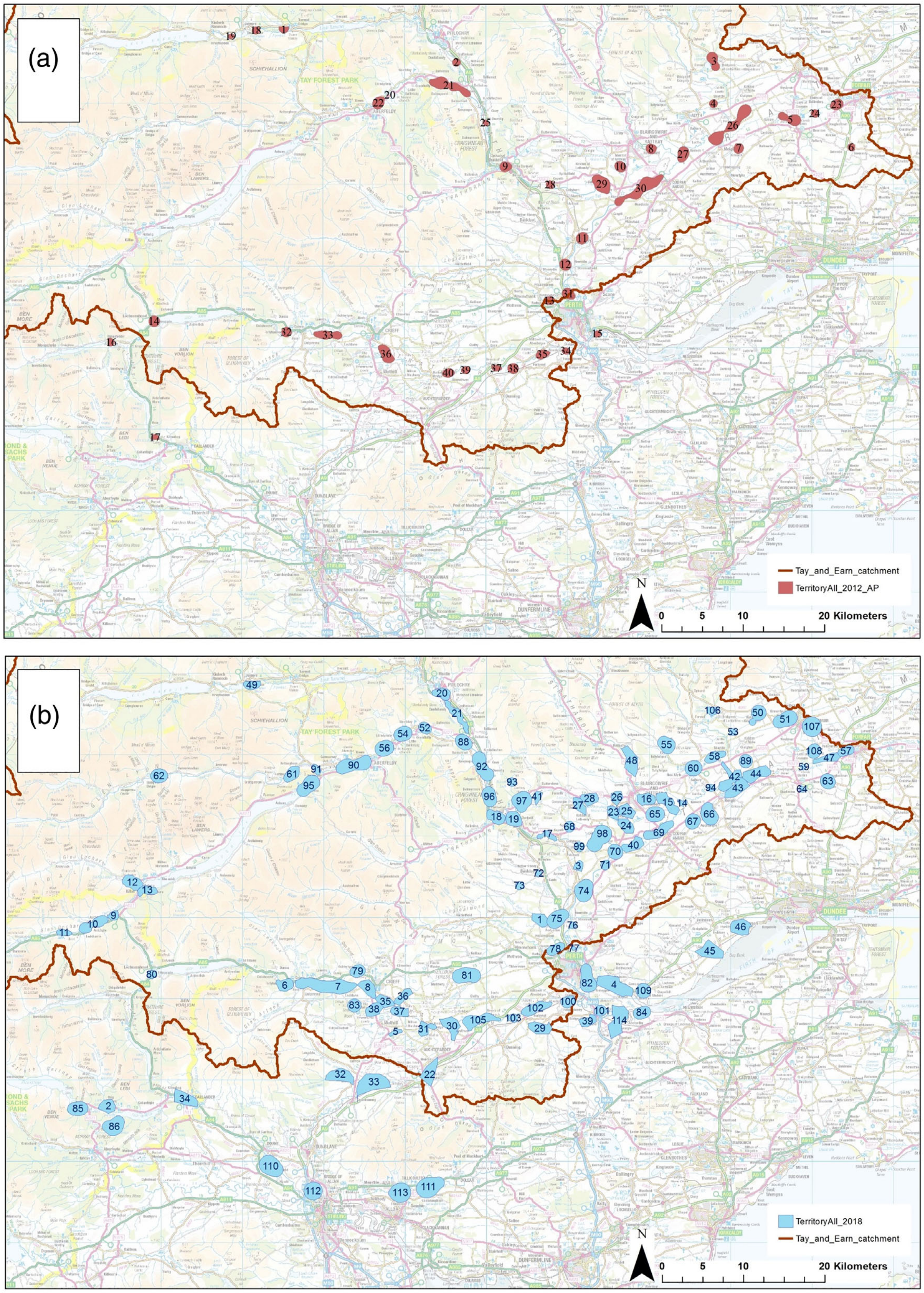
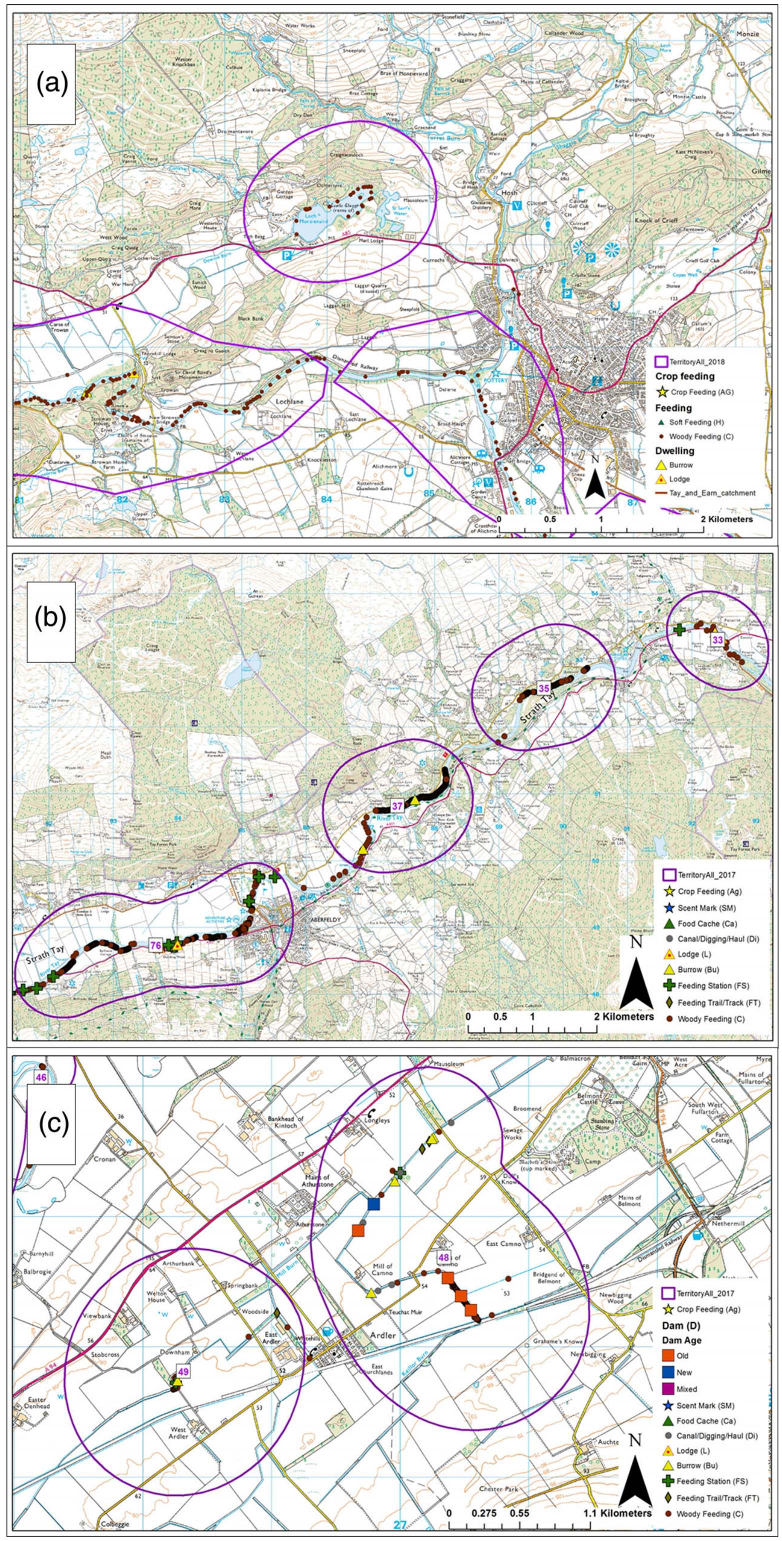


FIGURE 5 Comparison of 2012 and 2017/2018 beaver territory extent and identification number. Contains OS data © Crown copyright (and database rights) 2018 OS 100017908 [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 6 Zoomed in examples to illustrate beaver sign data collected and territory determination. Contains OS data © Crown copyright (and database rights) 2018 OS 100017908. (a) Example of survey results for the Crieff area with both main channel and lake based territories. (b) Example of survey results for a section of Strathtay along stretches of a main river system with multiple territories. (c) Example of survey results for the Ardler area including activity in an agricultural ditch system. Full discussion in SI 2. Contains OS data © Crown copyright (and database rights) 2018 OS 100017908 [Colour figure can be viewed at wileyonlinelibrary.com]



included signs which may have been faked or attributed to other animals.

4.3 | Results

4.3.1 | Observed beaver signs

A total of 70 confirmed beaver signs, of mixed age, were identified including those classed as fresh thereby made between the periods of late winter 2018 to time of survey by March 2019 (Figure 8). All but two signs (one burrow and one beaver cadaver which dates back to 2017 and was verified during this survey) were feeding signs (woody feeding, herbaceous feeding and feeding stations) and 100% of these signs were judged as having involved a low level of effort expenditure. All woody feeding signs were minimal cutting of multiple small branches and no large-scale tree felling or dam building was observed.

4.3.2 | Active beaver areas

Nine main areas of activity on the River Wye (five areas in Wales and four in England) were observed during the survey (Figure 8). However, the widely dispersed, low density, type, and age of observed signs indicated a low number of dispersing individuals. Therefore, kernel density analysis was not required or deemed appropriate to delineate established beaver territories to which estimations of population numbers can be attached.

4.3.3 | Land use and management concern

Due to the type and low density of signs (i.e., woody feeding, with no damming), no notable incidents of land use impacts and management concerns were observed, such as inundated land or dams blocking or threatening infrastructure such as roads or culverts. The only possible reports involved a burrow, which could be regarded as undesirable bankside burrowing in a recreational fishpond. Tree felling on more modified land-use areas may be undesirable to landowners but was not constituted as a management issue here as evidence demonstrated extremely low-level activity on non-amenity or crop trees.

Overall, this is reflective of small numbers of beaver dispersing along main river systems that are too large to dam. If beaver densities increase or if beavers are found to have established in smaller associated tributary systems where damming is likely then this would be expected to change rapidly with time.

5 | DISCUSSION

5.1 | Field survey method assessment

This study deployed a replicable and standardized field survey method to assess beaver distribution, and territories, which could be applied across diverse study areas and different stages of beaver colonization. Application could be widely employed, allowing for standardized data collection to facilitate a greater understanding of beaver distribution and population dynamics across Europe. With a little more time and expertise, study methods can be adjusted to collect additional data that can be adapted for asking more specialist questions that is, recording of management conflicts, or recording of individual tree species etc. (as shown in Brazier et al., 2020a).

Any territory-based survey techniques have limitations when estimating total beaver population sizes (refs). They may omit dispersers travelling through the catchment, by missing subtler field signs left by one individual. They may also attribute sporadic and dispersed field signs to the nearest beaver family as opposed to estimating additional single animals.

The survey method and associated data presented here should be viewed as providing a snapshot in time in a dynamic situation. Colonization of other catchments is part of an ongoing natural process. Dispersing sub-adults tend to colonize habitats close to their natal territory, although they are capable of travelling tens of kilometers per day (Nolet & Rosell, 1994; Saveljev et al., 2002) and may move hundreds of kilometers in a season to find suitable territories (Hartman, 1995). Several studies have found that after initial population establishment, dispersers tend to infill habitats within an occupied area, before expanding into new catchments (Barták, Vorel, Símová, & Pus, 2013; Fustec et al., 2001). Simunková and Vorel (2015) found that there is more rapid population growth when the proximity of source populations (i.e., maternal territories) is small. Additionally, they found that animals dispersing long-distances are more influenced by mating opportunities, rather than purely influenced by habitat selection. Therefore, during the initial phase of population growth, individuals will make longer journeys to seek mating opportunities (Halley & Rosell, 2002). This natural ecology and dispersal ability of beavers make the colonization of closely associated catchments very plausible. Beavers do not require permanent watercourses for dispersal and will even follow damp ditch-type systems. It is also completely feasible that some individuals remain undiscovered in smaller backwater areas away from the main river stem and may not become apparent until breeding and/or landowners report any impacts.

As with any wildlife population, densities will vary over time and with habitat quality (Novak, 1987). One of the greatest areas of uncertainty in determining territories via spatially discrete zones of activity is that, where there are continuous stretches of river with high intensity activity recorded, it is hard to differentiate between territories. With continued population expansion over time, this uncertainty will most likely increase and so should be incorporated into any future sampling strategy and population size calculations.

Caution must be used when interpreting results due to the unknown factors that impact on population dynamics and territory extents such as the composition and location of the original founders, the intensity of any culling that has taken place, and the extent of any further unofficial animal releases.

The following sections discuss survey results across the two contrasting catchments, including Tayside where there are a large number

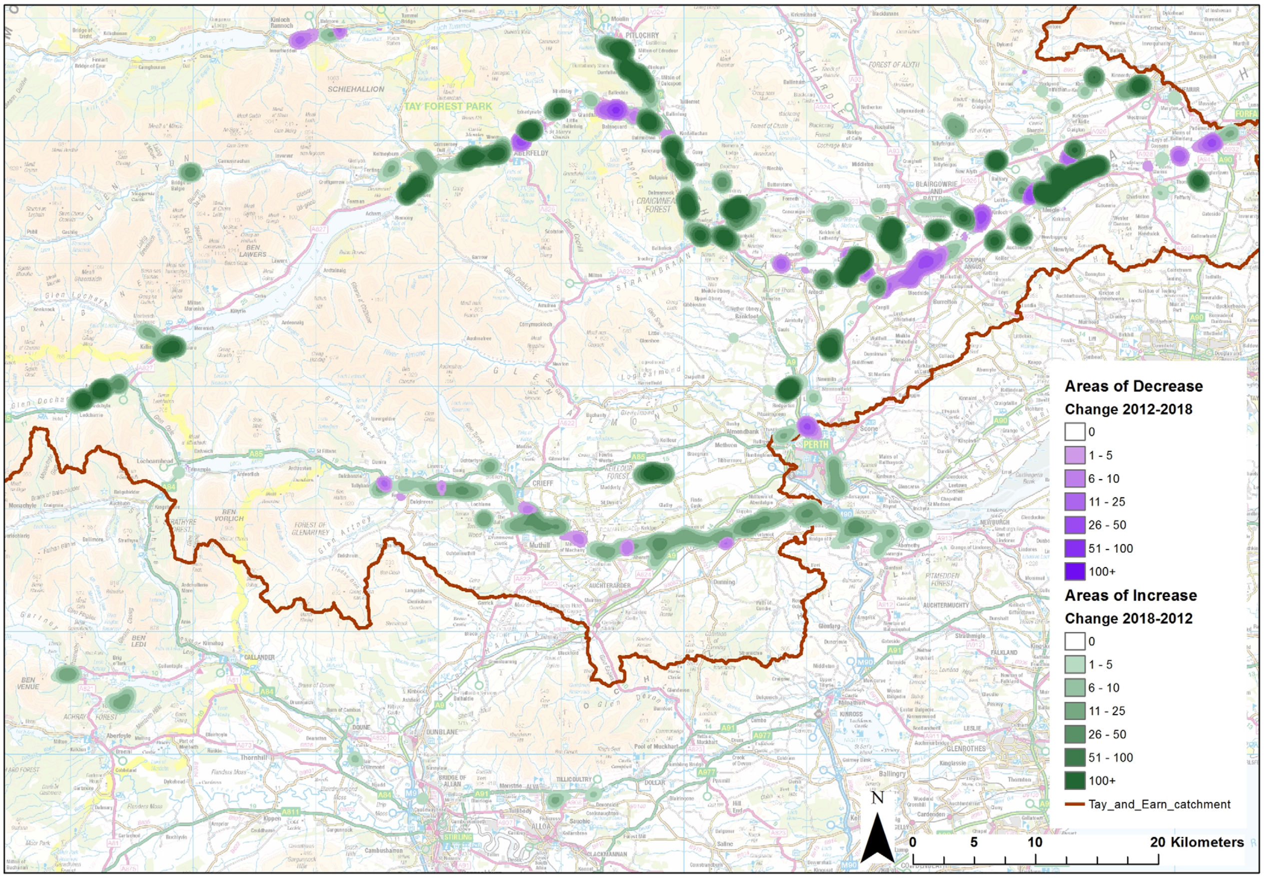


FIGURE 7 Areas of increased beaver field sign density (green) and reduced field sign density (purple) between 2012 and 2017/2018 surveys. Change is measured in number of field sign data points per km^2. Contains OS data © Crown copyright (and database rights) 2018 OS 100017908 [Colour figure can be viewed at wileyonlinelibrary.com]

of established territories and the Wye where results indicate a low number of animals are in the initial colonization stage.

5.2 | Survey findings and implications in Case Study 1: Tayside, Scotland

A total of 114 active beaver territories were recorded. This was a significant increase since 2012, yet it is unlikely that the populations are operating at carrying capacity. Culling in some areas has removed animals and therefore created vacant territories at time of survey. Such activity has slowed down progression toward carrying capacity and therefore stabilization of the population in these areas. In the short term, empty territories are likely to be filled by dispersing beavers. Over the long term, the population may respond to culling by changing their reproductive patterns through reproducing at a younger age and/or increasing number of kits (Payne, 1984).

Results from Tayside indicated that all territories contained the areas identified as potential beaver woodland. The majority (95%) were contained within "core beaver woodland" (Stringer et al., 2015). As beaver populations grow and densities increase, successive generations are forced to travel greater dispersal distances and/or occupy "suboptimal" habitats in more minor watercourses. This is occurring within Tayside as increasing numbers of beavers are now occupying smaller tributaries and artificial drainage systems, associated with some of the larger river systems where they have been resident for many years (TBSG, 2015). These provide suitable habitat for beavers as some of these watercourses can easily be dammed, banks tend to be suitable for burrowing and can provide a ready supply of food. Since beavers often need to modify such habitats, particularly to stabilize and deepen water levels, this tends to lead to increased conflicts with people. Damming is one of the most common causes of conflict, especially in flatter landscapes, and requires reactive management. Drainage systems are essential for many agricultural practices in such areas, and their failure or blockage can cause problems, including increased ground water levels and direct flooding of crops (Schwab & Schmidbauer, 2003). In the Tayside survey, damming and localized flooding accounted for the greatest number of potential sources of conflict identified.

FIGURE 8 Confirmed field signs recorded across the River Wye and according to age. Contains OS data © Crown copyright (and database rights) 2018 OS 100017908 [Colour figure can be viewed at wileyonlinelibrary.com]

5.3 | Survey findings and implications in Case Study 2: Wye

In contrast to Tayside, the range of beaver activity confirmed was limited. Signs were indicative of small numbers of animals, most likely singletons, moving through a large linear river system without long-term residency. No high-density clusters of feeding signs, damming or lodges were found, all of which would represent a more residential animals/breeding.

For all signs, the level of impact was deemed as very low, with no notable management implications or conflicts. This is not dismissing any perception of impact from specific landowners, in which the felling of even a single tree may be considered as a personal conflict. On examination of field signs observed, no notable conflicts with land-use were assumed given the low level of signs and lack of typical management issues such as damming or burrowing leading to bank collapse. However, similar situations have been observed in other British catchments when beavers were only present at very low densities. It should be anticipated that this would change if population changes to breeding status and numbers increase and/or beavers establish on smaller streams in the headwaters of the Wye. In smaller rivers, typically below fifth order (Graham et al., 2020), damming may be expected which would result in greater management implications (both positive and negative). Similarly, at higher population densities, feeding on vegetation deemed valuable (i.e., crops or prestige/ornamental trees) may be more likely.

Whilst the impact of nascent beaver activity in the Wye catchment is limited, beavers are clearly present. Presuming that the population increases in the future; beaver impacts are likely to occur. It is recommended that reports of beaver sightings and signs continue to be recorded and survey efforts repeated in the future. The same repeated approach could be applied to the Rivers Wye, Tay, and indeed other sites throughout Europe to obtain a continuous, up-to-date assessment of distribution whilst determining any changes in territories and population numbers.

6 | SUMMARY AND FUTURE RECOMMENDATIONS

This paper presents the deployment of a beaver sign survey across two large catchments to determine current distribution of beaver and active territories (or lack of) in addition to quantifying change. The two case studies herein illustrate the survey method is applicable both for established beaver territories and catchments where beavers have recently been reintroduced. The deployment of a standardized survey will inform future management decisions and forms a template by which expanding populations of beaver across Europe can be quantified. Given the significant potential for beaver to impact upon land use and modify habitats on a catchment scale, their presence and subsequent management requirements need due consideration. As beaver populations continue to expand across Europe being able to undertake replicable geospatial analysis of beaver population dynamics has increasing value for scientific understanding and inform future decision making.

These survey results provide a wealth of opportunities for more detailed research into beaver population dynamics (both spatial and temporal) across catchments, with widespread relevance for identifying potential release sites for restoration efforts. In addition to identifying risk and the management of conflicts, expanding beaver populations may provide opportunities for ecosystem service provision that is, for water resources and biodiversity (Puttock et al., 2017; Puttock et al., 2018; Law, McLean, & Willby, 2016; Law et al., 2017; Gaywood, 2018). Such survey methods can extend our understanding of beaver behavior in densely populated and managed environments, informing management and modeling approaches to help mitigate conflict and maximize benefits (Brazier, Elliott, et al., 2020).

This paper illustrates that detailed field surveys of beaver signs, combined with geospatial analysis and expert evaluation, can allow estimates of active beaver spatial extent and territories. As populations of Eurasian beaver expand across Europe, such survey-based approaches can be used to increase understanding of their distribution, population dynamics and territorial behavior. Additionally, as beaver engineering and feeding activities have increasingly well recognized management implications (both positive and negative), results from surveys such as this can be used to design and implement management strategies at both the national and local level.

ACKNOWLEDGMENTS

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DATA AVAILABILITY STATEMENT

Original field survey data was collected on behalf of Scottish Natural Heritage for the Tayside survey and full results are published in Campbell-Palmer et al. (2018). For the Wye survey, full data are available from the Environment Agency and Natural England. Data are available from these organizations on request.

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SUPPORTING INFORMATION

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

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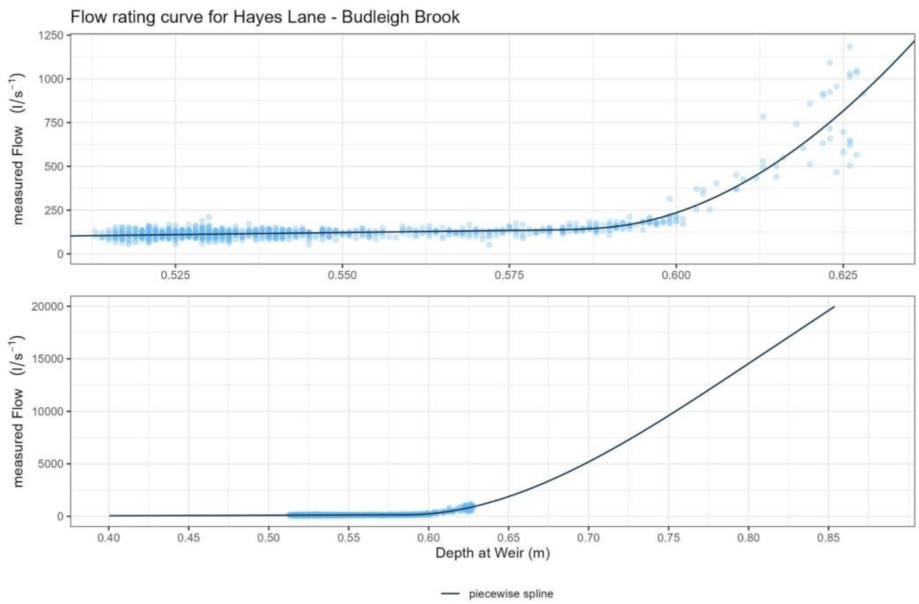
Appendix 6. Supplementary Information: Chapter 2

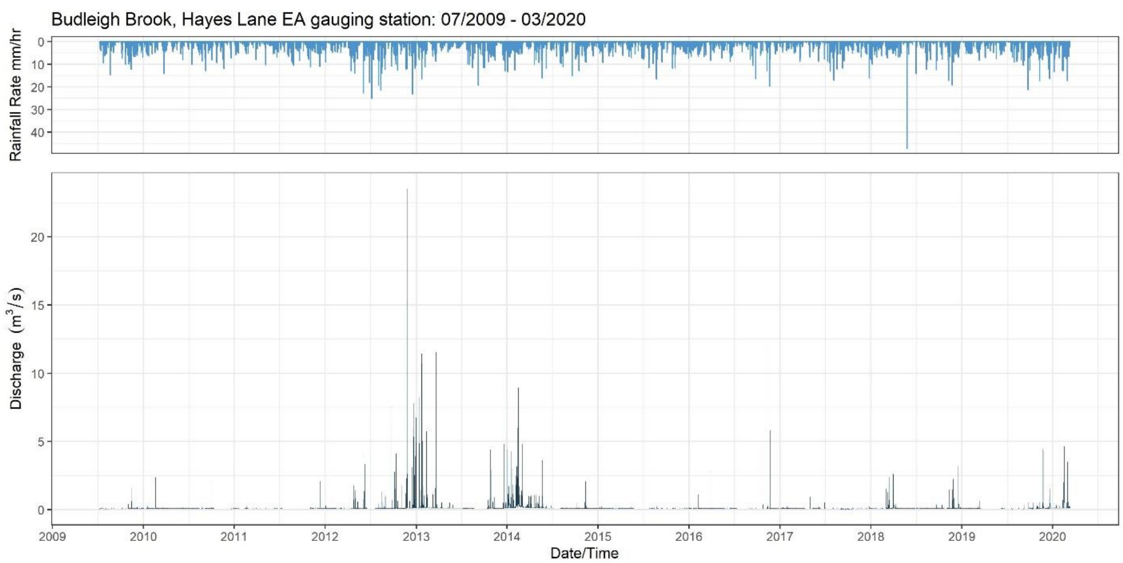
SI 1: **A** - Hayes Lane gauging station and weir at East Budleigh. **B**- Location of flow gauge installation ~50 m upstream of the weir pictured in panel A. The gauge remained in situ for 2 months to measure flows, allowing for the creation of a rating curve to estimate flow from the depth gauge downstream.

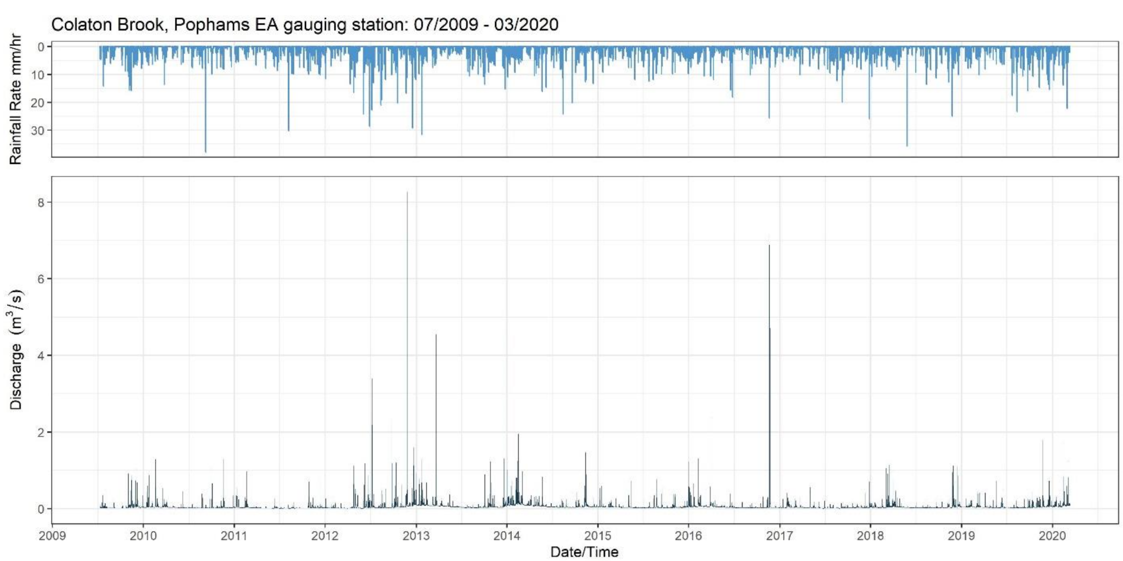
SI 2: stage-discharge rating using spline regression for Budleigh Brook EA gauging station. Upper plot shows the curve fit for the measured flow range. Lower plot shows extrapolation of curve to maximum and minimum flow limits from full time series. The equation denotes the piecewise polynomials that describe the curve.



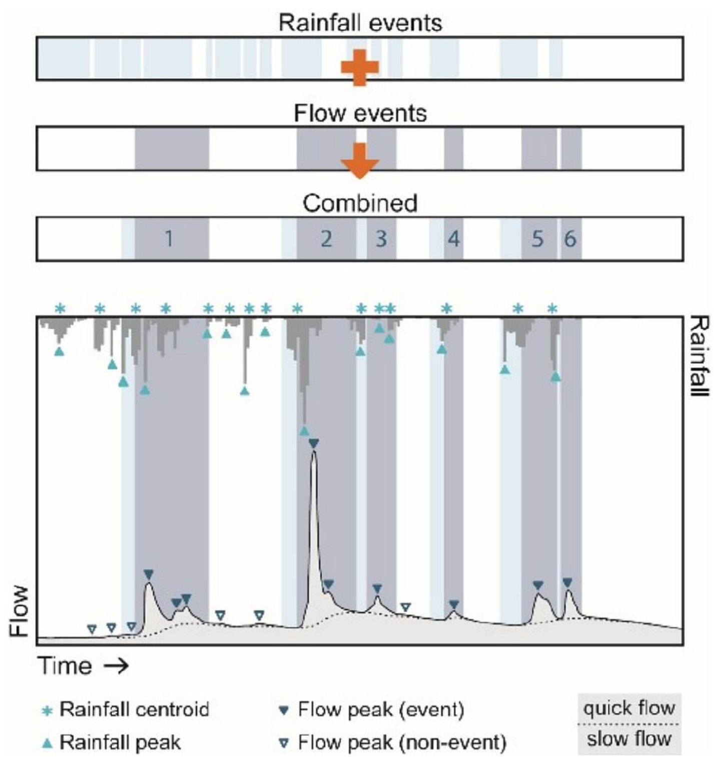
Piecewise polynomials of degree 3:
*y = 7.24e-14 + 474 * (x - 0.58) + 4.69e-08 * (x - 0.58) ^ 2 + 1.17e+07 * (x - 0.58) ^ 3*
*y = 31.9 + 6.42e+03 * (x - 0.593) + 4.57e+05 * (x - 0.593) ^ 2 - 7.36e+05 * (x - 0.593) ^ 3*

SI 3: Hydrological time series for Budleigh and Colaton Brook.

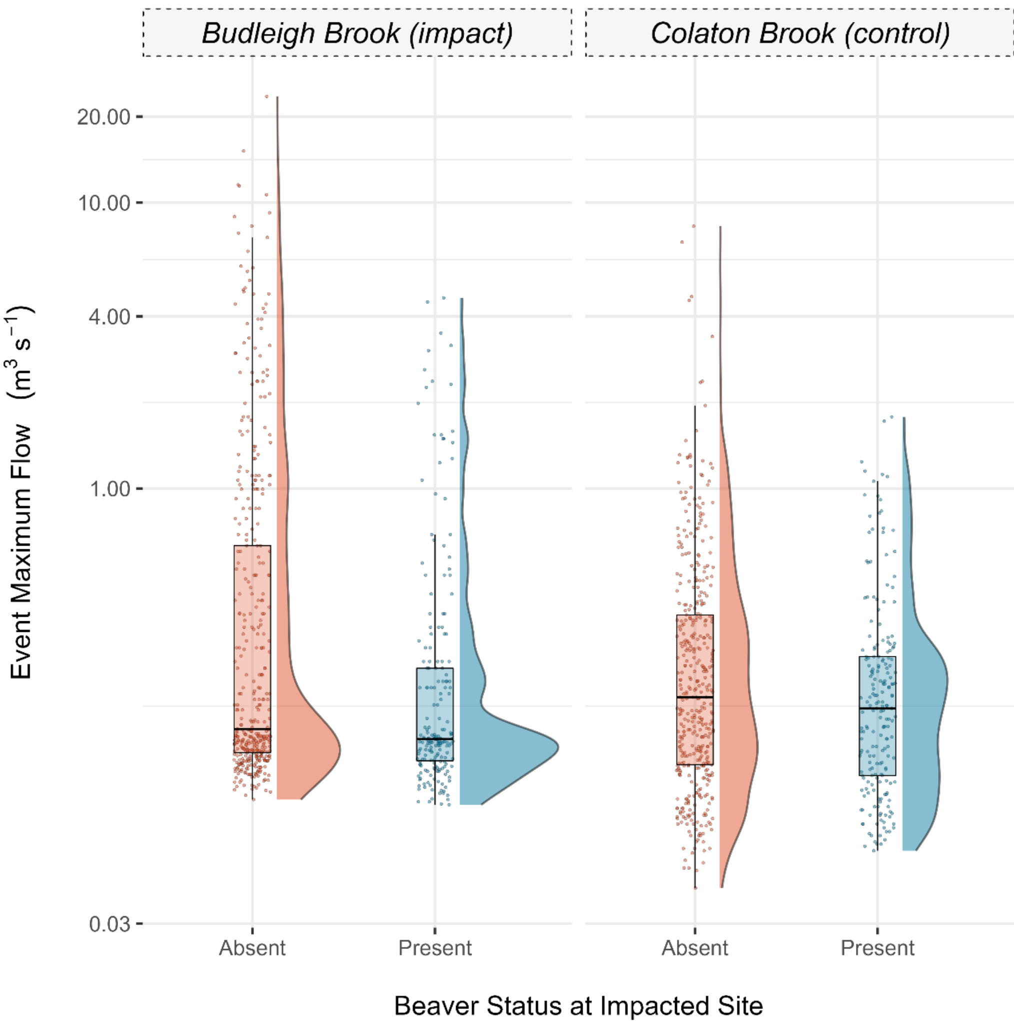




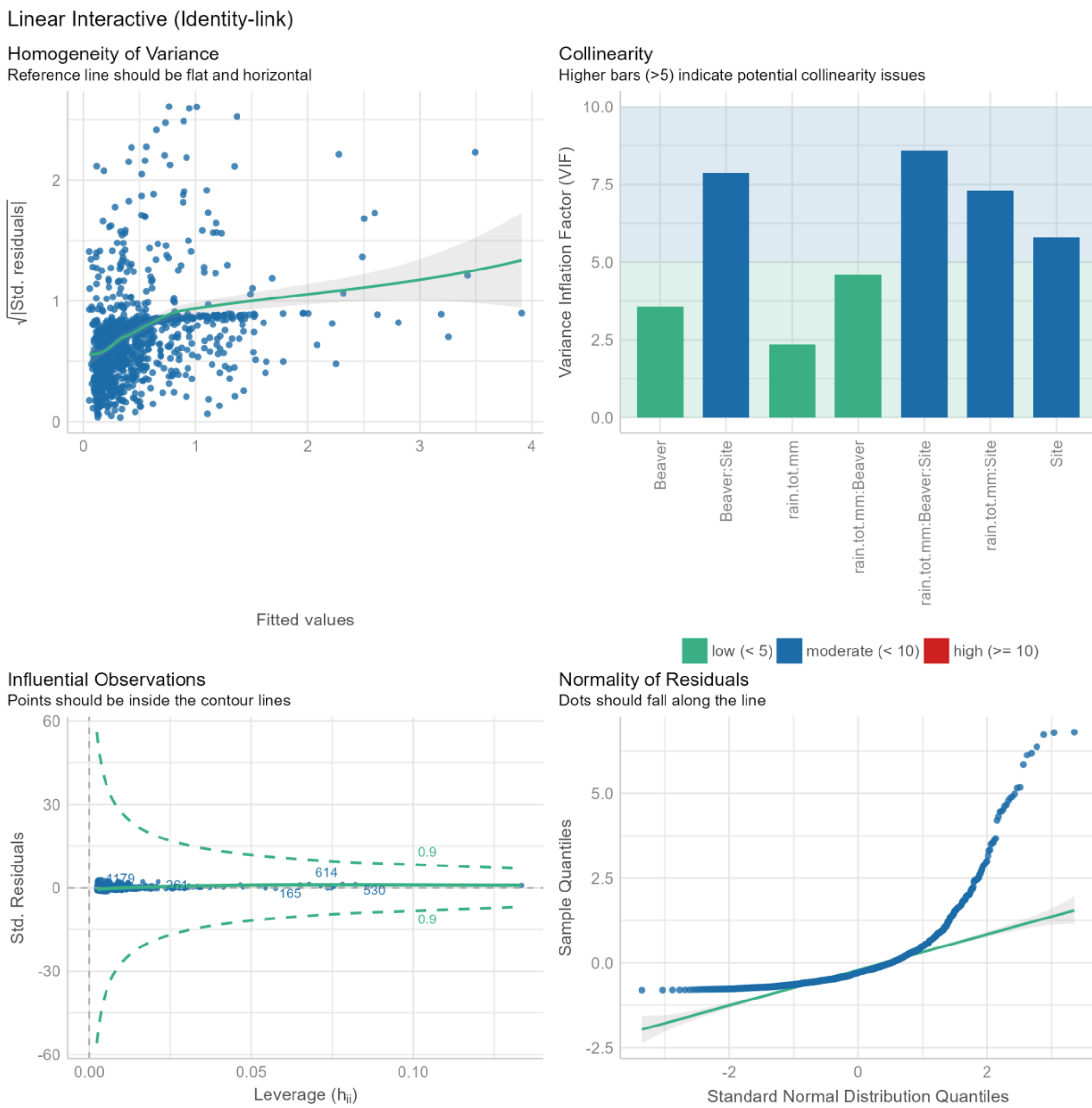
SI 4: Schematic describing the method used to automatically extract discrete hydrological events. From Puttock et al., (2021).



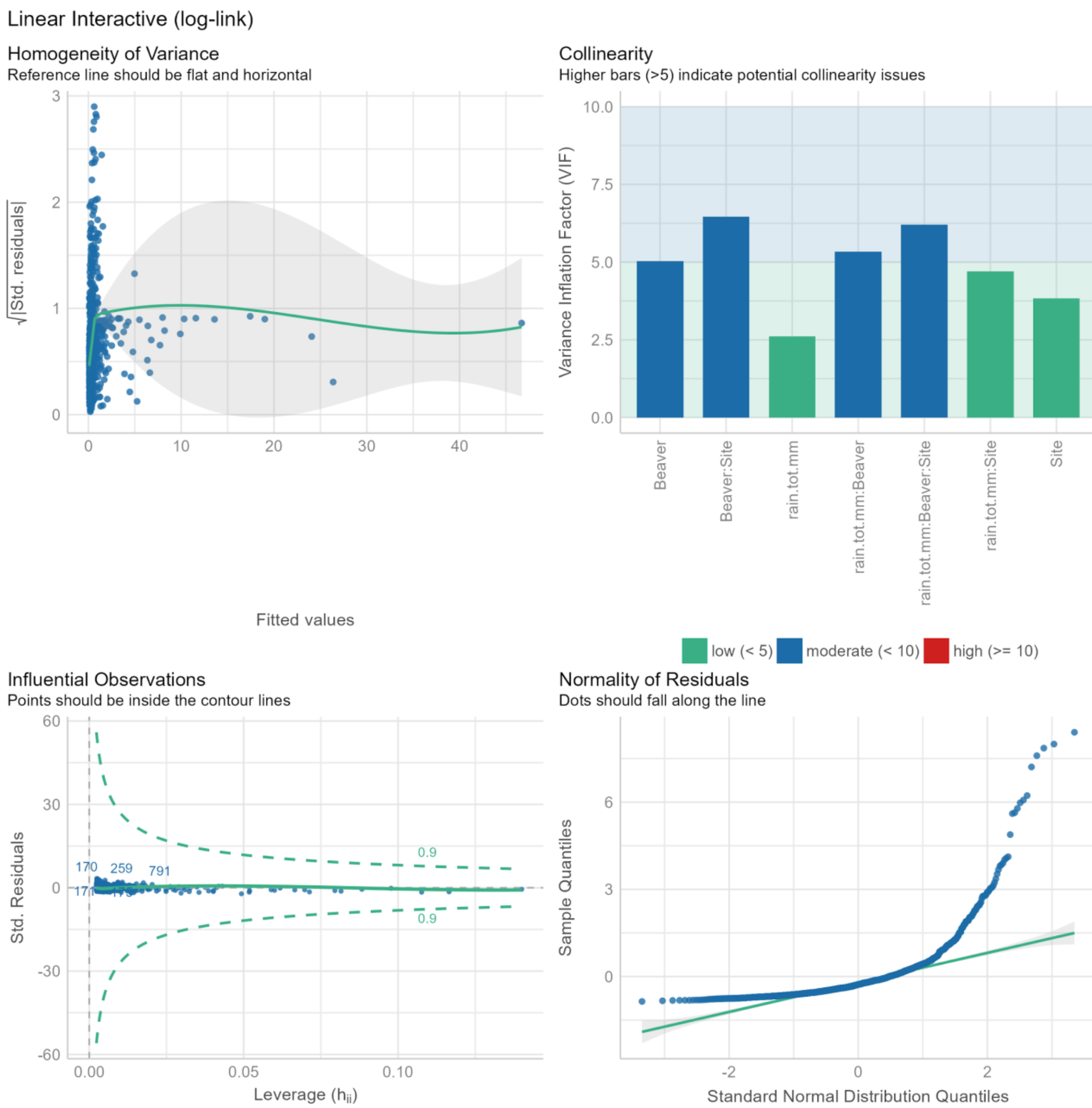
SI 5: Raincloud Plot showing the raw data, boxplot statistics and density distribution of peak flows for hydrological events in both Budleigh Brook and Colaton brook, before and after beaver complex was established in Budleigh Brook



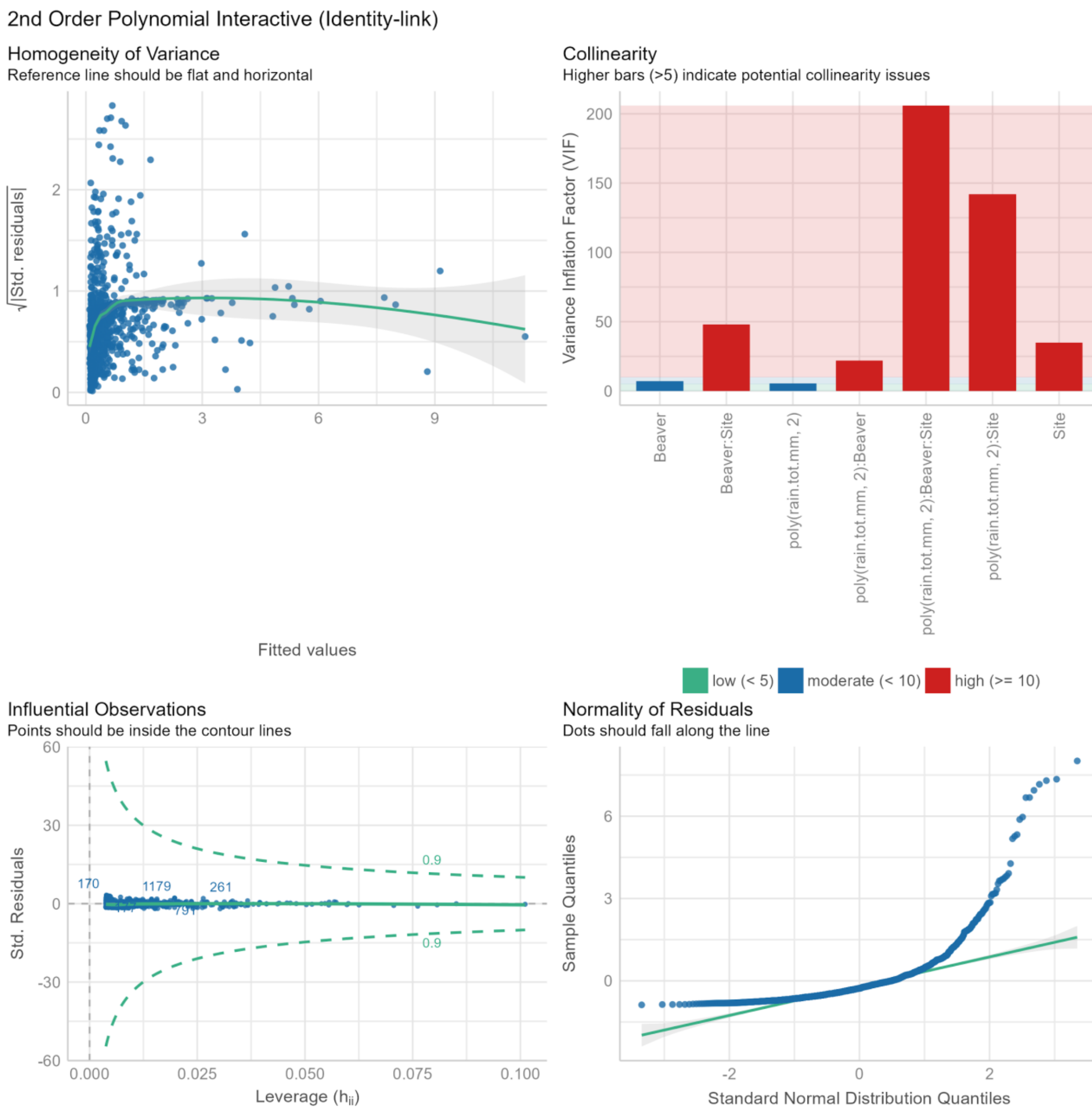
SI 6: General Linear Model validation plots produced using the {performance} R package (Lüdecke et al., 2021). The key diagnostic in these figures is the residual plots in the upper left; here, heteroscedasticity is not of such importance because we have adopted a Gamma error distribution. Critically, we are interested in the deviance in the fitted line through the residuals. It is clear that in M1 and M2, there is considerable skew in this line, indicating that the model is not appropriately describing the trend in the data, particularly for higher predicted flows. For M3, we some improvement but there is generally a poorer model fit. M4 and M5 provide better fit for larger predictions with less deviation in the trend line – of the two M5 provides the least deviation in the trend line, especially for larger values. Heavy tails in the bottom right (normality of residuals or QQ plot) indicate that for all models, there is likely to be some uncertainty in the predicted standard errors for extreme values.

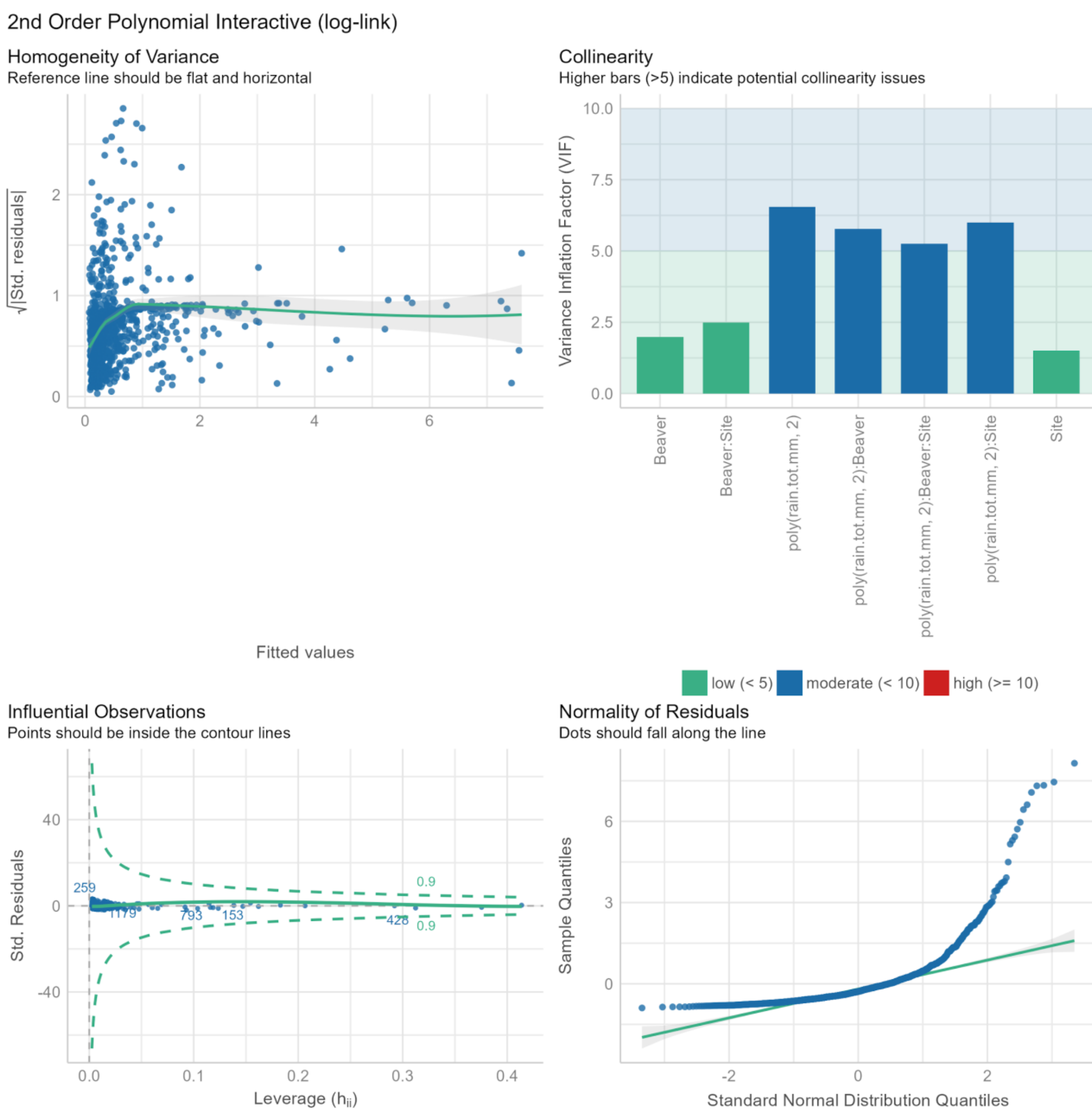


Linear Interactive (Identity-link)
Homogeneity of Variance
Reference line should be flat and horizontal
√|Std. residuals|
Fitted values
Collinearity
Higher bars (>5) indicate potential collinearity issues
Variance Inflation Factor (VIF)
Beaver
Beaver:Site
rain.tot.mm
rain.tot.mm:Beaver
rain.tot.mm:Beaver:Site
rain.tot.mm:Site
Site
low (< 5)
moderate (< 10)
high (>= 10)
Influential Observations
Points should be inside the contour lines
Std. Residuals
Leverage (h_{ii})
0.9
614
165
530
Normality of Residuals
Dots should fall along the line
Sample Quantiles
Standard Normal Distribution Quantiles



Linear Interactive (log-link)
Homogeneity of Variance
Reference line should be flat and horizontal
√|Std. residuals|
Fitted values
Collinearity
Higher bars (>5) indicate potential collinearity issues
Variance Inflation Factor (VIF)
Beaver
Beaver:Site
rain.tot.mm
rain.tot.mm:Beaver
rain.tot.mm:Beaver:Site
rain.tot.mm:Site
Site
low (< 5)
moderate (< 10)
high (>= 10)
Influential Observations
Points should be inside the contour lines
Std. Residuals
Leverage (h_{ii})
170
259
791
0.9
0.9
Normality of Residuals
Dots should fall along the line
Sample Quantiles
Standard Normal Distribution Quantiles


2nd Order Polynomial Interactive (Identity-link)
Homogeneity of Variance
Reference line should be flat and horizontal
√|Std. residuals|
Fitted values
Collinearity
Higher bars (>5) indicate potential collinearity issues
Variance Inflation Factor (VIF)
Beaver
Beaver:Site
poly(rain.tot.mm, 2)
poly(rain.tot.mm, 2):Beaver
poly(rain.tot.mm, 2):Beaver:Site
poly(rain.tot.mm, 2):Site
Site
low (< 5)
moderate (< 10)
high (>= 10)
Influential Observations
Points should be inside the contour lines
Std. Residuals
Leverage (h_{ii})
170
1179
261
0.9
Normality of Residuals
Dots should fall along the line
Sample Quantiles
Standard Normal Distribution Quantiles


2nd Order Polynomial Interactive (log-link)
Homogeneity of Variance
Reference line should be flat and horizontal
√|Std. residuals|
Fitted values
Collinearity
Higher bars (>5) indicate potential collinearity issues
Variance Inflation Factor (VIF)
Beaver
Beaver:Site
poly(rain.tot.mm, 2)
poly(rain.tot.mm, 2):Beaver
poly(rain.tot.mm, 2):Beaver:Site
poly(rain.tot.mm, 2):Site
Site
low (< 5)
moderate (< 10)
high (>= 10)
Influential Observations
Points should be inside the contour lines
Std. Residuals
Leverage (h_{ii})
Normality of Residuals
Dots should fall along the line
Sample Quantiles
Standard Normal Distribution Quantiles

SI 7: General Linear Model Summary tables for the five general linear model presented in Figure 5. Corresponding Model evaluation plots are presented in SI6.

M1 Linear Add.				
term	estimate	std.error	T.statistic	p.value
(Intercept)	0.042	0.016	2.641	0.008 *
rain.tot.mm	0.025	0.002	12.567	< 0.001 **
BeaverPresent	0.000	0.021	0.016	0.987
SiteBudleigh Brook (impact)	0.326	0.042	7.766	< 0.001 **
BeaverPresent:SiteBudleigh Brook (impact)	-0.315	0.049	-6.418	< 0.001 **

M2 Linear Int.				
term	estimate	std.error	T.statistic	p.value
(Intercept)	0.051	0.016	3.090	0.002 *
rain.tot.mm	0.023	0.002	9.471	< 0.001 **
BeaverPresent	0.030	0.028	1.069	0.285
SiteBudleigh Brook (impact)	0.058	0.039	1.516	0.130
rain.tot.mm:BeaverPresent	-0.009	0.004	-2.454	0.014 *
rain.tot.mm:SiteBudleigh Brook (impact)	0.039	0.007	5.923	< 0.001 **
BeaverPresent:SiteBudleigh Brook (impact)	-0.084	0.050	-1.662	0.097 .
rain.tot.mm:BeaverPresent:SiteBudleigh Brook (impact)	-0.028	0.008	-3.436	< 0.001 **

M3 Linear Int. (log-link)				
term	estimate	std.error	T.statistic	p.value

(Intercept)	-2.168	0.091	-23.743	< 0.001 **
rain.tot.mm	0.070	0.006	12.064	< 0.001 **
BeaverPresent	-0.022	0.159	-0.141	0.888
SiteBudleigh Brook (impact)	0.793	0.131	6.075	< 0.001 **
rain.tot.mm:BeaverPresent	-0.015	0.010	-1.418	0.156
rain.tot.mm:SiteBudleigh Brook (impact)	0.014	0.009	1.581	0.114
BeaverPresent:SiteBudleigh Brook (impact)	-1.044	0.230	-4.547	< 0.001 **
rain.tot.mm:BeaverPresent:SiteBudleigh Brook (impact)	0.031	0.016	1.936	0.053 .

M4 Poly. Int.				
term	estimate	std.error	T.statistic	p.value
(Intercept)	0.342	0.025	13.771	< 0.001 **
poly(rain.tot.mm, 2)1	12.997	2.355	5.519	< 0.001 **
poly(rain.tot.mm, 2)2	4.608	1.683	2.739	0.006 *
BeaverPresent	-0.084	0.036	-2.338	0.020 *
SiteBudleigh Brook (impact)	0.631	0.086	7.362	< 0.001 **
poly(rain.tot.mm, 2)1:BeaverPresent	-4.741	3.405	-1.392	0.164
poly(rain.tot.mm, 2)2:BeaverPresent	-1.368	2.488	-0.550	0.583
poly(rain.tot.mm, 2)1:SiteBudleigh Brook (impact)	29.677	8.050	3.687	< 0.001 **
poly(rain.tot.mm, 2)2:SiteBudleigh Brook (impact)	11.093	5.247	2.114	0.035 *
BeaverPresent:SiteBudleigh Brook (impact)	-0.398	0.110	-3.634	< 0.001 **

poly(rain.tot.mm, 2)1:BeaverPresent:SiteBudleigh Brook (impact)	-8.101	10.333	-0.784	0.433
poly(rain.tot.mm, 2)2:BeaverPresent:SiteBudleigh Brook (impact)	1.544	6.788	0.227	0.820

M5 Poly. Int. (log-link)				
term	estimate	std.error	T.statistic	p.value
(Intercept)	-1.362	0.055	-24.812	< 0.001 **
poly(rain.tot.mm, 2)1	23.149	1.846	12.540	< 0.001 **
poly(rain.tot.mm, 2)2	-4.280	1.791	-2.390	0.017 *
BeaverPresent	-0.189	0.096	-1.967	0.049 *
SiteBudleigh Brook (impact)	0.950	0.078	12.110	< 0.001 **
poly(rain.tot.mm, 2)1:BeaverPresent	-5.441	3.280	-1.659	0.097 .
poly(rain.tot.mm, 2)2:BeaverPresent	0.738	3.162	0.233	0.815
poly(rain.tot.mm, 2)1:SiteBudleigh Brook (impact)	3.137	2.758	1.138	0.256
poly(rain.tot.mm, 2)2:SiteBudleigh Brook (impact)	-2.579	2.736	-0.943	0.346
BeaverPresent:SiteBudleigh Brook (impact)	-0.703	0.137	-5.138	< 0.001 **
poly(rain.tot.mm, 2)1:BeaverPresent:SiteBudleigh Brook (impact)	6.317	5.138	1.229	0.219
poly(rain.tot.mm, 2)2:BeaverPresent:SiteBudleigh Brook (impact)	-1.701	5.390	-0.316	0.752

Appendix 7. Supplementary Information: Chapter 3

SI 1: Ground control point location map. The spatial distribution of ground control points used for constraining evaluating the accuracy of the models

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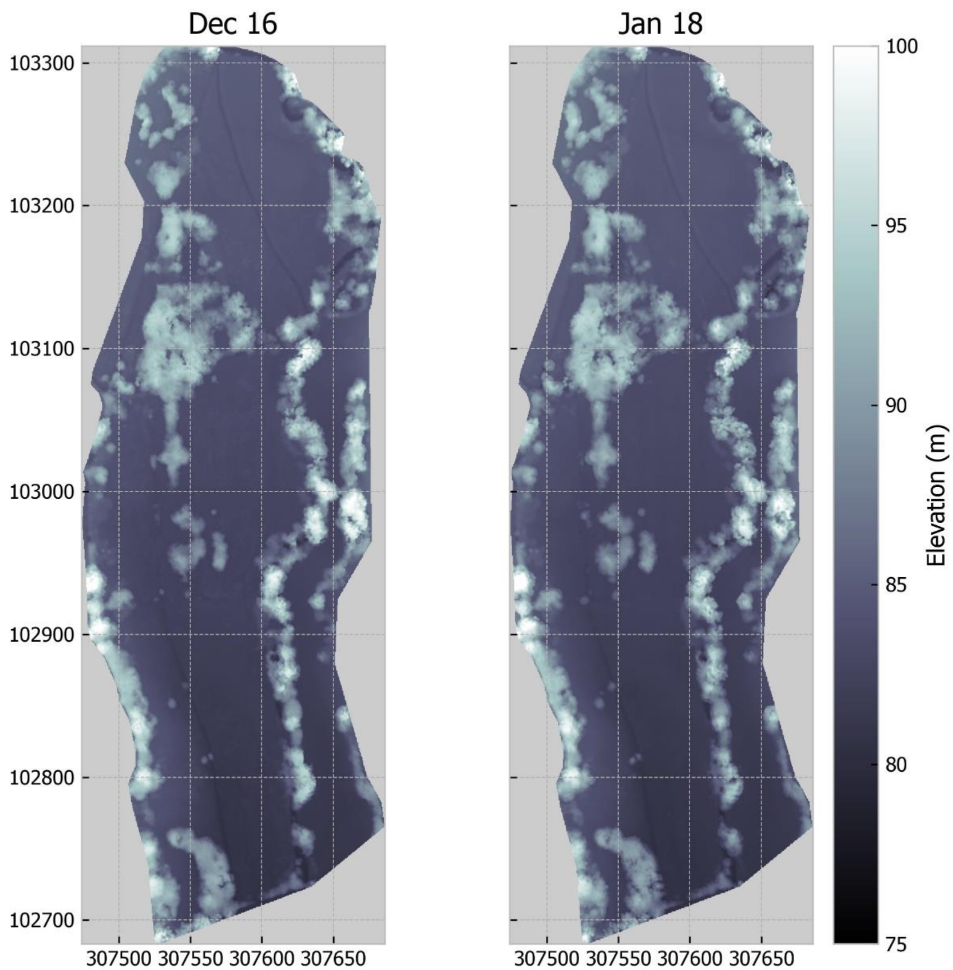
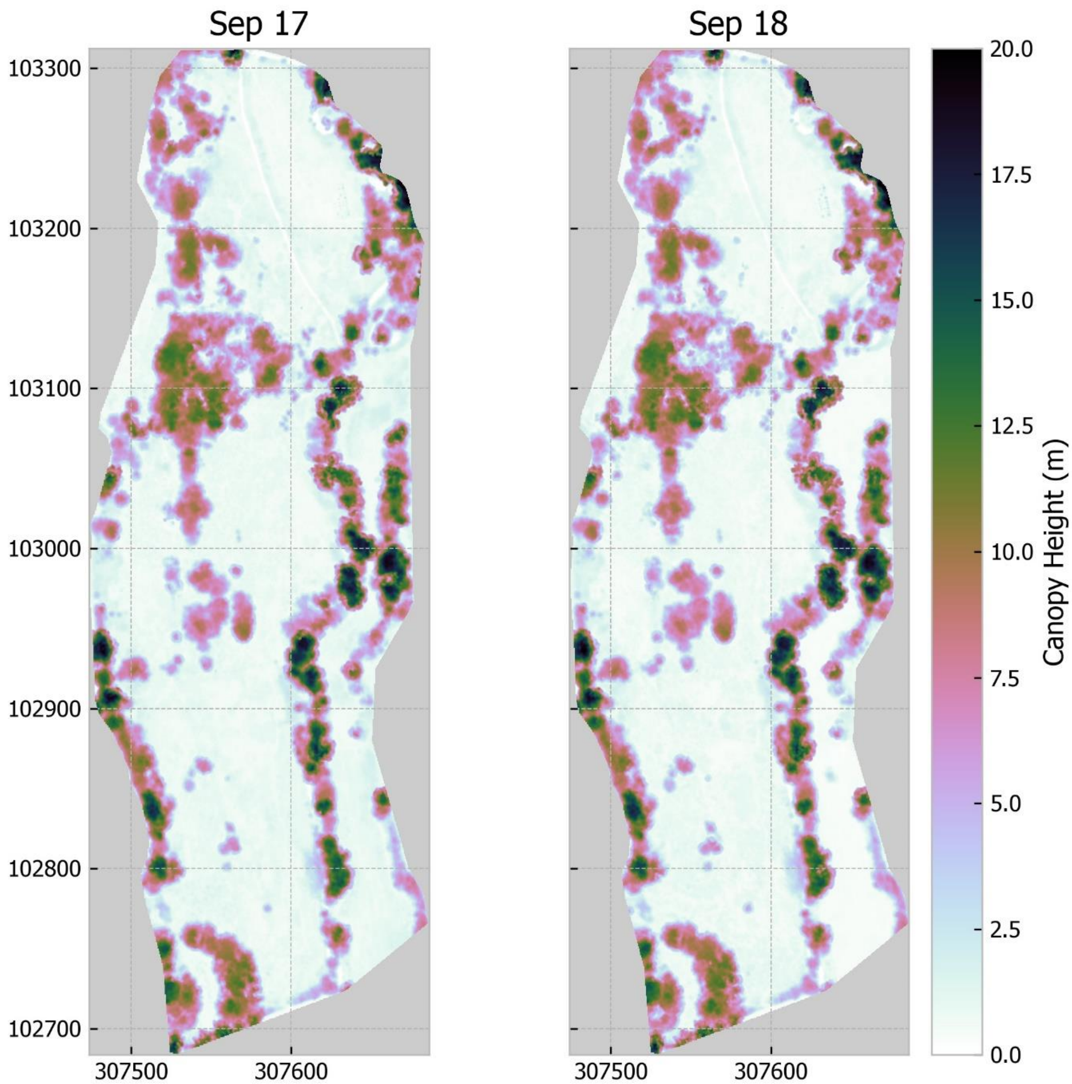
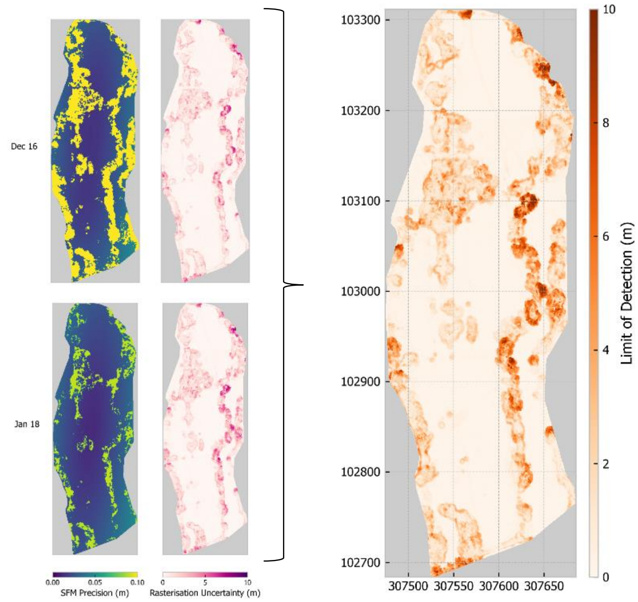
SI 2: Digital Surface Models (DSM) for summer surveys (Sep 17 – Sep 18).



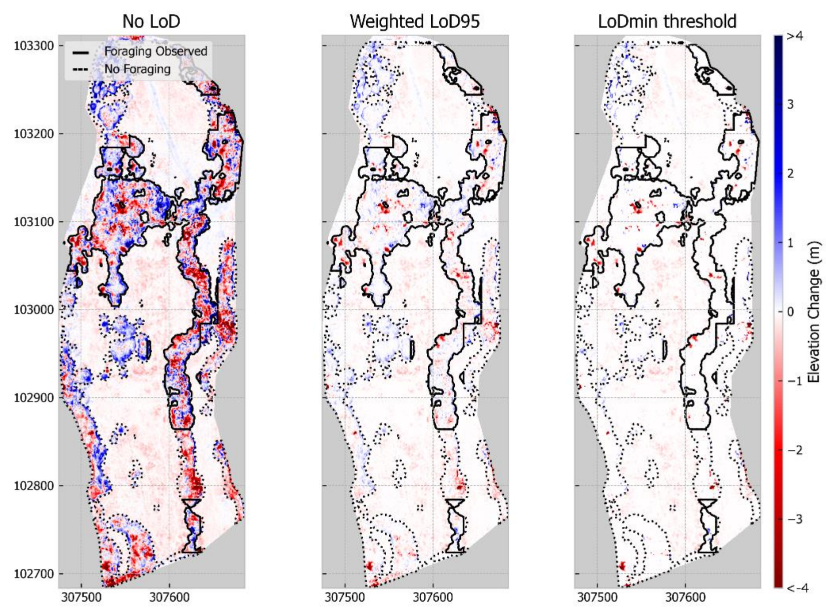
SI 3: Canopy Height Models (CHM) for each time step; calculated by subtracting Terrain Elevation (Figure 1) from each DSM.



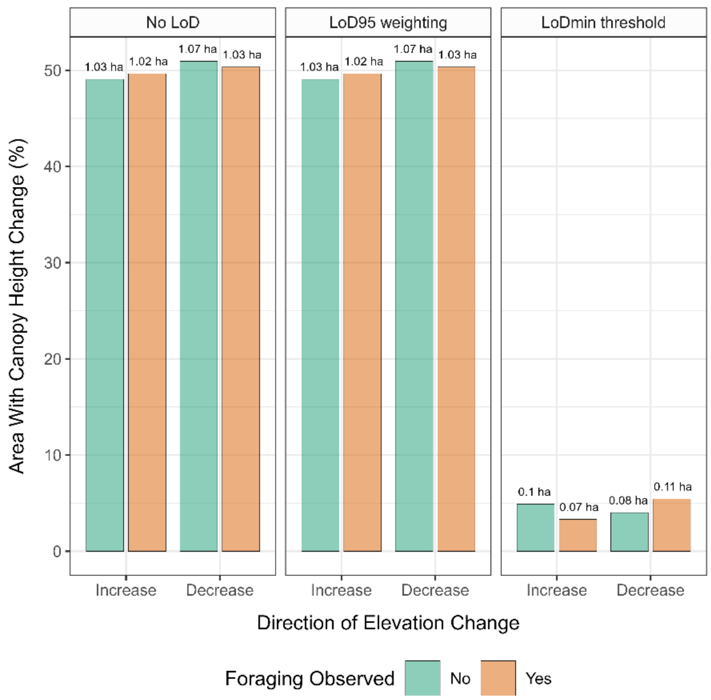
SI 4 Results from winter surveys (Dec 16 – Jan 18). Attached as 'SI4_WINTER_RESULTS.zip'



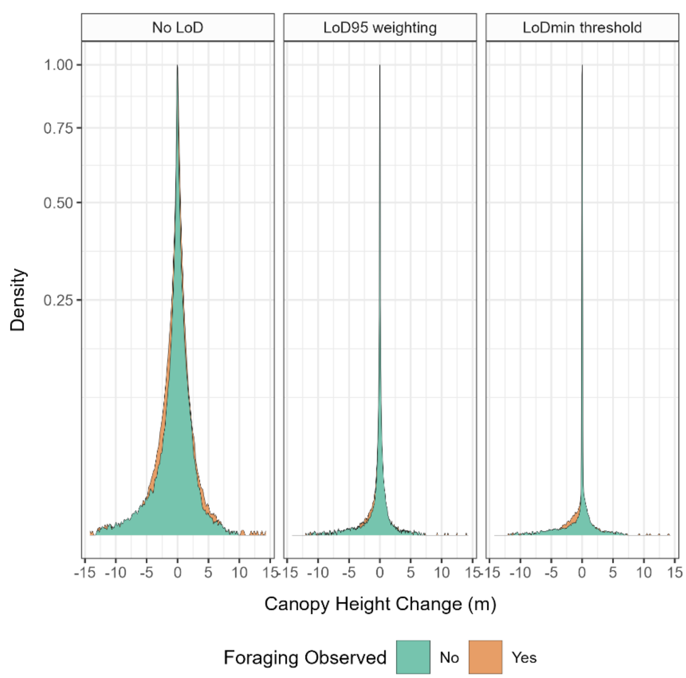
SFM precision maps (viridis palette – left) and Rasterisation uncertainty maps (pink palette – right) for the Dec 16 and Jan 18 surveys are shown on the left. The Limit of Detection map is shown on the right (orange palette) which is derived from the precision and rasterisation uncertainty maps using Equation 2. Winter survey version of Figure 3 (in Chapter 3).



Digital elevation models of difference showing the change in elevation between the two survey intervals computed using three different change detection approaches. Foraging and no foraging regions are differentiated by the solid and dotted polygon areas, respectively. Winter survey version of Figure 5 (in Chapter 3).



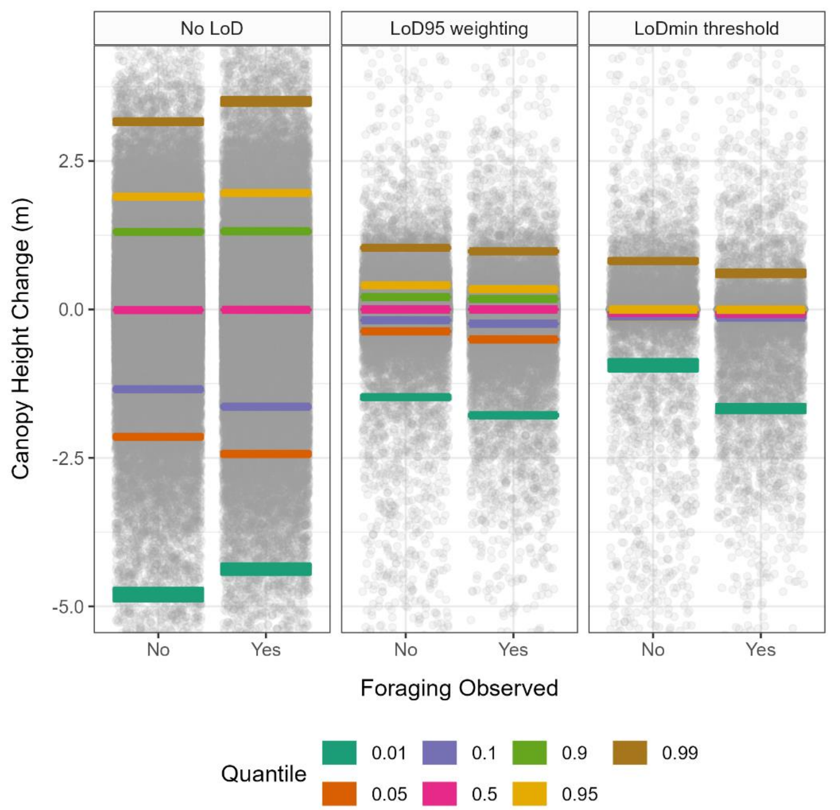
The areal percentage of each zone that experiences elevation increase and decrease. The total area of this change is given in the label above each bar. Winter survey version of Figure 6 (in Chapter 3).



Density plots for canopy elevation change in zones with and without beaver foraging for each change detection method. Winter survey version of Figure 6 (in Chapter 3).

Mean Canopy Change (m): Dec16 - Jan18			
Zone	***mean***	***conf.low***	***conf.high***
No LoD			
No Foraging	-0.048	-0.057	-0.039
Foraging Observed	-0.089	-0.099	-0.080
LoD95 weighting			
No Foraging	-0.013	-0.017	-0.010
Foraging Observed	-0.036	-0.039	-0.033
LoDmin threshold			
No Foraging	-0.009	-0.012	-0.006
Foraging Observed	-0.029	-0.032	-0.027

Mean canopy height change across each foraging zone: conf.low and conf.high refer to the 95% confidence intervals of the mean. Winter survey version of Table 1 (in Chapter 3).

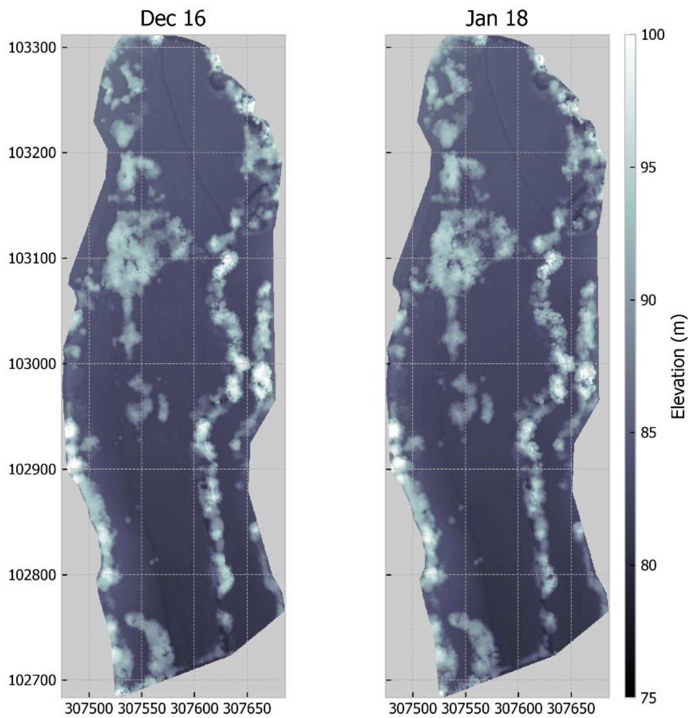


Spatially filtered unconditional quantile regression results showing the effect of beaver foraging on canopy elevation at different quantile levels of the canopy height change distribution. Results are presented for all three change detection methods, detailing the key differences between results derived from each method. Winter survey version of Figure 8 (in Chapter 3).

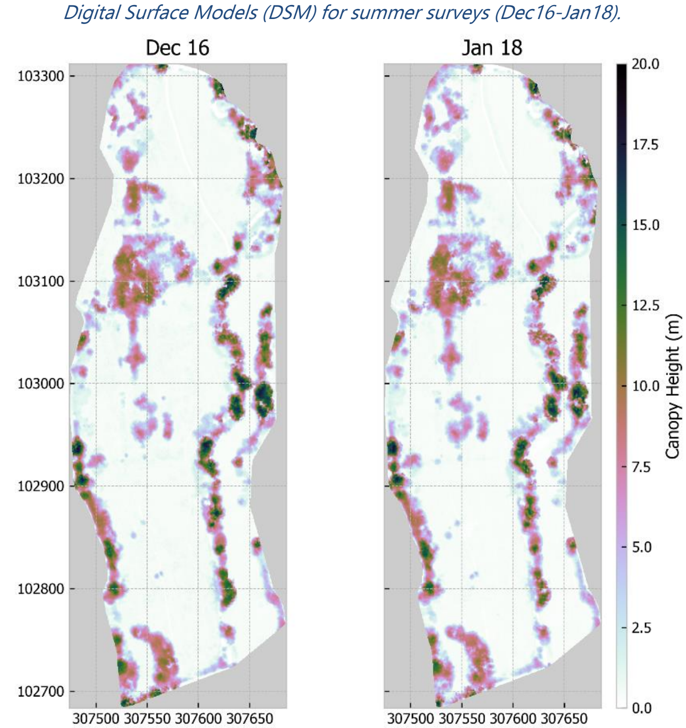
Quantile Regression Summary (Dec16-Jan18)

term	*quantile*	*estimate*	*conf.low*	*conf.upper*
No LoD				
Intercept	0.01	-4.803	-4.909	-4.696
Foraging Observed	0.01	0.434	0.448	0.409
Intercept	0.05	-2.146	-2.174	-2.114
Foraging Observed	0.05	-0.289	-0.292	-0.287
Intercept	0.10	-1.343	-1.364	-1.324
Foraging Observed	0.10	-0.294	-0.294	-0.295
Intercept	0.50	-0.011	-0.014	-0.007
Foraging Observed	0.50	0.006	0.005	0.007
Intercept	0.90	1.306	1.291	1.322
Foraging Observed	0.90	0.009	0.006	0.009
Intercept	0.95	1.900	1.877	1.921
Foraging Observed	0.95	0.061	0.060	0.063
Intercept	0.99	3.160	3.114	3.208
Foraging Observed	0.99	0.345	0.324	0.360
LoD95 weighting				
Intercept	0.01	-1.476	-1.511	-1.446
Foraging Observed	0.01	-0.306	-0.289	-0.319
Intercept	0.05	-0.370	-0.373	-0.366
Foraging Observed	0.05	-0.135	-0.136	-0.135
Intercept	0.10	-0.182	-0.183	-0.180
Foraging Observed	0.10	-0.059	-0.059	-0.059
Intercept	0.50	0.000	0.000	0.000
Foraging Observed	0.50	0.000	0.000	0.000
Intercept	0.90	0.208	0.206	0.210
Foraging Observed	0.90	-0.032	-0.031	-0.033
Intercept	0.95	0.407	0.404	0.410
Foraging Observed	0.95	-0.065	-0.064	-0.066
Intercept	0.99	1.038	1.027	1.050
Foraging Observed	0.99	-0.060	-0.061	-0.061
LoDmin threshold				
Intercept	0.01	-0.947	-1.036	-0.844
Foraging Observed	0.01	-0.713	-0.703	-0.755
Intercept	0.05	-0.117	-0.122	-0.100
Foraging Observed	0.05	0.093	0.099	0.076
Intercept	0.10	-0.110	-0.116	-0.094
Foraging Observed	0.10	-0.025	-0.032	-0.009
Intercept	0.50	-0.058	-0.062	-0.050
Foraging Observed	0.50	-0.015	-0.018	-0.006
Intercept	0.90	-0.007	-0.007	-0.006
Foraging Observed	0.90	-0.004	-0.004	-0.002
Intercept	0.95	0.000	0.000	0.000
Foraging Observed	0.95	-0.003	-0.003	-0.002
Intercept	0.99	0.814	0.782	0.857
Foraging Observed	0.99	-0.207	-0.229	-0.196

Spatially filtered quantile regression summary table showing estimates and confidence intervals of observed elevation change for the Winter surveys. Comparable results for the Sep17-Sep18 period are presented in SI 5.



Digital Surface Models (DSM) for summer surveys (Dec16-Jan18).



Canopy Height Models (CHM) for Dec16 and Jan18 Winter time steps; calculated by subtracting Terrain Elevation (Figure 1) from each DSM.

SI 5 Table containing the full regression summary of all inspected quantiles for the comparison of canopy elevations in beaver and non-beaver foraging zones.

Quantile Regression Summary (Sep17-Sep18)

term	quantile	estimate	conf.low	conf.upper
No LoD				
Intercept	0.01	-2.101	-2.157	-2.039
Foraging Observed	0.01	-1.690	-1.730	-1.663
Intercept	0.05	-0.874	-0.888	-0.859
Foraging Observed	0.05	-0.987	-1.000	-0.964
Intercept	0.10	-0.536	-0.544	-0.529
Foraging Observed	0.10	-0.565	-0.575	-0.556
Intercept	0.50	0.103	0.100	0.105
Foraging Observed	0.50	-0.060	-0.061	-0.059
Intercept	0.90	0.791	0.780	0.800
Foraging Observed	0.90	0.104	0.104	0.106
Intercept	0.95	1.133	1.121	1.146
Foraging Observed	0.95	0.154	0.150	0.156
Intercept	0.99	1.994	1.961	2.036
Foraging Observed	0.99	0.396	0.380	0.413
LoD95 weighting				
Intercept	0.01	-0.505	-0.514	-0.495
Foraging Observed	0.01	-1.594	-1.621	-1.566
Intercept	0.05	-0.113	-0.115	-0.112
Foraging Observed	0.05	-0.311	-0.315	-0.307
Intercept	0.10	-0.051	-0.052	-0.051
Foraging Observed	0.10	-0.105	-0.106	-0.104
Intercept	0.50	0.003	0.003	0.003
Foraging Observed	0.50	-0.002	-0.002	-0.002
Intercept	0.90	0.114	0.113	0.115
Foraging Observed	0.90	0.009	0.009	0.009
Intercept	0.95	0.191	0.189	0.192
Foraging Observed	0.95	0.034	0.034	0.034
Intercept	0.99	0.434	0.430	0.438
Foraging Observed	0.99	0.135	0.135	0.137
LoDmin threshold				
Intercept	0.01	-0.208	-0.232	-0.181
Foraging Observed	0.01	-1.860	-1.937	-1.791
Intercept	0.05	-0.048	-0.058	-0.046
Foraging Observed	0.05	-0.048	-0.040	-0.048
Intercept	0.10	-0.045	-0.053	-0.040
Foraging Observed	0.10	-0.060	-0.056	-0.054
Intercept	0.50	-0.024	-0.028	-0.021
Foraging Observed	0.50	-0.032	-0.030	-0.029
Intercept	0.90	-0.004	-0.004	-0.003
Foraging Observed	0.90	-0.005	-0.004	-0.004
Intercept	0.95	-0.001	-0.001	-0.001
Foraging Observed	0.95	-0.001	-0.001	-0.001
Intercept	0.99	0.199	0.187	0.209
Foraging Observed	0.99	0.152	0.141	0.164

SI 6: Check and control marker root mean square error (RMSE) summaries. Non-dimensional RMSE was calculated by dividing mean flight altitude by control/check marker accuracy.

	Mean flight altitude	*Control RMSE (m)*	*non-dimensional Control RMSE*	*Check RMSE (m)*	*non-dimensional Check RMSE*
September 2017	68.5	0.030	1: 2280	0.052	1: 1370
September 2018	64	0.034	1:1880	0.052	1: 1230

SI 7: Flight Paths of Drone surveys. In total 4 flights were undertaken to cover the north and south of the site with nadir imagery captured from a height of 55 m above ground level (AGL) and convergent imagery captured from a height of 60 m AGL.

Appendix 8. Supplementary Information: Chapter 4

SI 1 - Description of Beaver Foraging Index (BFI) values

BVI Value	Definition
0	No Vegetation
1	Unsuitable
2	Barely Suitable
3	Moderately Suitable
4	Suitable

SI 2 - OS Vector Layer Descriptions and assigned BFI value.

Land Use or Vegetation Type	BFI Value
Boulders	0
Boulders and Sand	0
Boulders and Shingle	0
Broad-leafed woodland	5
Broad-leafed woodland and Shrub	5
Building polygon	0
Coniferous woodland	3
Coniferous woodland and Shrub	5
Custom landform polygon	0
Glasshouse polygon	0
Grass And Shingle	1
Gravel Pit	0
Heathland	1
Heathland and Boulders	1
Heathland and Marsh	1
Heathland and Unimproved Grass	1
Heathland And Unimproved Grass And Boulders	1
Inland Rock	0
Inland water polygon	0
Marsh	1
Marsh and Unimproved Grass	1
Mixed woodland	5
Mixed woodland and Shrub	5
Mud	0
Orchard	5
Reeds	2
Refuse or Slag Heap	0
Sand	0
Sand Pit	0
Sea polygon	0
Shingle	0

Shingle and Mud	0
Shingle and Sand	0
Shrub	5
Shrub and Boulders	2
Shrub and Heathland	2
Shrub and Heathland and Boulders	2
Shrub and Heathland and Unimproved Grass	2
Shrub and Marsh	3
Shrub and Marsh and Heath	3
Shrub and Marsh and Unimproved Grass	3
Shrub and Unimproved Grass	3
Shrub And Unimproved Grass And Boulders	3
Unimproved Grass	1
Unimproved Grass and Boulders	1
Unimproved Grass and Sand	1
Unimproved Grass and Shingle	1

SI 3 - Centre for Ecology and Hydrology (CEH) 2015 land cover map feature descriptions and assigned BFI value

Land Cover Type	BVI Score
Acid grassland	1
Arable and horticulture	2
Broadleaf woodland	5
Bog	1
Calcareous grassland	1
Coniferous woodland	3
Fen, marsh and swamp	1
Freshwater	0
Heather	1
Heather grassland	1
Improved grassland	1
Inland rock	0
Littoral rock	0
Littoral sediment	0
Neutral grassland	2
Saltmarsh	0
Saltwater	0
Suburban	0
Supralittoral rock	0
Supralittoral sediment	0
Urban	0

SI4 - Copernicus Tree Cover Density range and assigned BFI value

Tree Cover Density Range (%)	BFI score
0	0
1-3	1
4-10	2
11-50	3
51-100	4

SI 5- Rules list for the vegetation Fuzzy inference system

Rule	Foraging Area Cat.		Riparian Area Cat.		Dam capacity Category
1	unsuitable	&	unsuitable	then	none
2	barely	&	unsuitable	then	none
3	moderately	&	unsuitable	then	rare
4	suitable	&	unsuitable	then	occasional
5	preferred	&	unsuitable	then	frequent
6	unsuitable	&	barely	then	rare
7	barely	&	barely	then	rare
8	moderately	&	barely	then	occasional
9	suitable	&	barely	then	frequent
10	preferred	&	barely	then	frequent
11	unsuitable	&	moderately	then	occasional
12	barely	&	moderately	then	occasional
13	moderately	&	moderately	then	occasional
14	suitable	&	moderately	then	frequent
15	preferred	&	moderately	then	frequent
16	unsuitable	&	suitable	then	occasional
17	barely	&	suitable	then	frequent
18	moderately	&	suitable	then	frequent
19	suitable	&	suitable	then	frequent
20	preferred	&	suitable	then	pervasive
21	unsuitable	&	preferred	then	frequent
22	barely	&	preferred	then	frequent
23	moderately	&	preferred	then	frequent
24	suitable	&	preferred	then	pervasive
25	preferred	&	preferred	then	pervasive

SI6 - Combined Fuzzy Inference System (FIS) Rules List

Rule	Veg FIS Category		Stream Power Q2		Stream Power Q80		Slope		BDC Category
1	none	&	…	&	…	&	…	then	none
2	…	&	…	&	cannot	&	…	then	none
3	…	&	…	&	…	&	cannot	then	none
4	rare	&	persists	&	can	&	…	then	rare
5	occasional	&	persists	&	can	&	…	then	occasional
6	frequent	&	persists	&	can	&	can	then	frequent
7	frequent	&	persists	&	can	&	probably	then	occasional
8	pervasive	&	persists	&	can	&	flat	then	pervasive
9	pervasive	&	persists	&	can	&	can	then	pervasive
10	pervasive	&	persists	&	can	&	probably	then	occasional
11	rare	&	breach	&	can	&	…	then	rare
12	occasional	&	breach	&	can	&	…	then	occasional
13	frequent	&	breach	&	can	&	can	then	frequent
14	frequent	&	breach	&	can	&	probably	then	occasional
15	pervasive	&	breach	&	can	&	flat	then	occasional
16	pervasive	&	breach	&	can	&	can	then	frequent
17	pervasive	&	breach	&	can	&	probably	then	occasional
18	rare	&	occasional blowout	&	can	&	…	then	rare
19	occasional	&	occasional blowout	&	can	&	…	then	occasional
20	frequent	&	occasional blowout	&	can	&	can	then	frequent
21	frequent	&	occasional blowout	&	can	&	probably	then	occasional
22	pervasive	&	occasional blowout	&	can	&	flat	then	occasional
23	pervasive	&	occasional blowout	&	can	&	can	then	frequent
24	pervasive	&	occasional blowout	&	can	&	probably	then	occasional
25	rare	&	blowout	&	can	&	…	then	none
26	occasional	&	blowout	&	can	&	…	then	rare
27	frequent	&	blowout	&	can	&	can	then	rare
28	frequent	&	blowout	&	can	&	probably	then	none
29	pervasive	&	blowout	&	can	&	flat	then	rare
30	pervasive	&	blowout	&	can	&	can	then	occasional
31	pervasive	&	blowout	&	can	&	probably	then	rare
32	rare	&	breach	&	probably	&	…	then	rare
33	occasional	&	breach	&	probably	&	…	then	occasional
34	frequent	&	breach	&	probably	&	can	then	frequent
35	frequent	&	breach	&	probably	&	probably	then	occasional
36	pervasive	&	breach	&	probably	&	flat	then	occasional
37	pervasive	&	breach	&	probably	&	can	then	frequent
38	pervasive	&	breach	&	probably	&	probably	then	occasional

39	rare	&	occasional blowout	&	probably	&	...	then	rare
40	occasional	&	occasional blowout	&	probably	&	...	then	occasional
41	frequent	&	occasional blowout	&	probably	&	can	then	occasional
42	frequent	&	occasional blowout	&	probably	&	probably	then	rare
43	pervasive	&	occasional blowout	&	probably	&	flat	then	occasional
44	pervasive	&	occasional blowout	&	probably	&	can	then	frequent
45	pervasive	&	occasional blowout	&	probably	&	probably	then	occasional
46	rare	&	blowout	&	probably	&	...	then	none
47	occasional	&	blowout	&	probably	&	...	then	rare
48	frequent	&	blowout	&	probably	&	can	then	rare
49	frequent	&	blowout	&	probably	&	probably	then	none
50	pervasive	&	blowout	&	probably	&	flat	then	rare
51	pervasive	&	blowout	&	probably	&	can	then	occasional
52	pervasive	&	blowout	&	probably	&	probably	then	rare
53	rare	&	persists	&	probably	&	...	then	rare
54	occasional	&	persists	&	probably	&	...	then	rare
55	frequent	&	persists	&	probably	&	flat	then	occasional
56	frequent	&	persists	&	probably	&	can	then	frequent
57	frequent	&	persists	&	probably	&	probably	then	occasional
58	frequent	&	breach	&	can	&	flat	then	frequent
59	frequent	&	breach	&	probably	&	flat	then	occasional
60	frequent	&	occasional blowout	&	can	&	flat	then	occasional
61	frequent	&	occasional blowout	&	probably	&	flat	then	occasional
62	frequent	&	blowout	&	can	&	flat	then	rare
63	frequent	&	blowout	&	probably	&	flat	then	rare
64	pervasive	&	persists	&	probably	&	...	then	frequent

SI7 - Beaver Foraging Index (BFI) pseudo code describing the inference system used to derive the final GB BFI Raster file

1) TCD conversion – convert Tree cover Density (TCD) from continuous description of cover (TCDi) to a value between Null-4 (TCDo).

If TCDi = 0% then TCDo = Null

If TCDi > 0% and < 3% then TCDo = 1

If TCDi >= 3% and < 10% then TCDo = 2

If TCDi >= 10% and < 50% then TCDo = 3

If TCDi >= 50% then TCDo = 4

2) To produce the next intermediate data (referred to here as VA), TCDo is combined with the other classified datasets (OS Vector, CEH Land Cover Map (LCM), CEH Woody Linar Features Framework (WLF)). Layers are simply merged based on the reliability of the data. Where no data is present, the next most reliable data is used to fill this step. As the LCM is continuous and the coarsest in detail, it is final layer to be selected if the other datasets are of NULL value in a given location. This inference step takes place as follows:

If OS is not NULL then VA = OS

If OS is NULL then VA = LWF

If WLF is NULL then VA = TCD

If TCD is NULL then VA = LCM

3) However, depending on the landuse types, other data may be more reliable at predicting the presence of woody material or buildings. As false positives are rare in all datasets it was decided to, as a secondary process, prioritise those data that are of higher value. The following sequence of commands was used to achieve this where VB:VD are intermediate datasets:

If VA < WLF then VB = LWF else VB = VA

If VB < TCD and ConLCM = Null then VC = TCD else VC = VB

If VC < LCM then VD = LCM else VD = VC

If OS < 1 then BVI = OS else BVI = VD

SI8 – Beaver Dam Capacity Python Code

https://github.com/exeter-creww/Graham-et-al-2020-Supporting-Information/tree/master/SI8_BDC_BFI_Python_code

SI9 – Beaver Dam Capacity Model Validation and statistical analysis R code:

https://github.com/exeter-creww/Graham-et-al-2020-Supporting-Information/tree/master/SI9_Model_Validation_R_Code

SI10-Zero Inflated Negative Binomial (ZINB) Regression Summary Table

n_dams refers to the number of observed dams

n_dams_mod refers to the modelled dam capacity

Call:

zeroinfl(formula = n_dams ~ n_dams_mod, data = Act_reaches, dist = "negbin")

Pearson residuals:

Min	1Q	Median	3Q	Max
-0.32620	-0.21442	-0.01955	-0.01955	19.54168

Count model coefficients (negbin with log link):

predictor	Estimate Std.	Error z	value	Pr(>z)
(Intercept)	-2.4588	0.2560	-9.605	< 2e-16 ***
n_dams_mod	0.2655	0.1072	2.477	0.0132 *
Log(theta)	-1.9394	0.2701	-7.180	6.98e-13 ***

Zero-inflation model coefficients (binomial with logit link):

predictor	Estimate	Std. Error	z value	Pr(>z)
(Intercept)	4.884	1.202	4.065	4.8e-05 ***
n_dams_mod	-54.411	19.741	-2.756	0.00585 **

Signif. codes: 0 '*' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1**
Theta = 0.1438 Number of iterations in BFGS optimization: 45 Log-likelihood: -258 on 5 Df

SI11-Examples of beaver dams and examples of model performance.

A - Example of a valley-wide beaver dam from the Otter Catchment, B - Example of mature and stable dam from the Mid Devon Beaver Trial (Puttock, et al., 2017), C - Bankfull dam in a 4th order tributary of the River Otter, D - Small dam (~40cm) made of soft vegetation and sediment in an agricultural ditch within the Otter catchment.

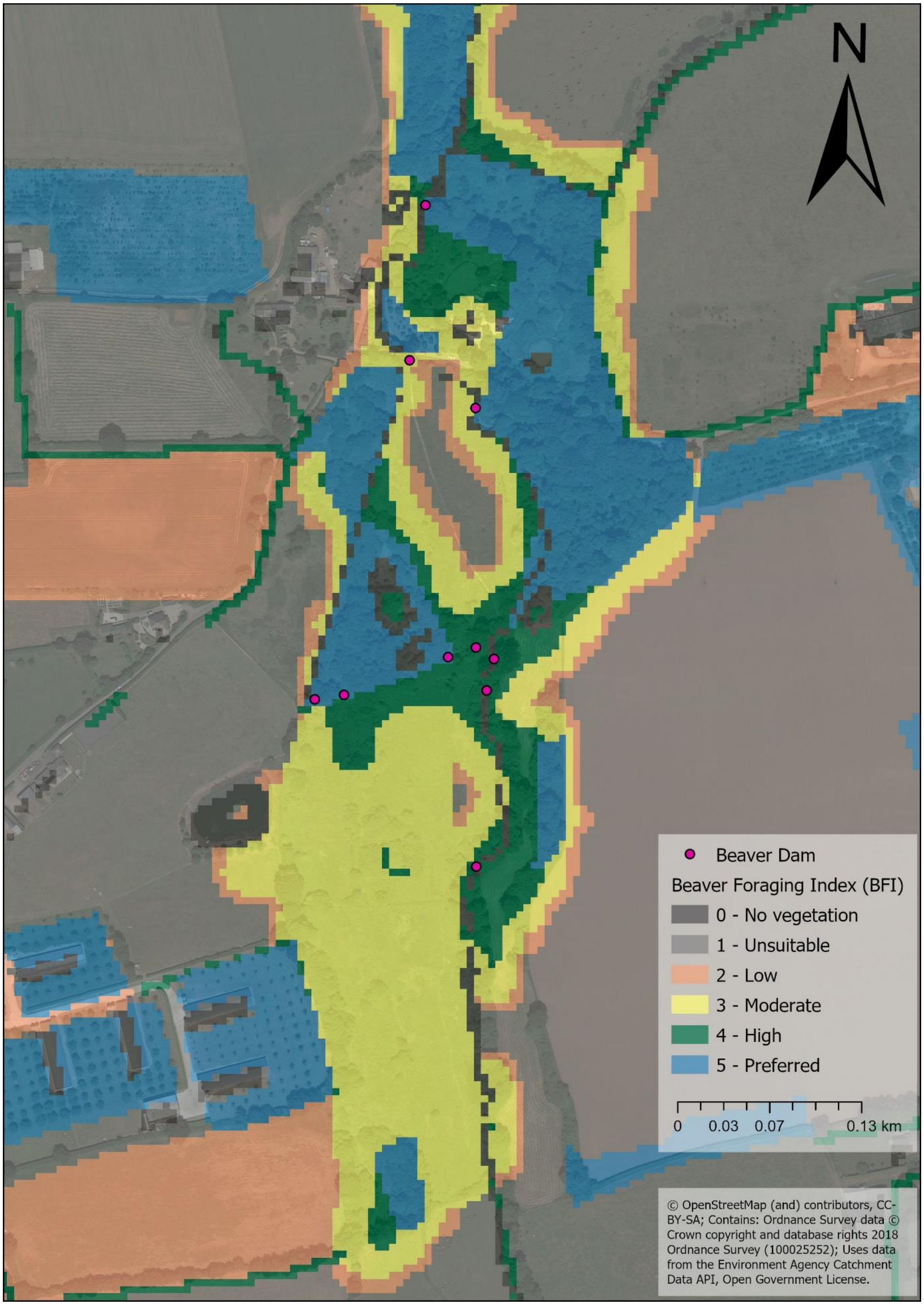
SI.11 continued… A selection of maps to provide examples of BDC and BFI results at local scale

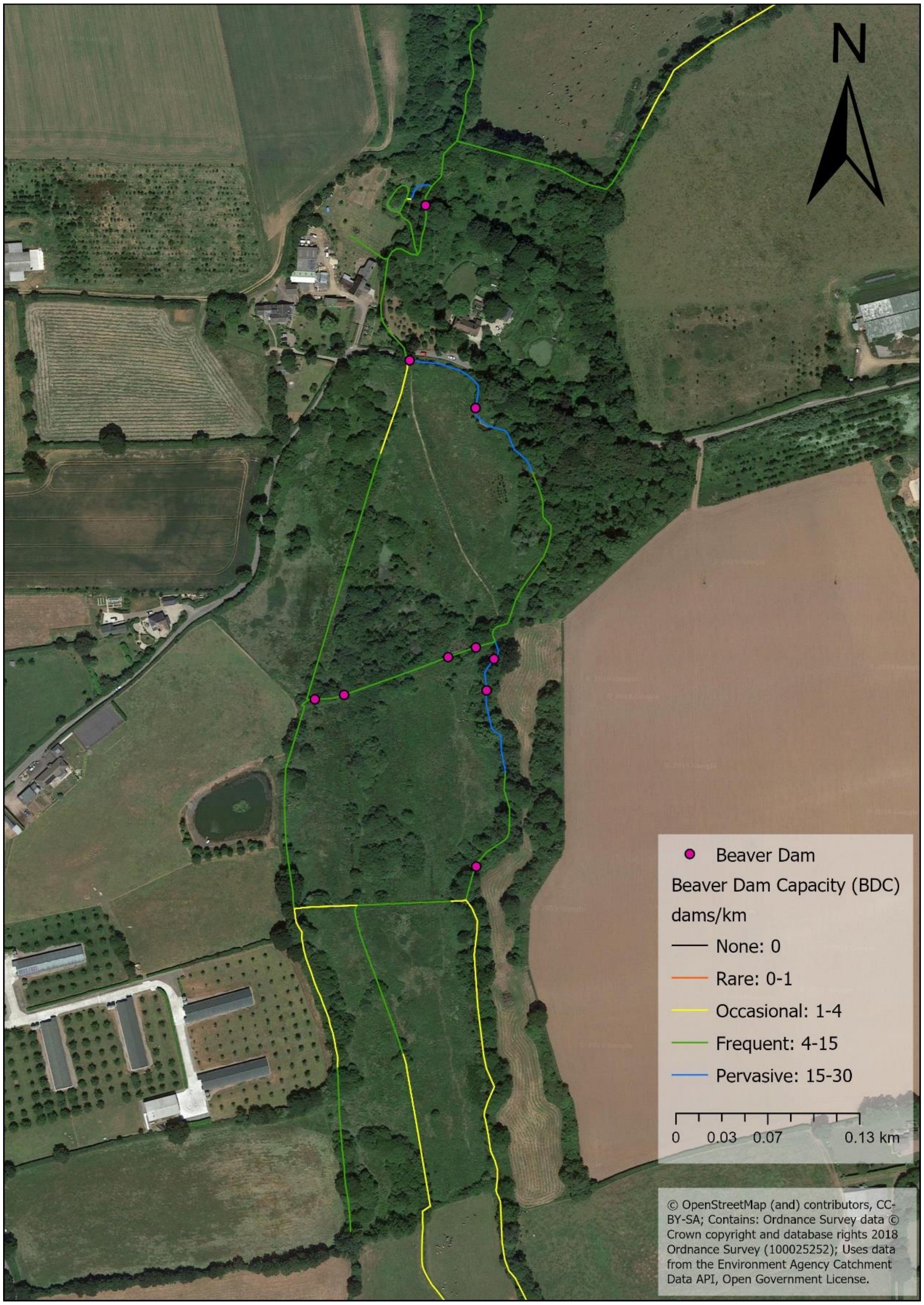
locations of these sites are not provided to maintain land-owner privacy

River Otter Catchment Examples

Low intensity Agricultural Landscape.

This is the site of a beaver release in 2016. The animals have since remained in this reach and have also reproduced. The site composes a semi-natural grassland site with riparian woodland and encroaching willow shrub. The surrounding land is largely dominated by mixed grazing and arable farmland. The maximum number of dams constructed at this site, at any one time, is 10 by approximately 4 animals. These dams frequently incur damage during high flows being either partially or fully "blown-out". Often, following their destruction, the dams are then reconstructed during periods of low flow.

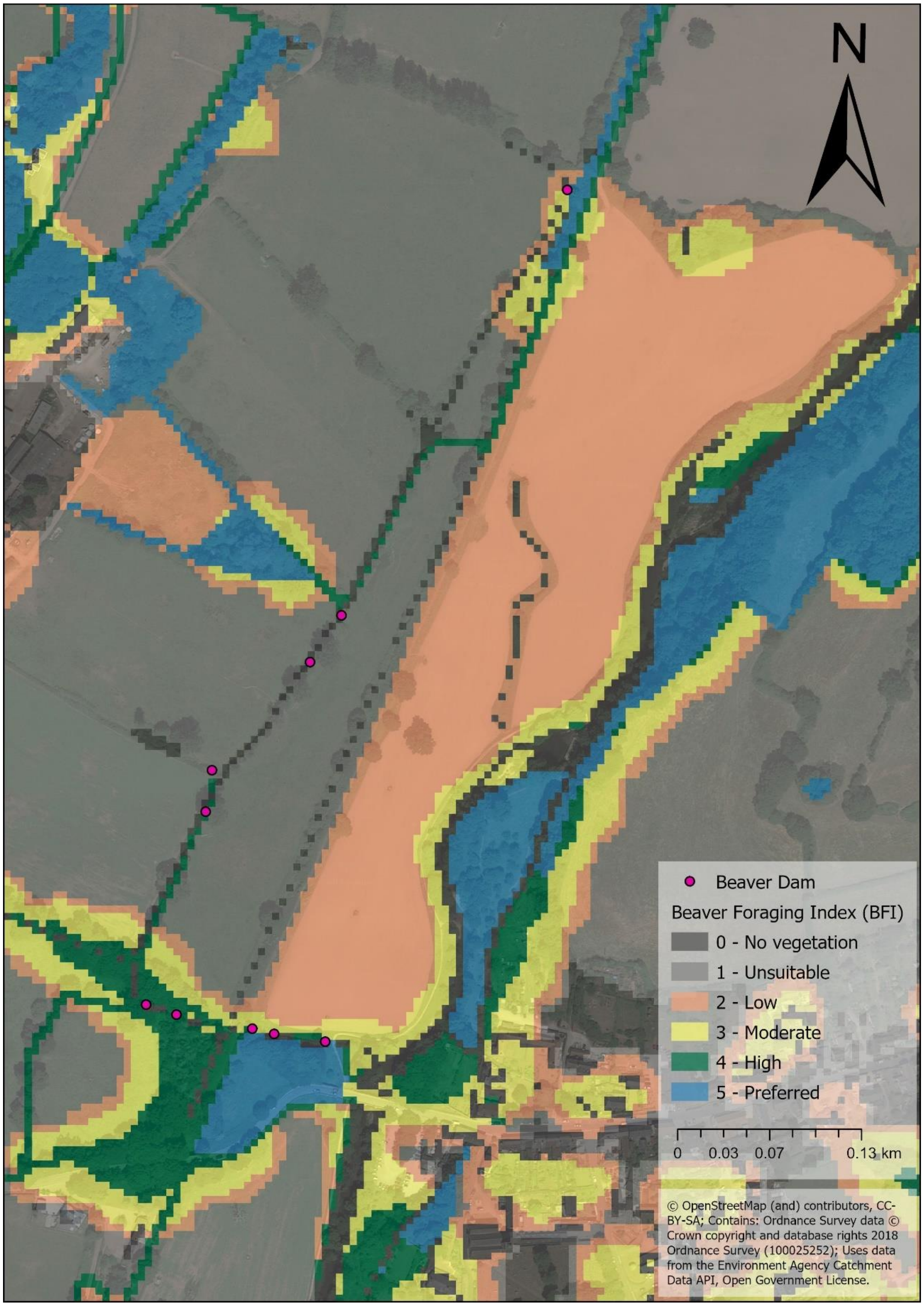

N
Beaver Dam
Beaver Foraging Index (BFI)
0 - No vegetation
1 - Unsuitable
2 - Low
3 - Moderate
4 - High
5 - Preferred
0 0.03 0.07 0.13 km
© OpenStreetMap (and) contributors, CC-BY-SA; Contains: Ordnance Survey data © Crown copyright and database rights 2018 Ordnance Survey (100025252); Uses data from the Environment Agency Catchment Data API, Open Government License.



All dams within this area have been constructed along reaches classified as pervasive or frequent. This example illustrates that the model effectively discriminates between those more densely wooded areas to the north of the site which offer more building and foraging materials than the southern part of the site where vegetation is confined to a narrower riparian strip. The Beaver at This site have clearly expressed a preference to dam construction around their dwelling, located in the more heavily wooded north of the site.

Intensively-managed grassland landscape

Beaver were first identified at this site in 2016. Initially, the dwelling and related damming activity was located in a small isolated wet woodland in the centre of the site. Beaver have since established a dwelling in the mixed woodland to the south of the site

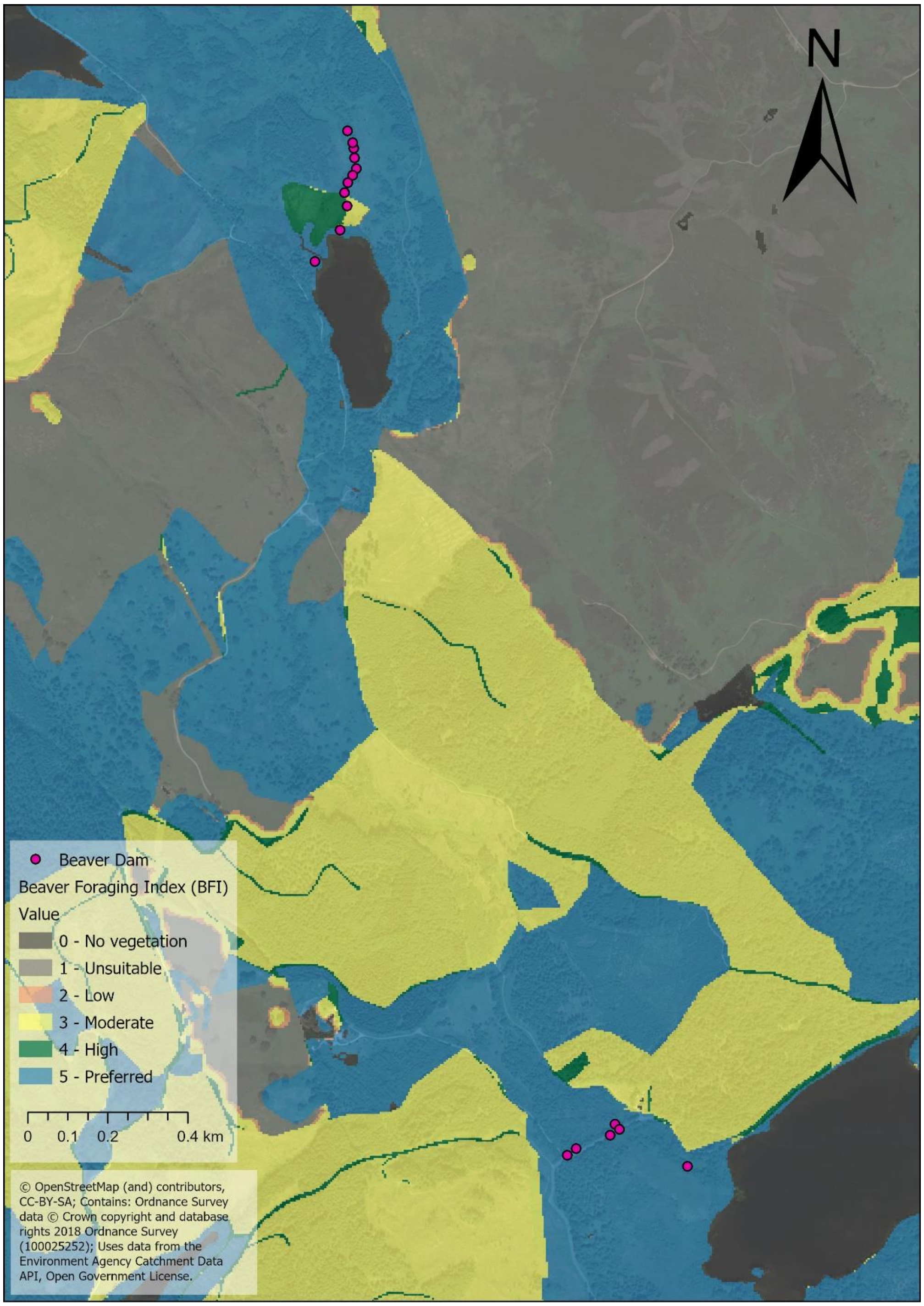


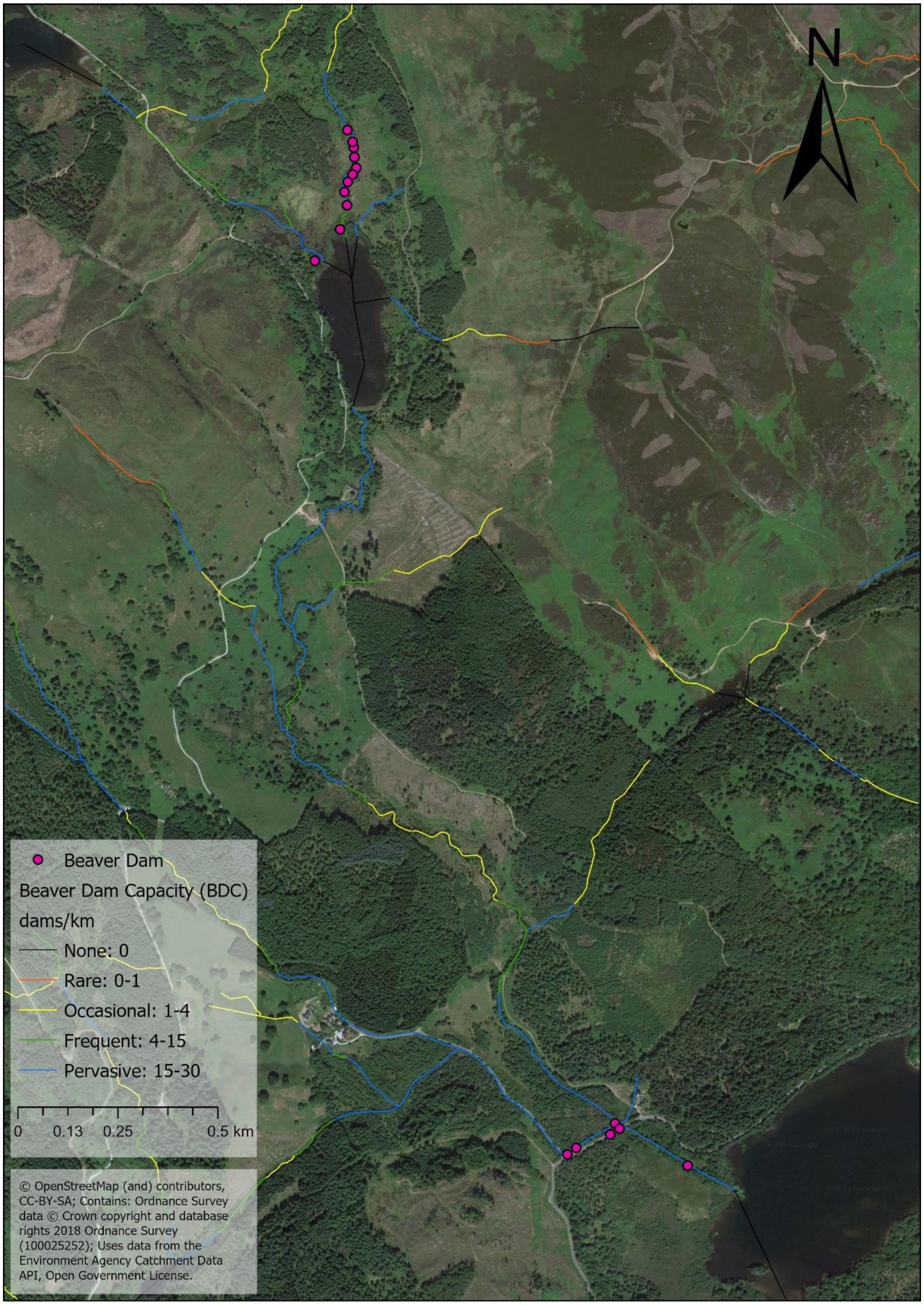
As shown by the BFI map, this is an example where some discontinuous woodland is not captured. This could explain why three dams occur in reaches classified as rare. However, all three of these dams have since been abandoned in favour of the more densely wooded area to the south of the site. where six dams have been built.

River Tay Catchment Examples

Tay Catchment Semi-Natural/Low Intensity grazing landscape

BFI and BDC maps of two beaver dam complexes in a semi-natural setting within the Tay catchment. There are two dam complexes in this area, both of which are located on the inflow to lakes.





Both dam complexes are positioned on reaches classified as pervasive. In this example, there are clear distinctions between reaches with plentiful surrounding woody vegetation and those where grassland prevails. Additionally, lakes are correctly classified as having no capacity for dams.

Tay Catchment Arable farming setting.

BFI and BDC maps of a sequence of beaver dams in an agricultural (arable) landscape within the Tay Catchment

The five dams within this sequence are located within reaches classified as rare (n=1), occasional (n=2) and frequent (n=2). The model effectively locates reaches with minimal streamside vegetation that is capable of supporting beaver dams and can differentiate between these reaches and those less favourable. It is also notable that other patches of woodland within this scene are also competently characterised by the model.

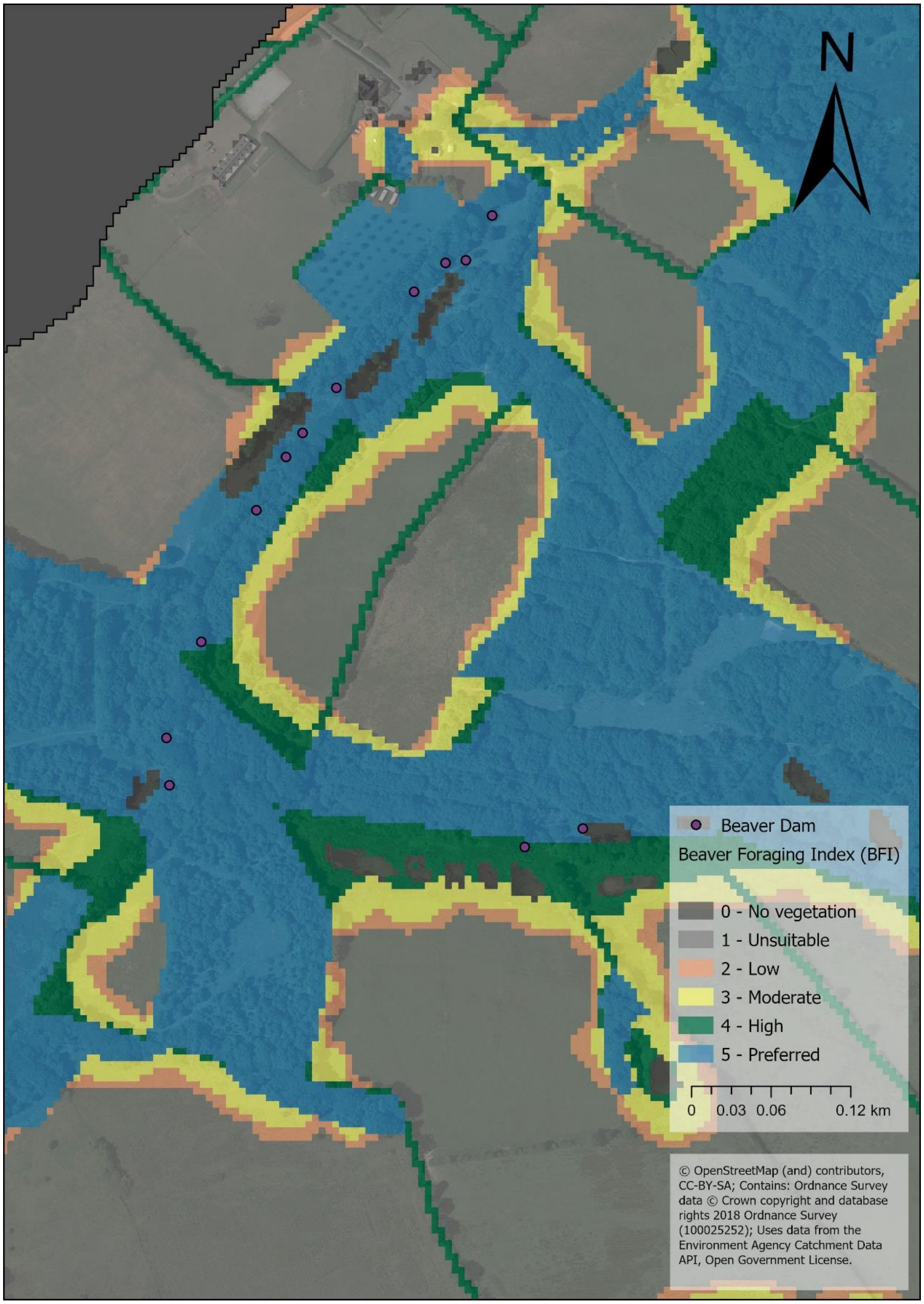
Tay Catchment Semi-Urban Landscape.

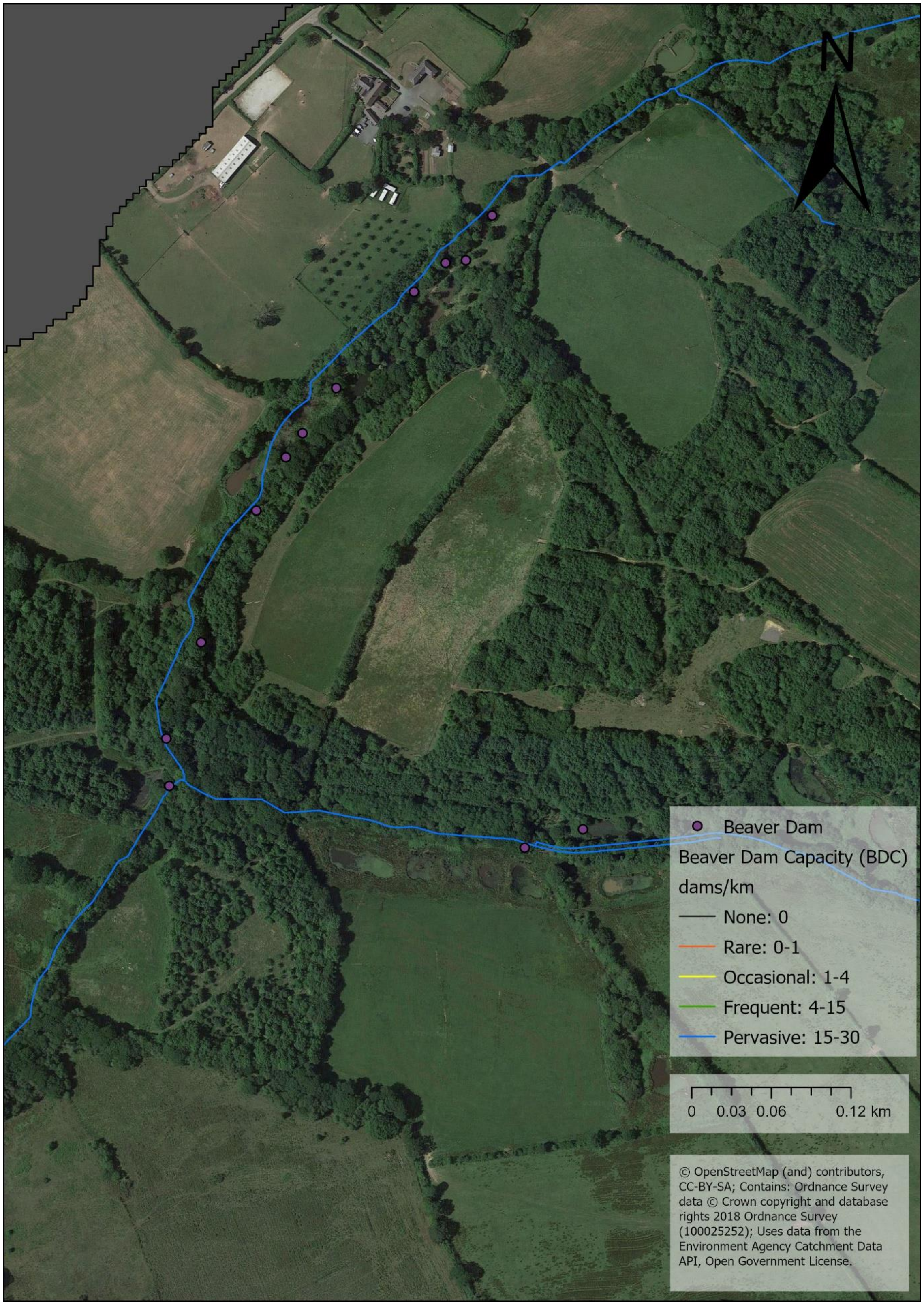
Map of Beaver Dam capacity model in a semi-urban setting within the Tay Catchment. A sequence of three beaver dams that have been constructed in a small area of woodland within a settlement.

All three dams are located in reaches classed as frequent. This is good example of how beavers can often make use of localised areas of key habitat within a wider landscape of less suitable habitat.

Coombeshead Sub-catchment

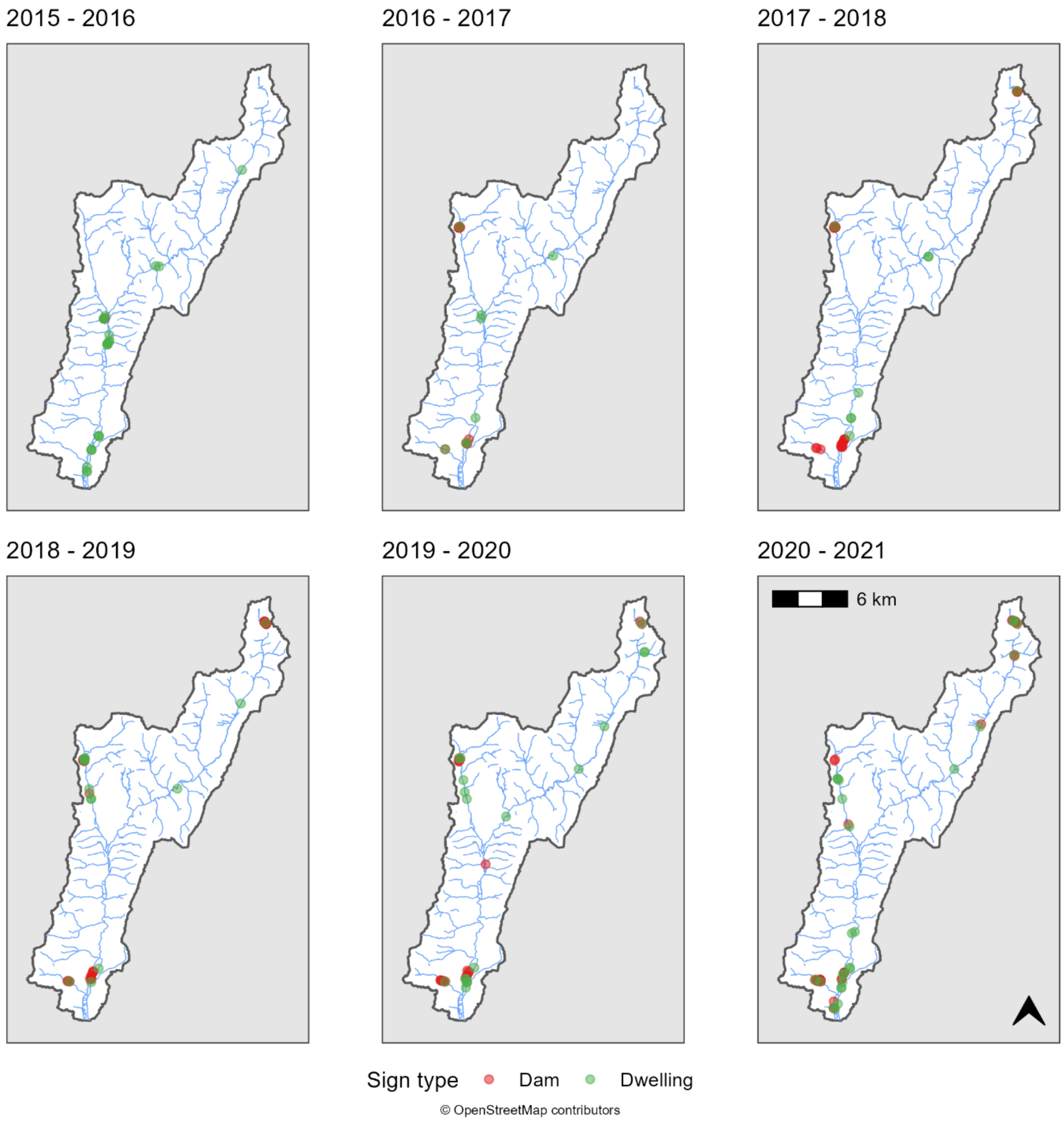
The following BFI and BDC maps show the full extent of the damming activity in the Coombeshead sub-catchment. A total of 13 dams were constructed at the time of surveying.



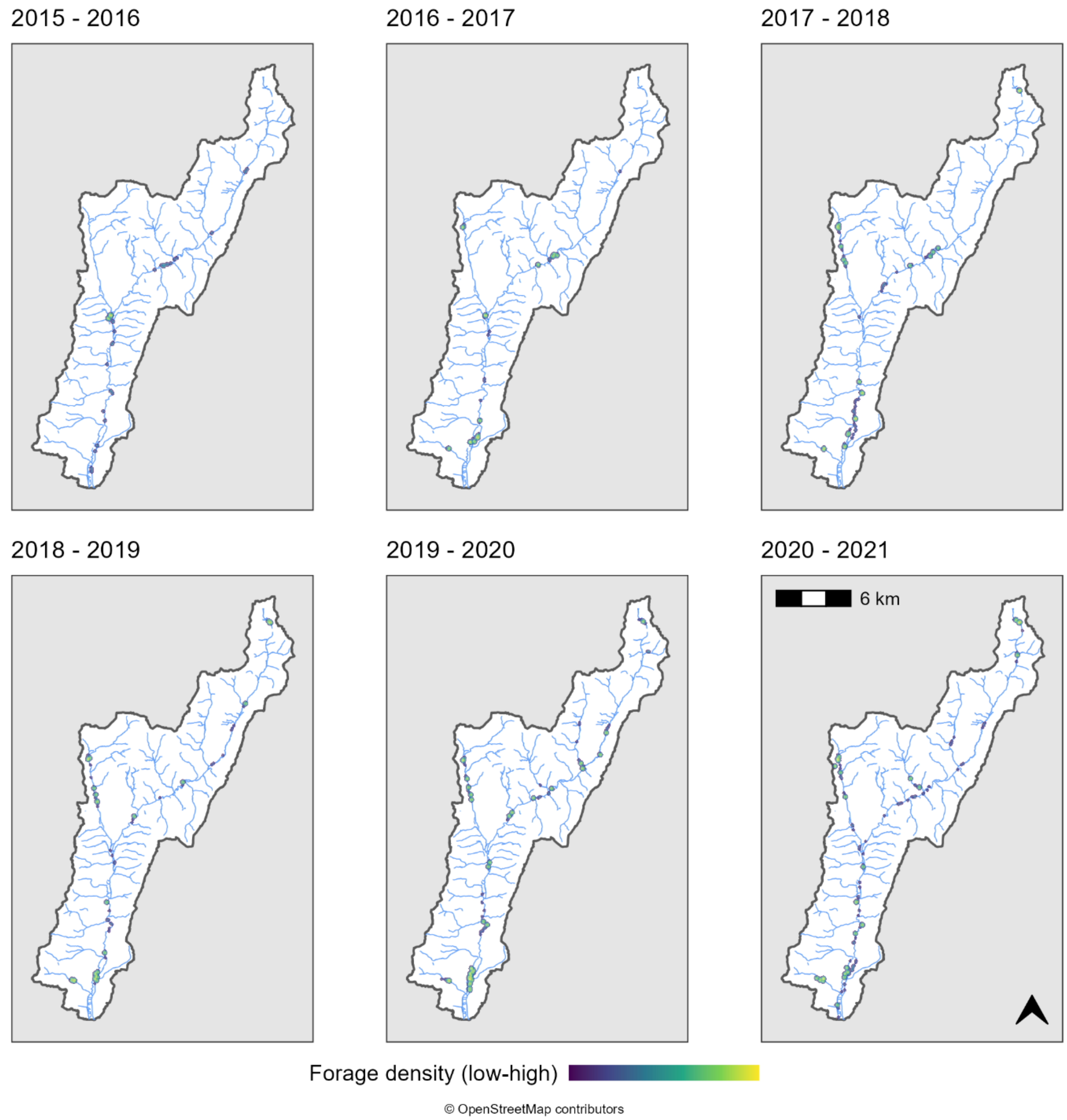


All reaches within the inhabited area were classified as pervasive. The BFI here highlights the efficacy of identifying areas of substantive woodland and in addition narrow hedgerows which also provide important forage resources for beaver in some landscapes.

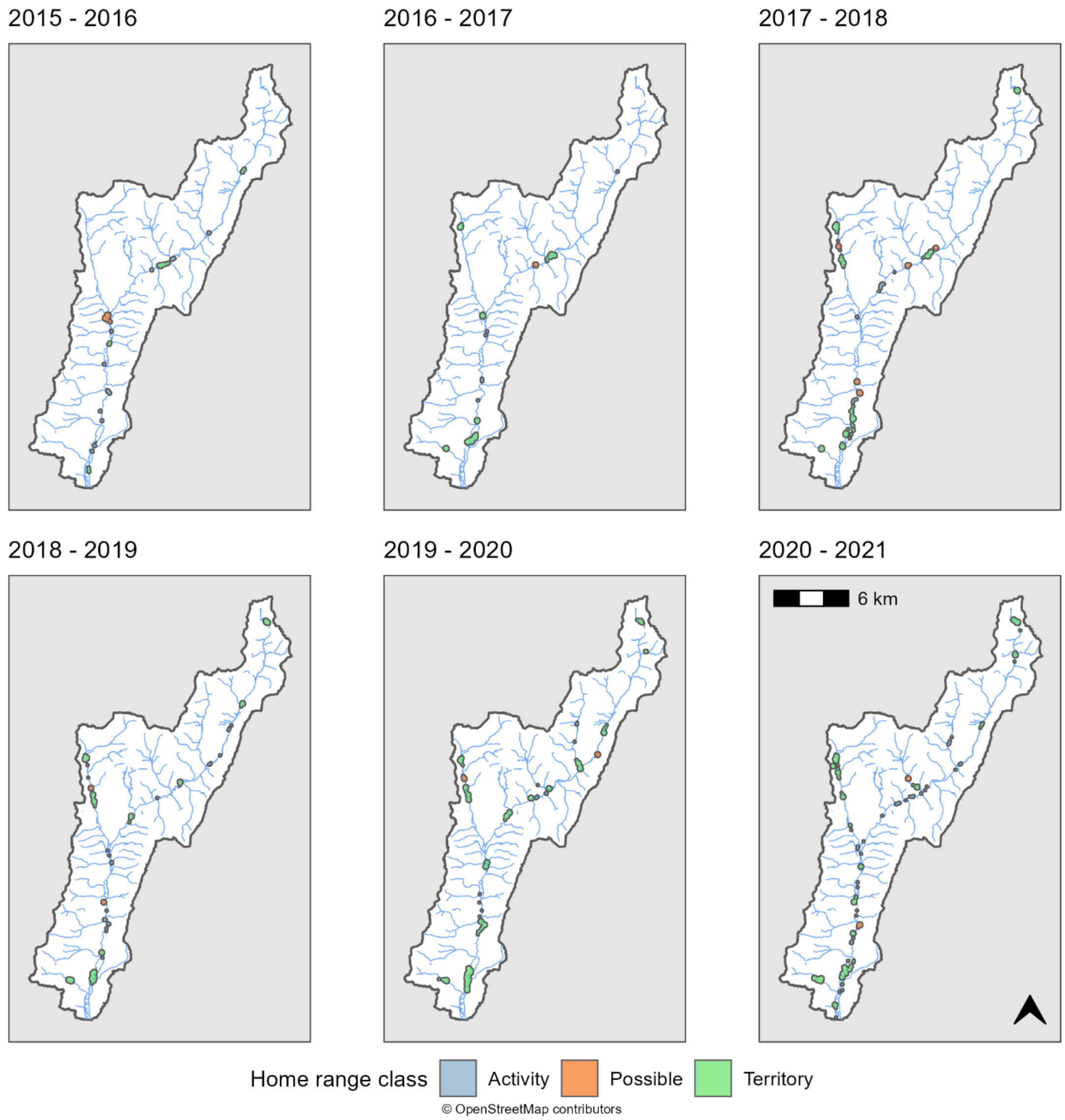
Appendix 9. Supplementary Information: Chapter 5



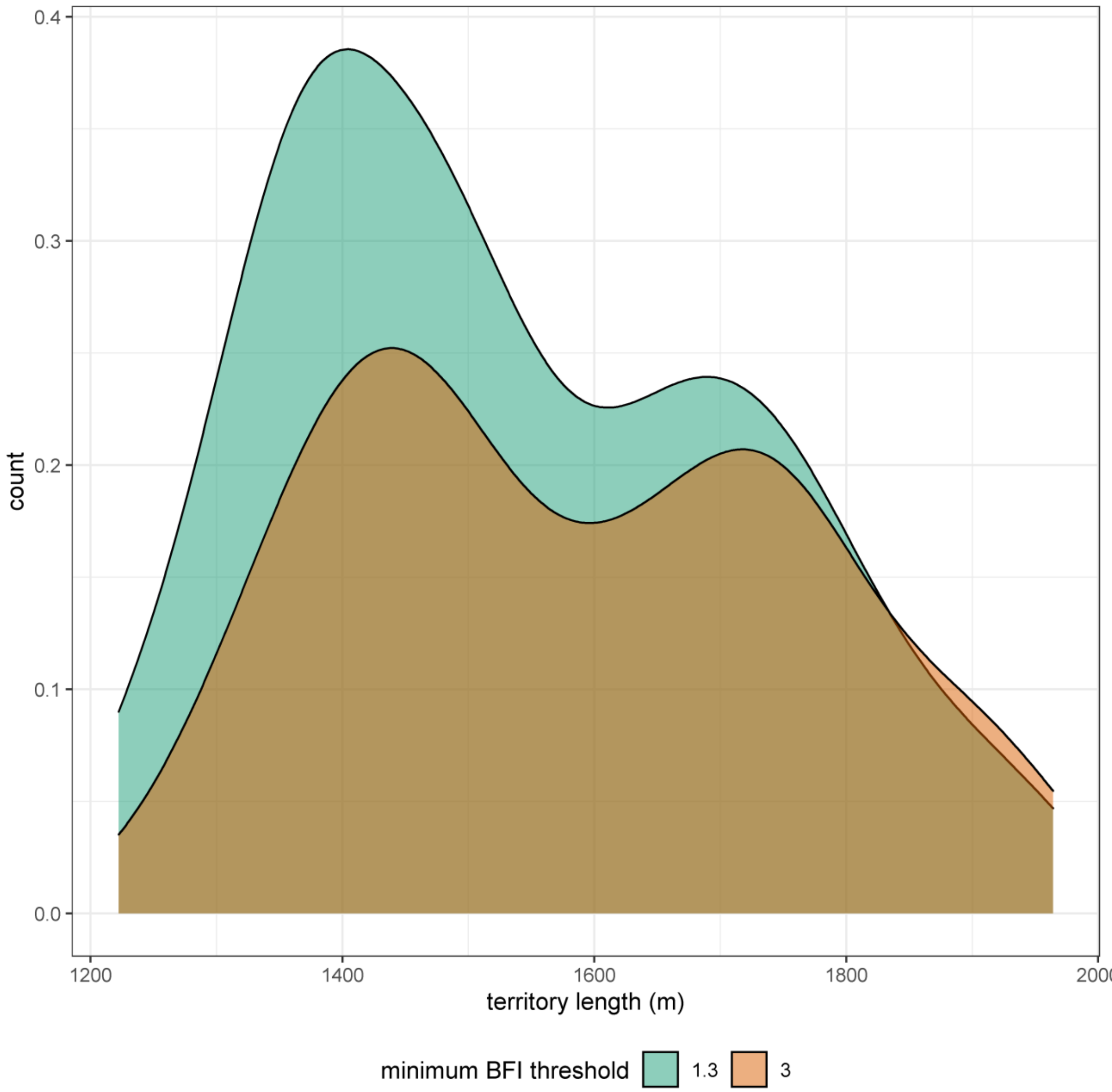
SI 1: Beaver dwelling and dam locations.



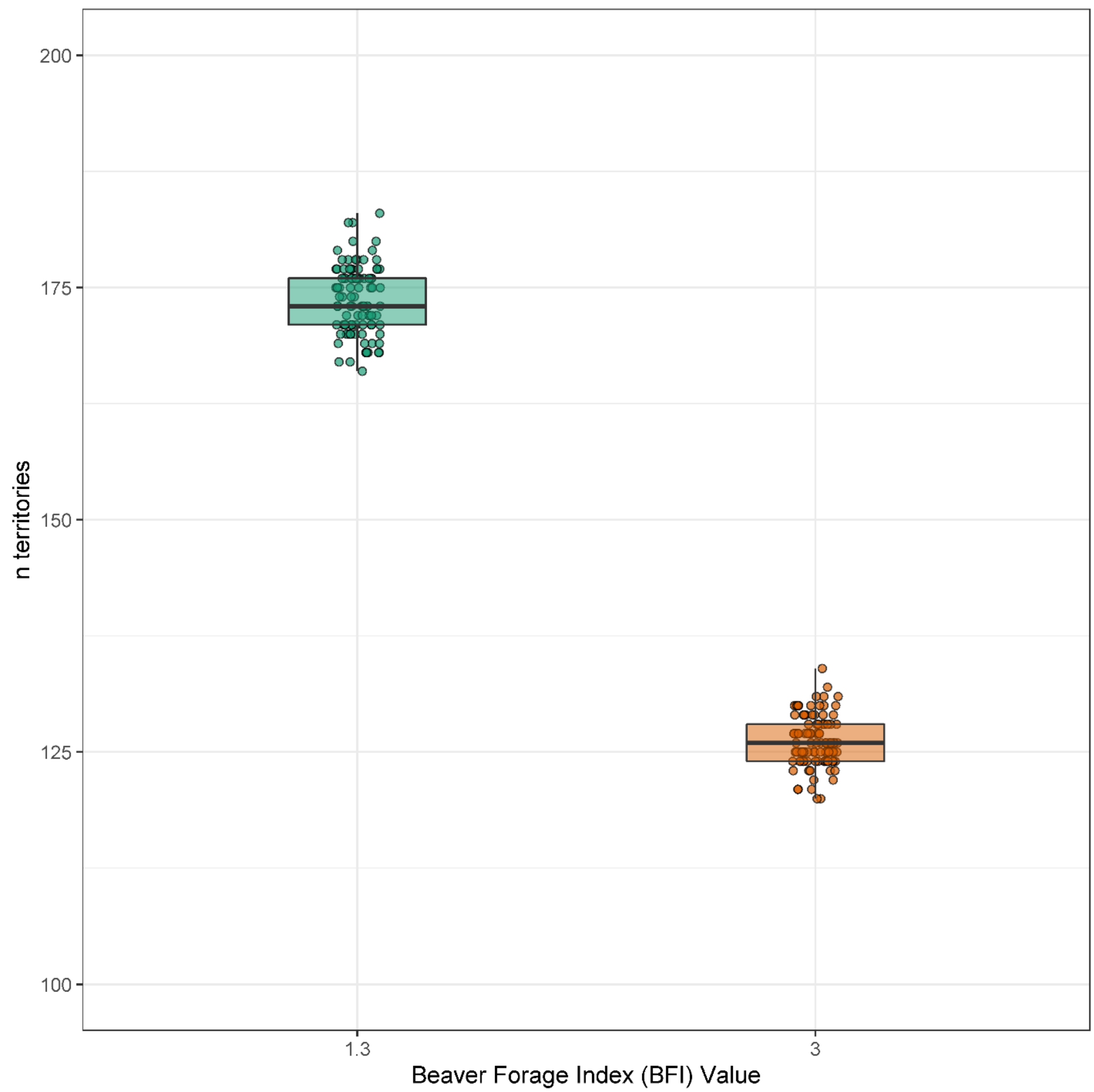
SI 2: Foraging density with bandwidth of 200m and low threshold of $1e^{-10}$.



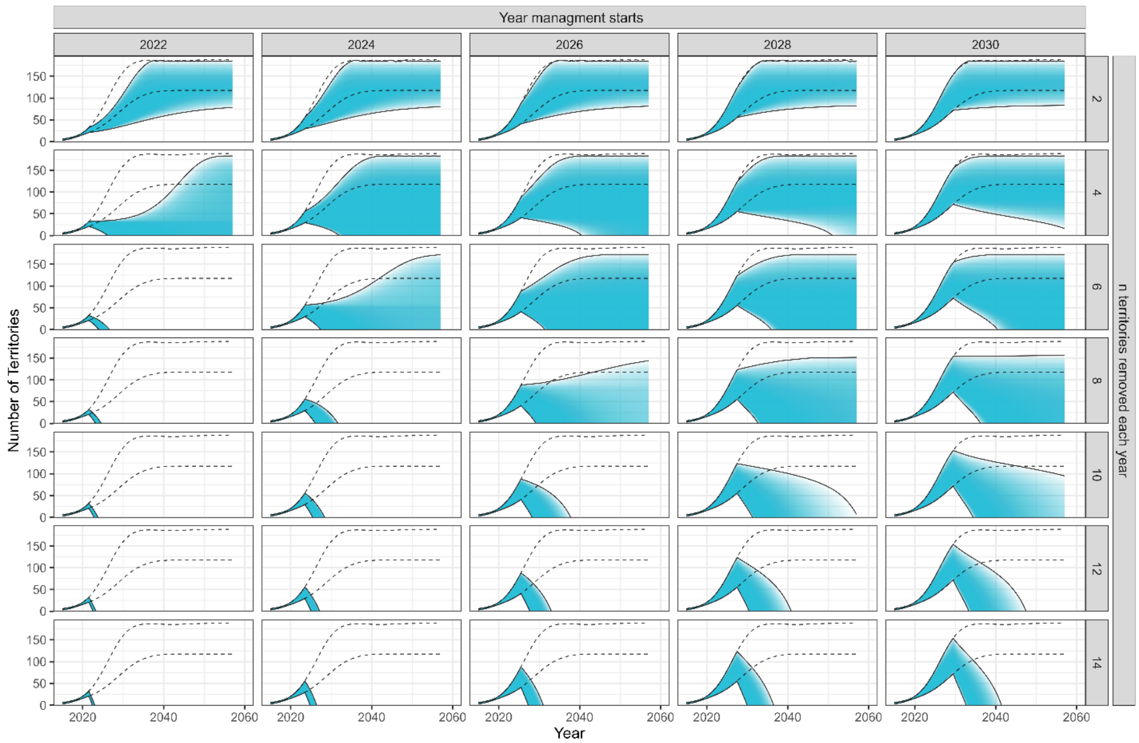
SI 3: Semi-automated home range locations and classes presented without the additional 100m buffer for visualisation.



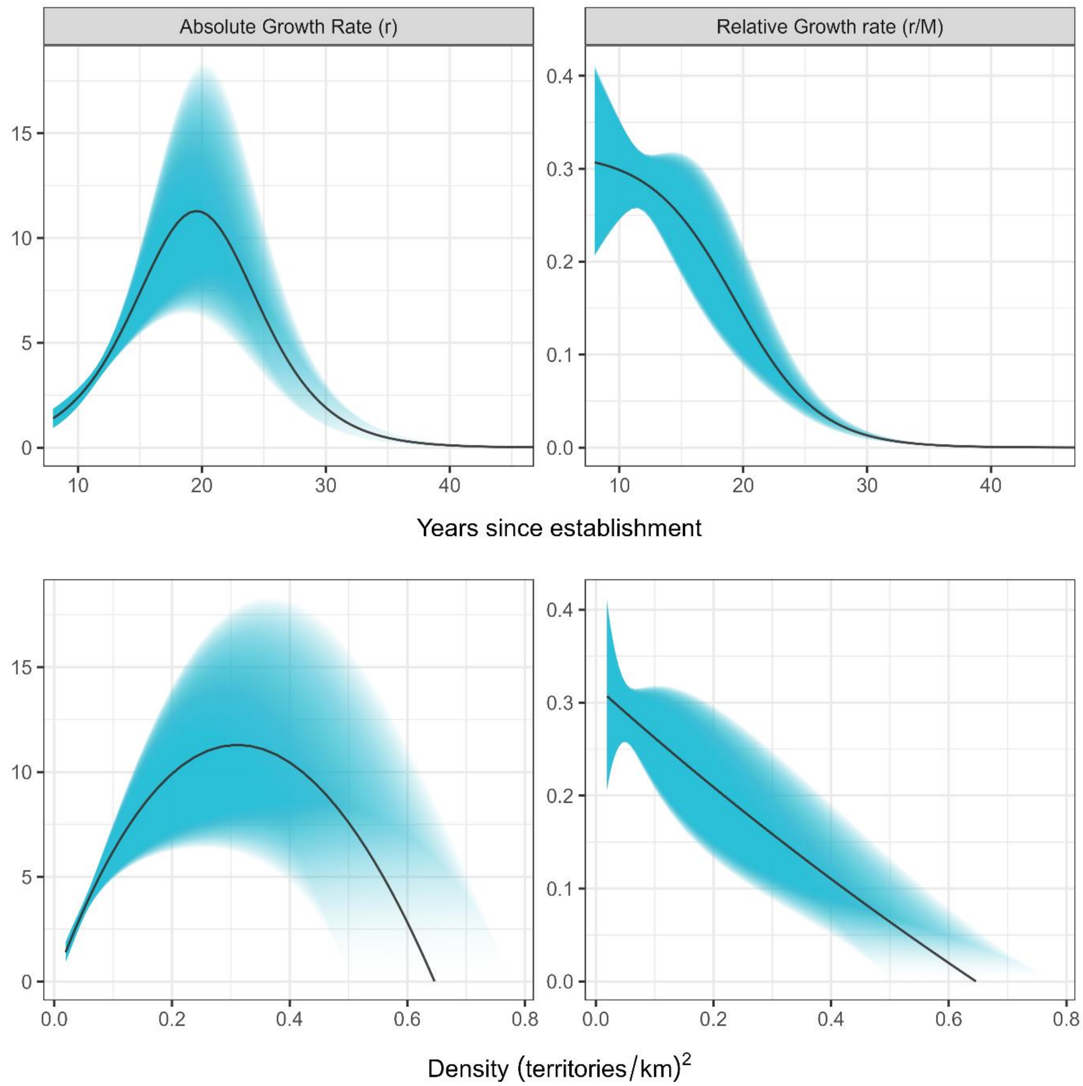
SI 4: The density distribution of territory lengths produced from a simulation of beaver territory capacity. The scenario was tested for both the minimum (1.3) and mean (3.0) BFI values of observed territories.



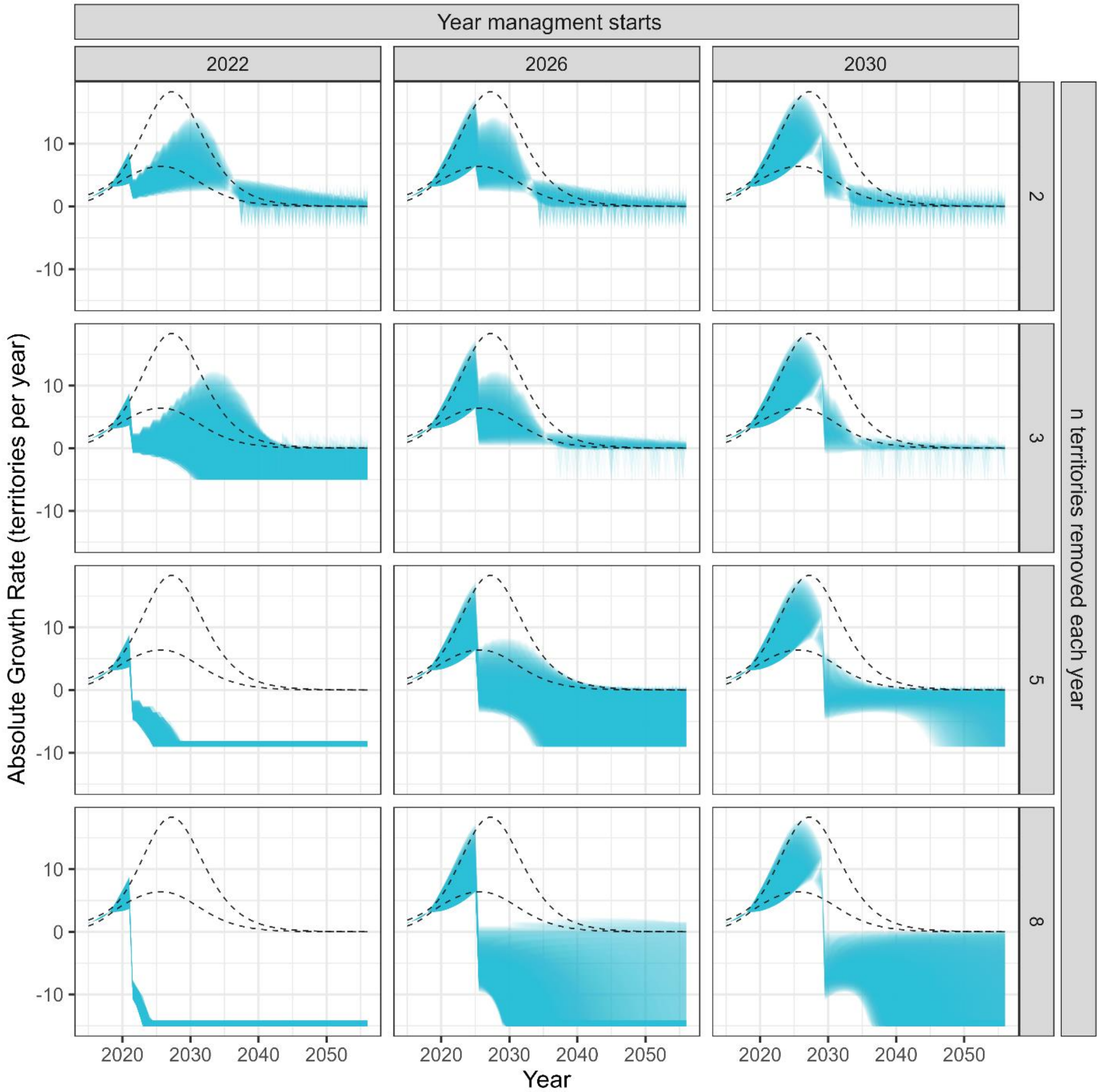
SI 5: Territory capacity simulation results showing the distribution of territory capacity estimates for the lower (1.4) and upper (3.1) beaver forage index thresholds. Mean estimates of 126 (2.7 SD) and 174 (3.7 SD) were recorded for the low and high BFI scenarios respectively. 100 random territory generation scenarios were carried out with each scenario tested with low and high BFI thresholds.



SI 6: Beaver territory removal management scenario matrix. This plot is an extension of figure 8 and includes a greater range and number of scenarios that were tested to evaluate the impact of beaver territory removal beginning on different years at different intensities.



SI 7: Population dynamics analysis comparing the predicted absolute growth rate and relative growth rate with time and population density. Solid lines show the mean trend, shaded areas define the 95% confidence interval. These models are a composite of 63 different models across the estimated territory capacity range; darker shading implies stronger agreement across these (sub) models.



SI 8: Corresponding to figure 8, this matrix describes the impact of territory removal on growth rates. Dotted lines show the growth rate range in the absence of management, shaded areas define the 95% confidence interval of the growth rate following territory removal. These models are a composite of 63 different models across the estimated territory capacity range; darker shading implies stronger agreement across these (sub) models.

Appendix 10. National-scale Beaver Dam Capacity (BDC)