CENTRE OF EXPERTISE FOR WATERS

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Josie Geris, Katya Dimitrova-Petrova, Mark Wilkinson

Hydro Nation International Centre

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Contents

Executive Summary

Research Questions

i. How does beaver activity affect the functioning of rivers and streams and water resources?

ii. What are the potential benefits and limitations of the ecosystem engineering capabilities of beavers for ecosystem restoration and environmental management in Scotland?

iii. What are the remaining knowledge gaps for which further research is needed?

Background

Beavers are well known for their ability to transform ecosystems through dam building and other activities. By modifying physical processes in streams and rivers, beavers have the potential to play a role in providing ecosystem services that link to key water resource management issues in Scotland, alongside wider benefits such as carbon sequestration and river restoration. The water management benefits include improvement of water quality, water supply, and the management of floods and droughts. However, the evidence for the role of beaver activity in these various ecosystem services is typically diffuse or incomplete, especially for Scotland and Europe generally. In addition, beavers are increasingly spreading to prime agricultural land and other intensively used land in Scotland which has led to a range of conflicts.

This report provides an independent evidence review of the role of beavers in modifying physical processes, and the potential benefits they may bring for the provision of ecosystem services. It will inform the dialogue on the benefits and limitations of beaver expansion, including where trade-offs are required. It will also support decision making and policy related to the development of a National Strategy for beavers in Scotland.

Research undertaken

Two mechanisms for capturing evidence were used: an international literature review of quantifiable metrics of beaver activity effects, specifically of dam building; and an expert evaluation and interpretation of the effects and remaining knowledge gaps. The review builds on NatureScot's 2015 'Beavers in Scotland' report (Gaywood *et al.,* 2015) and other recent international reviews. It specifically:

- Collates measurable evidence for trends (i.e., increase, decrease, or no change) associated with the effects of beaver dam building on water quantity and quality and the geomorphological characteristics of Scottish rivers.
- Provides confidence levels for the evidence of these trends, determined as a function of the amount of evidence and the level of agreement between different evidence sources.
- Explores the limits of knowledge on beaver activity effects, e.g., in terms of the types of environments, and the spatial and temporal scales for which evidence has been collected.
- Evaluates the results in the context of ecosystem services in Scotland.

Key Outcomes

What is known

- Most of the evidence of beaver activity effects on the physical functioning of streams and rivers points to positive contributions to local ecosystem services. There is strong evidence that beaver dam-building results in wetland creation and the trapping of suspended sediment, nutrients and contaminants. In addition, high flows are typically lowered and delayed, while recharge, water storage and residence times increase. Beaver activity can therefore contribute to water supply and purification, the moderation of extreme events, nutrient cycling and river restoration.
- Enabling positive contributions to ecosystem services may also involve compromises and care must be taken to manage any disbenefits. Beaver activity effects may include the loss of land because of habitat creation and increased flooding behind dams. While flooding increases in the area behind beaver dams, beaver activity contributes to small-scale downstream decreases and delays in the flood peak. The relative effects will therefore depend on the location in relation to the beaver activity, as well as the surrounding land use (e.g., in most cases any flooding in built-up areas is likely to have larger socio-economic effects than the flooding of forested areas).
- Depending on site characteristics, other effects that could be considered as disbenefits include interruptions to fish passage because of decreased hydrological connectivity within a river network. In addition, average water temperature typically increases locally, but beaver activity is also associated with decreases in the maximum temperature. Changes in water temperature can have implications for in-stream ecology and private/industry water users.
- For carbon storage, beaver activity is simultaneously paired with increased carbon storage and increased methane and carbon dioxide emissions; the offsets between these two effects are highly variable and less

known.

- Dam-breaching - part of the evolution of beaver systems - can have detrimental effects. These include exacerbating flood events and the release of sediment and contaminants that were being retained by a dam. The significance of these effects will depend on the timing and extent of breaching.

Remaining questions (future research needs)

- How do beaver activity effects scale to rivers that drain larger catchment areas? Most evidence has been recorded at the local scale, i.e., up to about 1 km^2; policy and practice for ecosystem services would benefit from evidence at larger scales.
- What are the effects of beaver activity on the full range of stream discharge? There is less evidence of the effects of beaver activity on low flows and storage-discharge relationships.
- What is the net effect of beaver activity on greenhouse gas emissions and carbon sequestration and so the carbon budget, and what controls the balance locally?
- What are the site-specific controls on the magnitude of beaver effects? Some effects depend strongly on local beaver activity and landscape characteristics. This poses problems for the transferability of effects to other sites, especially with different characteristics. The evidence base lacks studies from Scotland and the UK, non-forested environments, and at larger scales.

Recommendations

- The potential for beaver activity to contribute to a wide range of ecosystem services should be considered in relevant riparian management appraisals. These services include water supply and purification, the moderation of extreme flow events, nutrient cycling, and river restoration.
- To inform an appraisal and mitigate local adverse effects of beaver activity, discussion with landowners and wider societal groups is required. This should consider (i) the wider ecological and socio-economic aspects of beaver translocation and expansion, as well as (ii) mechanisms to ensure that those negatively affected are involved and appropriate 'payment for public goods' models are identified alongside other mitigation strategies.
- More empirical research is required to address the fundamental knowledge gaps, particularly on the scaling and magnitude of beaver activity effects. This needs to be supported by long-term experimental monitoring in Scotland and modelling. Monitoring efforts should involve interlinked characteristics of water quantity, water quality and geomorphology alongside effects on ecology, so that a holistic evaluation can be made for ecosystem services.

Glossary for quantifiable metrics and technical terms used in this report

1. Quantifiable metrics used in this report	Definition
Ammonium (NH4+)	A form of nitrogen. Here it a product of the breakdown of organic material under anaerobic conditions and can be re-oxidised to nitrate (NO_3-) in aerobic conditions.
Area of (new) sediment	A measurement of the area (usually measured in m^2) of newly accumulated sediments.
Average flow	The discharge of a stream or river, often given in cubic metres per second, which is equalled or exceeded for 50% of the time.
Carbon (C) sequestration	The process of removing carbon from the atmosphere and storing it in a reservoir, e.g., in vegetation, sediment, or soil.
CH_4 (methane) and CO_2 (carbon dioxide) release	Two forms of carbon gas release into the atmosphere. These occur naturally in wetlands and can be enhanced by increased nutrient and carbon cycling.
Dissolved organic carbon (DOC)	The concentration of dissolved organic carbon. It has a key role in many freshwater processes. DOC is largely derived from (terrestrial) vegetation transported by streamflow and/or produced in situ by algae and macrophytes.
Dissolved oxygen (DO)	The amount of oxygen dissolved in water. Oxygen is essential for both plants and animals, but extremely high or low levels in water can be harmful to fish and other aquatic organisms.
Groundwater (GW) recharge	A hydrological process through which water moves downward from the surface to replenish groundwater.
Heavy metals and contaminants	A heavy metal is one that can be poisonous to humans already at low concentrations. A contaminant is any unnatural i.e., anthropogenically produced substance. Soil and groundwater contamination with heavy metals and contaminants is an issue of global concern, thus retention and remediation of polluted soils and sediments is key for improving downstream water quality.
High flows (magnitude and lag-time)	The stream discharge during peak flows and/or equalled or exceeded for 10% of the time. Also referred to as peak flow or peak discharge. Here high flows are characterised based on magnitude (i.e., the amount of water passing through a point in the stream at a specific point in time) and lag time (i.e., the time from the centroid of the rainfall storm to the peak discharge).
In-stream storage	The storage of surface water within the stream course.
Low flows	The river flow which is equalled or exceeded for 95% of the time.
Nitrogen (N) and Nitrates (NO_3-)	Nitrogen (N) is a necessary nutrient for all organisms' growth. In the form of Nitrate (NO_3-) excessive amounts in water courses increase algae growth, which can starve the water of dissolved oxygen and eventually kill fish and other aquatic life. Sources of nitrates may include industrial pollutants and nonpoint-source runoff from heavily fertilized cropland.
Out of bank flow	Localised flooding whereby water flows out of the riverbank.
Phosphorus (P)	A key nutrient for the productivity of freshwater ecosystems. When in excess in water, it can speed up eutrophication and reduce dissolved oxygen. Input in streams in human-managed environments come from agricultural fertilizers, manure, sewage, etc. Soil and bank erosion is another major contributor of phosphorus to streams, especially during high flows.
Residence time	Residence time of water is a measure of the average time a unit of water spends in a system.
Sediment size class	An indication of the dominant sediment particle size. An increase is associated with coarser material accumulating in relatively larger proportions and a decrease is associated with more fine sediment.
Sediment volume pond	The amount of sediment from upstream or adjacent land deposited within one or multiple ponds within a beaver system.
Sedimentation rate	The rate at which sediment is deposited.
Storage-discharge (S-Q) relationships	The relationship between catchment storage and discharge, i.e., how much discharge leaves the catchment per unit storage. This relationship is highly non-linear.
Suspended sediment	Sediment fine enough to be held in suspension by water.
Variability of flows	A measure of stream flow dynamics characterised by the range of flows and the variability around the mean.
Water temperature (T)	The temperature of water. Its fluctuations and extremes directly influence the health of aquatic organisms as well as nutrient cycling and amount of dissolved oxygen.
Wetland creation	Wetland ecosystems occur between terrestrial and aquatic environments, with the degree of flooding being a main control on its vegetation. Wetlands are associated with high biodiversity and range of other ecosystem services.

2. Technical term	Definition
Hyporheic zone	The aquatic zone under the riverbed where groundwater and surface waters mix. Provides an important refuge and nursery habitat to aquatic organisms.
Lateral connectivity	A concept that quantifies the linkages between stream channels and habitats at the margins and on the floodplain, including the flow of water and exchange of sediments and organic material.
Longitudinal connectivity	The connections between upstream and downstream sections of the river network, as opposed to vertical or lateral (bank to bank) connections.
Aerobic and anaerobic conditions/ environments	An aerobic environment is characterised by the presence of free oxygen (O2) (e.g., in free-flowing stream reaches and unsaturated soils) while an anaerobic environment lacks free oxygen (e.g., in saturated soils or at the bottom of sediment in a pond).
Aggradation	Net accumulation of sediment leading to an increase in channel bed or floodplain surface elevation. This generally occurs where sediment transport capacity is exceeded by sediment input.
Ecosystem services and disservices	Ecosystem services: the aspects of healthy ecosystems valued by humankind for their contribution to human well-being, as e.g., provision of water supply, attenuation of high flows, etc. which are usually services to society at large.
Geomorphology	The study of landforms and landform evolution.
Hydrology	The study of the water cycle, including water evapotranspiration, precipitation, storage, distribution and stream discharge. Also used to refer to the flow characteristics of the stream of a catchment. Both water quantity and water quality are aspects of hydrology.

1 Introduction

Beavers (*Castor fiber* and *C. canadensis*) are well-known for their ability to transform ecosystems through dam building and other activities such as canal creation, lodge building, burrow creation and felling of riparian woody species. Beaver activity is typically associated with the creation of diverse habitats (Dalbeck *et al*., 2020; Stringer & Gaywood, 2016). These and other effects on catchment scale biodiversity (Nummi *et al*., 2021; Willby *et al*., 2018) and in-stream ecology (Kemp *et al.*, 2012; Tye *et al.*, 2021) have been relatively well documented. This report provides an evidence base review of the role of beavers in modifying physical processes and the potential benefits they may bring in delivering ecosystem services. It addresses the following three questions:

(1) How does beaver activity affect the functioning of river and streams and water resource management?

(2) What are the potential benefits and limitations of the ecosystem engineering capabilities of beavers for ecosystem restoration and environmental management in Scotland?

(3) What are the remaining knowledge gaps for which further research is needed?

By modifying physical processes in streams and rivers, beavers have the potential to play a role in important ecosystem services (Thompson *et al.*, 2021) such as: ameliorating flooding, reducing sediment loads, improving water quality, increasing rates of aquifer recharge and creating riparian wetland habitats. These link to key water resource management issues in Scotland, including water supply, management of floods and droughts, riverbank restoration and diffuse pollution (Figure 1). The reintroduction and natural expansion of beavers is therefore also increasingly considered as part of nature-based strategies for habitat restoration, adaptation to climate extremes and rewilding (Willby *et al.*, 2018).

However, evidence for the effects of beavers on physical processes and freshwater ecosystem services is typically diffuse or incomplete, especially for Scotland and Europe generally. In addition, beavers are increasingly spreading to prime agricultural land in Scotland. Co-existing with beavers in these and other human-managed landscapes has led to a range of different conflicts (Campbell-Palmer *et al.*, 2015; Coz and Young, 2020; Kinas *et al.*, 2021; NatureScot, 2021b). A comprehensive evidence base of beaver activity effects for Scotland is therefore also required to inform the dialogue on the benefits and limitations of beaver expansion (Devon Wildlife Trust, 2019; Mikulka *et al.*, 2020). This report will particularly inform decision making and policy related to the development of a National Strategy for beavers in Scotland.

The independent evidence review here provides an up-to-date overview of quantitative beaver activity effects. It also evaluates these in the context of ecosystem services in Scotland. It particularly focusses on the effects on the movement and distribution of water within rivers and their catchments, and on the physical processes responsible for the evolution and sustainable functioning of streams and rivers. In their 2015 'Beavers in Scotland' report, NatureScot provided a detailed review of beaver activities up to that point (Gaywood *et al*., 2015). Recent international reviews (e.g., Brazier *et al*., 2021; Larsen *et*

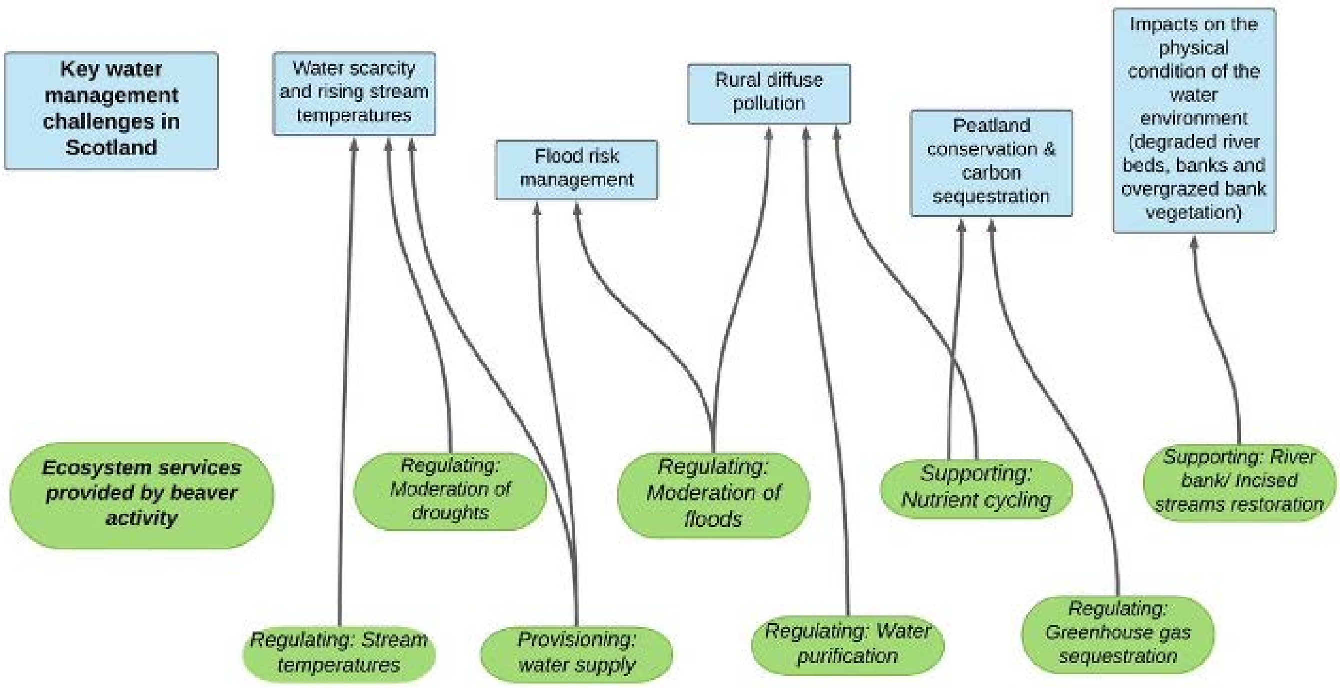

Figure 1. Links between key water management challenges in Scotland, as identified by Scottish Government, (2017); SEPA, (2020); NatureScot, (2014, 2021a) to ecosystem services provided by beaver activity, as evaluated by Thompson et al. (2021).

al., 2021) have provided more up to date overviews of the effects that beavers may have on water quantity, water quality and geomorphology. This study builds on these and specifically:

- Collates quantitative evidence for trends (i.e., increase, decrease or no change) associated with beaver activity effects on water quantity, water quality and geomorphological characteristics (metrics) of Scottish rivers. For water quantity these metrics include the effects on low flows, high flows, recharge. A full list of the metrics is provided in Table 1.
- Provides confidence levels for evidence on these trends, determined as a function of both the amount of evidence and level of agreement between different evidence sources.
- Explores the boundaries of knowledge on the types of environments, the spatial and temporal scale, and other aspects for which evidence of beaver activity effects has been collected. This enables insights into the applicability of the available evidence to Scotland.
- Evaluates the results in the context of ecosystem services for Scotland. This is supported by discussions with the steering group and other beaver experts from a wide range of backgrounds.

2 Methodology: Framework for capturing evidence

The methodology for this study is illustrated in Figure 2. Two mechanisms for capturing evidence were used: an international literature review of quantifiable metrics of beaver activity effects, and an expert evaluation and interpretation of (knowledge gaps of) these effects.

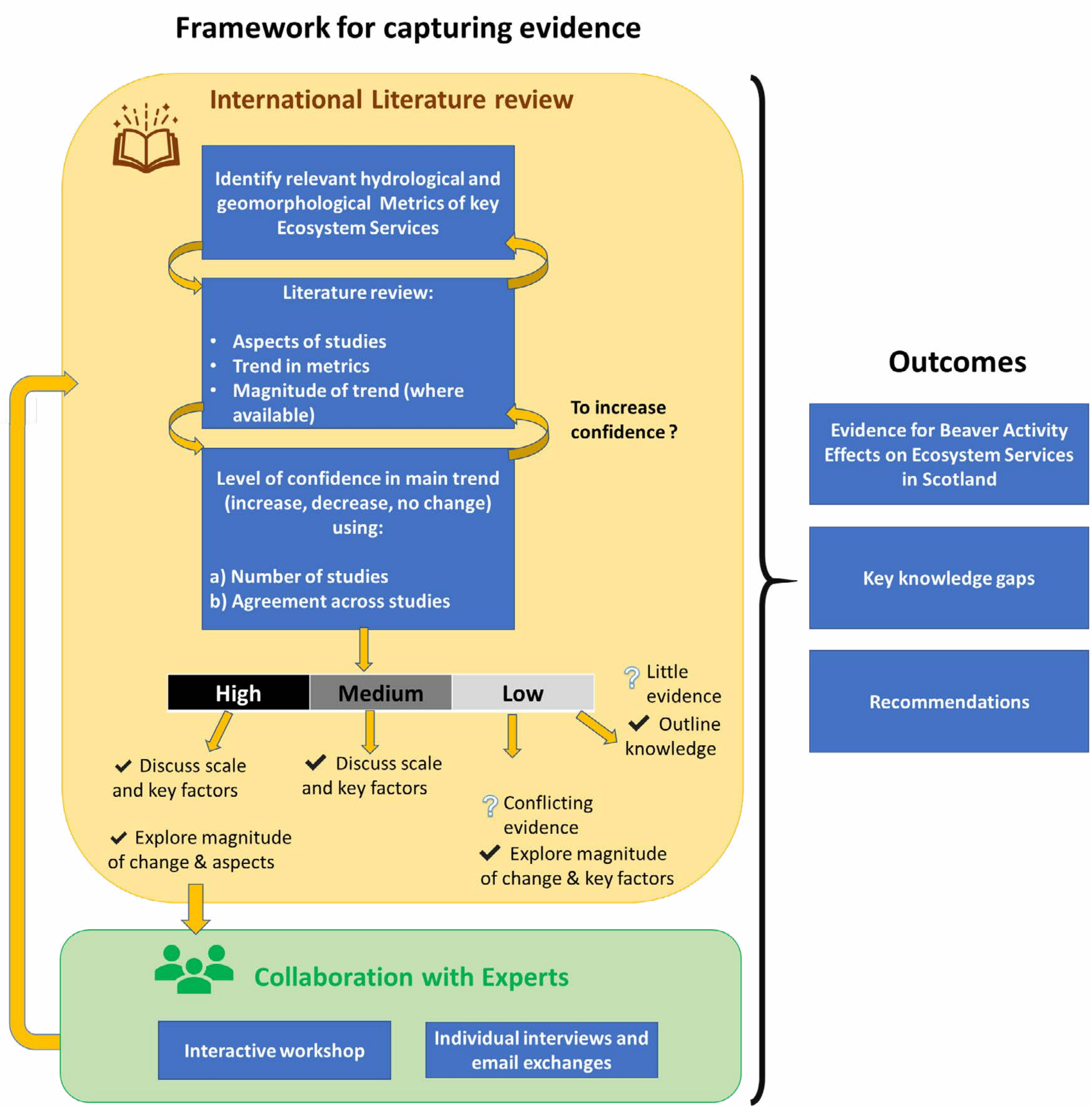

Figure 2. Flow chart of methodology followed in this project. See Section 2.1 for details on the approach used for the literature review and Section 2.2 for the approach on collaboration with other experts.

2.1 International literature review

2.1.1 Metrics and literature search to evaluate beaver activity effects

The international literature review focused on the effects of beaver activity on measurable characteristics (metrics) that describe the overall hydrology and geomorphology of Scottish Rivers (Table 1). These metrics were used because it is not possible to directly measure or quantify the effect of beaver activity on ecosystem services, as these typically depend on multiple factors. For example, moderation of floods depends on the available water storage, how well the river is connected to the floodplain, and the magnitude and timing of the flood peak, among other characteristics.

All metrics were identified via an iterative process at the start of the literature review (Figure 2). Many of the metrics are interlinked and contribute to multiple ecosystem services (Table 1) that Scotland's rivers can provide (Perfect *et al.*, 2013). Most of the metrics are also discussed in reviews elsewhere (e.g., Brazier *et al*., 2021; Larsen *et al*., 2021). Here the focus was specifically on characteristics for which effects were observed quantitatively. In this review, 'effect' is defined as an observed trend, i.e., an increase, decrease or no change in the value of the metric as it would be without beaver activity.

Google Scholar and Web of Science were used to identify peer reviewed and grey literature. This involved a combination of different search terms relating to "beaver", "dam", "hydrology", "geomorphology" and "water quality", combined with topic key words (see Appendix 1). Studies on the Eurasian (*C. fiber*) as well as the North American (*C. canadensis*) beaver activity effects were included. Differences between the activities of these two beavers are considered to be minimal (Danilov and Fyodorov, 2015; Alakoski *et al.*, 2019). Some additional literature and knowledge were identified via the expert group. Sources which reported a quantitative trend of change on one or more metrics were captured in an evidence table (see Appendix 2). For the relevant metrics, the evidence table includes (1) direction of change effect, *i.e.,* increase, decrease or no trend, (2) a measure of the effect magnitude and (3) additional study aspects under which the evidence was collected. These aspects relate to site and study specifics that are known to potentially affect the results of individual studies. This includes information on the location of where the study was conducted, study site landscape characteristics such as land use, and the spatial and temporal extent of the beaver activity that was monitored. Studies that report contrasting or extreme effects of beaver activity need to be considered within the context of these different study aspects. They were therefore used to explore possible bias towards, for example, a specific environment, but also to disentangle the evidence where conflicting results were found. Overall, these study aspects also provide insights into the relevance of the evidence base to Scotland and the remaining knowledge gaps.

The review focused primarily on the effects of beaver activity where dams are present[1]. While beaver presence and activity does not always result in damming (e.g., in large/wider rivers and lochs), the evidence is most abundant; and effects are most pronounced, for those locations where dams are present. Depending on the metric, 'effect' information was collected for either (1) across the area of beaver activity, (2) locally inside the beaver pond and/or (3) downstream of beaver activity. Most studies compared sites with beaver activity to reference sites without beaver activity (e.g., further upstream or in neighbouring reaches). Studies that compared metrics before and after the occurrence of beaver activity were also included.

It is recognised that the effects of beaver dam breaches can be large and are likely to be different. These differences in effects relate to the direction of the trend, the magnitude and the duration of the effect. Additionally, beaver dams are dynamic structures. Dam dimensions, construction materials and the type of throughflow, which together could be captured in a classification of beaver dams (Woo and Waddington, 1990; Burchsted and Daniels, 2014; Ronnquist and Westbrook, 2021), will also affect the results of site-specific studies. Because there is no systematic reporting dam classification in the general literature, it was not possible to include this as a study aspect.

1 See Textbox 1 for a summary of other beaver activity effects.

Table 1. Links between key water management challenges, ecosystem services and how they relate to the water quantity, water quality and geomorphology metrics considered in this study.

Key water management challenges in Scotland

- **Water scarcity & rising stream temperatures**
- **Rural diffuse pollution**
- **Flood risk management**
- **Carbon sequestration & Peatland conservation**
- **Impacts of physical condition of the water environment**

Metrics	*Ecosystem services provided by beaver activity*	*Stream Temperature*	*Moderation of droughts*	*Water supply*	*Moderation of floods*	*Water purification*	*Nutrient cycling*	*Greenhouse gas sequestration*	*Incised stream/ river bank restoration*
Geomorphology	Sediment volume (Pond)				✔	✔	✔		
	Sedimentation rate				✔	✔	✔		✔
	Suspended sediment (D/s)			✔	✔	✔	✔		
	Wetland creation			✔	✔	✔	✔	✔	✔
	Area of (new) sediment				✔		✔		✔
	Sediment size class				✔		✔		
	Longitudinal connectivity								
	Lateral connectivity	✔	✔	✔	✔		✔		✔
	High flows magnitude			✔	✔				
Water quantity	High flows lag-time			✔	✔				
	Residence time		✔	✔	✔				
	In stream storage		✔	✔	✔				
	Groundwater recharge		✔	✔	✔				
	Out of bank flow (upstream)			✔	✔				
	Storage-discharge (S-Q) relationships		✔	✔					
	Low flows	✔	✔	✔					
	Average flows		✔	✔					
	Variability of flows		✔	✔					
	Improved hyporheic flow	✔				✔			
Water quality	Nitrogen (N, NO_3^-) (Pond)					✔	✔		
	Nitrogen (N, NO_3^-) (D/s)			✔		✔	✔		
	Carbon sequestration						✔	✔	✔
	Carbon (CH_4,CO_2) release						✔	✔	✔
	Ammonium (NH_4^+) (Pond)					✔	✔		
	Ammonium (NH_4^+) (D/s)			✔		✔	✔		
	Dissolved organic carbon (DOC) (Pond)					✔	✔		
	Dissolved organic carbon (DOC) (D/s)			✔		✔	✔		
	Mean water Temperature (Pond)	✔							
	Mean stream Temperature (D/s)	✔		✔					
	Attenuation of Temperature fluctuations	✔	✔						
	Metals and contaminants (Pond)					✔			
	Metals and contaminants (D/s)			✔		✔			
	Phosphorus (P) (Pond)					✔	✔		
	Phosphorus (P) (D/s)			✔		✔	✔		
	Dissolved oxygen (DO) (Pond)					✔	✔		
	Dissolved oxygen (DO) (D/s)			✔		✔	✔		

2.1.2 Trends and levels of confidence

From across the evidence base, the dominant trend for each metric was determined. The level of confidence in the change trend for a metric was also provided. For this, a combination of the amount of evidence and the level of consensus was used (Figure 3). This method was adapted from Morison and Matthews (2016). Using this approach, the highest level of confidence can only be achieved if many studies show similar trends. A small amount of evidence, and/or conflicting results, will result in low levels of confidence. In the context of this study, a large amount of evidence was determined as 10 or more studies reporting quantifiable evidence on a metric. A medium amount was five to nine studies, and a low amount less than five studies. The level of agreement was classified as high when 75% or more of the studies reported the same trend. Medium and low percentages of studies reporting the same trend of change were 60-74% and less than 60%, respectively.

For the high confidence level metrics, the trends were reported and discussed. For the low and medium confidence level metrics, a distinction between low confidence due to a low number of studies or due to conflicting evidence, or both, was also provided. For cases with conflicting evidence, the role of study site characteristics (e.g., land use, or the extent of monitoring) was explored.

2.1.3 Magnitude of change

For decision making that relates to beaver activity and the provision of ecosystem services, the magnitude of the effect may be as important as the trend. An example, in the context of flood risk management, would be by how much a peak flow is increased/decreased. Information on the conditions under which effects are likely to be smaller or larger would be part of that. For example, does the magnitude of the effect change with catchment scale, or depend on land use. However, direct comparisons between studies were mostly not possible. For all metrics, there was much variation in reporting of the magnitude of effects, both with regards to the format and units. Nevertheless, for a sub-selection of the metrics, including those on high flows could be explored across studies. This was done by normalising the magnitude of the effect via the 'effect ratio' ($\Delta ratio$), following Ecke *et al.*, (2017):

$$\Delta ratio\_UD = \ln\left((Value\_beaver)/(Value\_reference\right)$$

(Equation 1)

In Equation 1, *Value_beaver* relates to the metric value for the overall beaver affected area, the beaver pond, or downstream of the pond, and *Value_reference* relates to the equivalent metric value for a reference site or time with no beaver activity. In the example of high flows, *Value_beaver* would be the peak flow at a site with

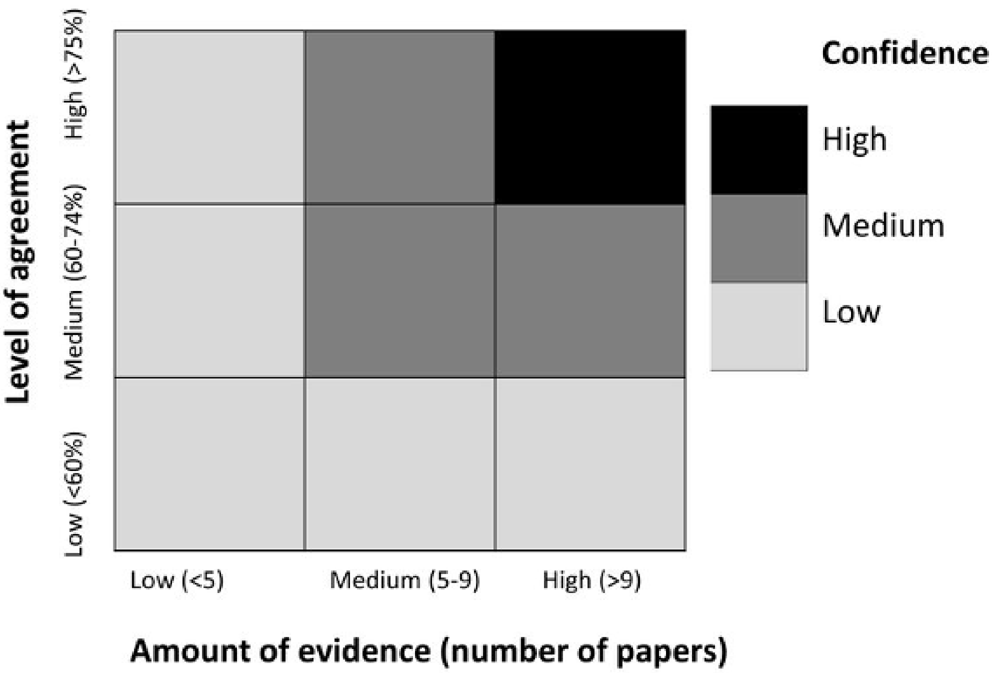

Figure 3. Assessment of the levels of confidence in the evidence from literature and trends of change. The level of confidence is a function of the number of papers or reports presenting quantifiable evidence (x-axis) and the level of agreement (y-axis). Thresholds are provided in the axis's labels. Level of confidence method adapted from Morison and Matthews (2016).

beaver activity, and *Value_reference* the comparable peak flow at a time or location without beaver activity.

The magnitude effect ratio was calculated for studies on the effects of high flows, nitrates, and dissolved organic carbon. These specific metrics were selected because: (1) they had a relatively high number of studies for which the magnitude was recorded, (2) studies had most consistency in the format in which the magnitude was reported and (3) together these metrics relate to ecosystem services where beaver impacts were considered to have high potential to address the key water management challenges in Scotland, as identified collectively by the stakeholders and expert contributors.

2.2 Incorporating expert knowledge

Beaver activity experts from a range of backgrounds (hydrologists, geomorphologists and ecologists) were identified. Together with the steering group, their role in the project was to: (1) provide feedback on the framework for capturing evidence, (2) help identify additional sources of evidence for the effects of beaver activity, and (3) discuss the beaver activity effects for ecosystem services, knowledge gaps and recommendations for future work. Information was gathered through: (1) individual unstructured interviews, (2) email exchange and/or attendance at a (3) 3 hr workshop held on June 16, 2021[2]. Discussion sessions were key elements of the workshop. In the first session, the importance and spatial extent of ecosystem services provided by beavers in Scotland was addressed. In the second, the focus was on knowledge gaps and ways to address these, for example via modelling or knowledge from beaver dam analogues (e.g., leaky barriers). Individual contributions were anonymised.

3 Beaver activity effects

3.1 General overview of evidence base

The evidence base includes a total of 119 studies which report quantifiable evidence on the effect of beaver dam activity on one or more metrics related to geomorphology, water quantity and water quality (see Appendix 2). An overview of the aspects related to this general evidence base is provided in Figure 4.

In summary, the international evidence base is large, but studies from Scotland and the UK, non-forested environments, and at larger catchment scales (> 1 km^2) are relatively sparse. Most studies originate from North America (Figure 4a). Only a quarter provide evidence for sites in Eurasia, including the UK (5% of total studies). Most studies come from environments with forest land use (56%), and secondly from agricultural environments (20%) (Figure 4b). A smaller proportion of studies was conducted in moorland (16%) and urban (6%) areas. There is a quite balanced representation of studies in

2 The agenda and key outcomes of the workshop are summarised in Appendix 6.

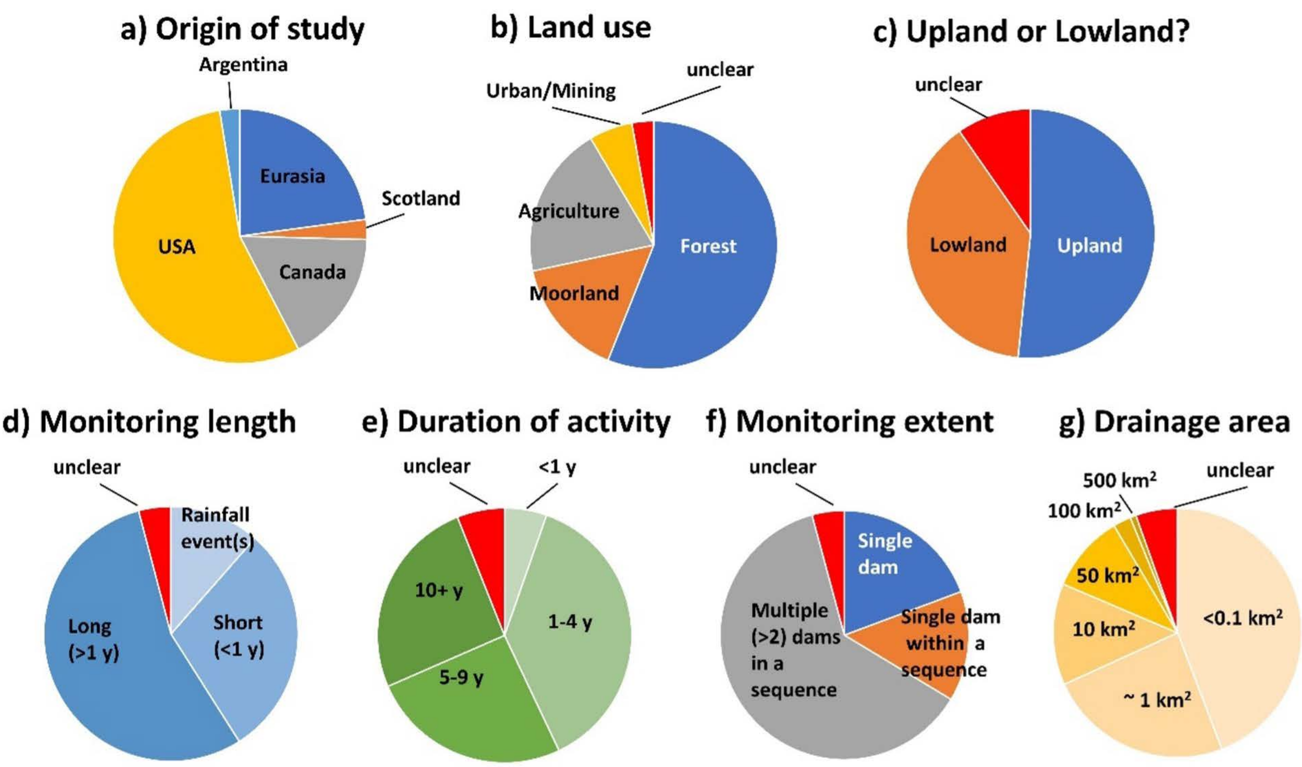

Figure 4. Selected aspects of evidence across all studies (n = 119) included in the evidence base.

upland and lowland locations (Figure 4c). Just over half of the studies (55%) include observations that spanned more than one year (Figure 4d). Long term monitoring allows for understanding beaver activity effects across a wider range of conditions (e.g., in the climate, time of year, hydrology, etc.). However, whether the variability in natural conditions is captured also depends on the frequency of the observations, which is likely to be higher during shorter term monitoring efforts. There was a relatively uniform spread in the duration of beaver activity across the studies (Figure 4e). Beaver activity may consist of a single dam or a beaver dam sequence. Across the studies, most evidence involved beaver activity with dam sequences (62%), as opposed to single dam systems (Figure 4f). There was a tendency for those studies carried out at larger catchment scales (10-100 km^2) to involve multiple beaver dam systems (i.e., producing cumulative effects over a large area). However, overall, there is large bias in evidence towards studies that were conducted at small scales (Figure 4g).

Aspects for individual metrics[3] mostly reflect the distribution indicated in Figure 4 (i.e., the bias in the evidence base is similar for most metrics). However, for several of the water quality metrics, including nutrients, carbon and dissolved oxygen, there is relatively more evidence from agricultural environments and lowland settings. Another noteworthy exception is that the larger scale studies report mainly the effects related to geomorphology metrics (e.g., sediment dynamics and wetland creation). This means that for the water quantity and water quality metrics, the bias towards small scale studies is even greater than as presented in Figure 4.

Since beavers were first formally reintroduced at Knapdale in 2009, evidence on the effects of beaver activity on physical processes has been collected in three Scottish environments: at the Scottish Beaver Trial in Knapdale, Argyll (Willby *et al.*, 2014), in Tayside near Blairgowrie (van Biervliet *et al.*, In Prep; Law *et al.*, 2016), and at an enclosed site near Inverness in north Scotland (Angus Tree, Pers. Comm). The results of these studies are included in the relevant sections below[4].

3.2 Effects of beaver activity on geomorphology

Beaver dams slow streamflow and limit sediment transport (Figure 5). In the beaver ponds upstream of the dams, sediment deposition rates and consequently, sediment volumes, tend to increase. Combined with raised water tables (see section 3.3) and multiple ecological processes (Gurnell, 1998; Stringer and Gaywood, 2016), wetlands are created or expanded. Over time, beaver activity can increase channel sinuosity (Burchsted *et al*., 2010; Levine and Meyer, 2014) and lateral connectivity with the floodplain. This lateral connectivity is also expanded via beaver burrowing activities[5] into the bank (Abbott *et al.*, 2013; Gorczyca *et al.*, 2018; Grudzinski *et al.*, 2020). Beaver structures decrease longitudinal connectivity. Comprehensive overviews of the geomorphological effects of beaver activity are provided e.g., by Gurnell (1998), Pollock *et al.* (2014), Brazier *et al.* (2021) and Larsen *et al.* (2021).

In total, 80 pieces of quantitative evidence, for six geomorphology metrics that can be linked to specific ecosystem services (Table 1), were identified[6]. The geomorphology metrics relate mainly to sediment transport and wetland creation. An overview of the high

3 Detailed representations of the various aspects for individual metrics are presented in Appendix 3.
4 Appendix 4 provides a summary for the findings in Scotland specifically.
5 See textbox 1 for more details on the effects of burrowing.
6 An overview of the spread of evidence among different aspects is reported in Appendix 3.

Textbox 1. Burrowing, lodge building, channel digging and felling

In addition to dam building, beavers also modify the geomorphology of their environment via burrowing, channel digging, felling and lodge building. These activities mostly influence the area within 50 meters from the water body (Willby et al., 2014; Mikulka et al., 2020).

Beavers live either in burrows or constructed lodges using cut branches, mud and stones. Often, multiple burrows are established within the beaver territory, which can contribute a significant amount of sediment and organic material to the water course. It can also lead to localised erosion (de Visscher et al., 2014; Harvey et al., 2019).

Digging of shallow channels facilitates easy access to resources (Brazier et al., 2021). These channels may act both as source and sink of sediment. Networks of beaver channels increase complexity in the topography and connectivity with the floodplain (Hood and Larson, 2015; Brazier et al., 2021). While burrowing and channel digging may be a source of sediment and cause erosion, quantifying the impact of burrowing remains a key knowledge gap (Harvey et al., 2019; Grudzinski et al., 2020).

Beaver activity also involves felling and increasing small and large woody material (Iason et al., 2014; Perfect et al., 2015). Small woody material can help riparian plant recruitment (Levine and Meyer, 2019). Large dead wood in streams provides a range of ecosystem services and constitutes an essential element of Scotland's rivers (Perfect et al., 2013). Large dead wood in small streams may remain in place for longer and so influence local geomorphology, by increasing stream bed heterogeneity and altering scour and sedimentation, alike beaver dam structures (Gurnell, 1998).

The burrowing, channel digging, felling and lodge building activities are often, but not always, paired with dam building. Dam building retains water levels that provide safe refuge and under water entrance to the burrow or lodge. In locations with wide rivers or in lochs (Hartman and Törnlöv, 2006; John et al., 2010) beaver colony establishment does not require dam building.

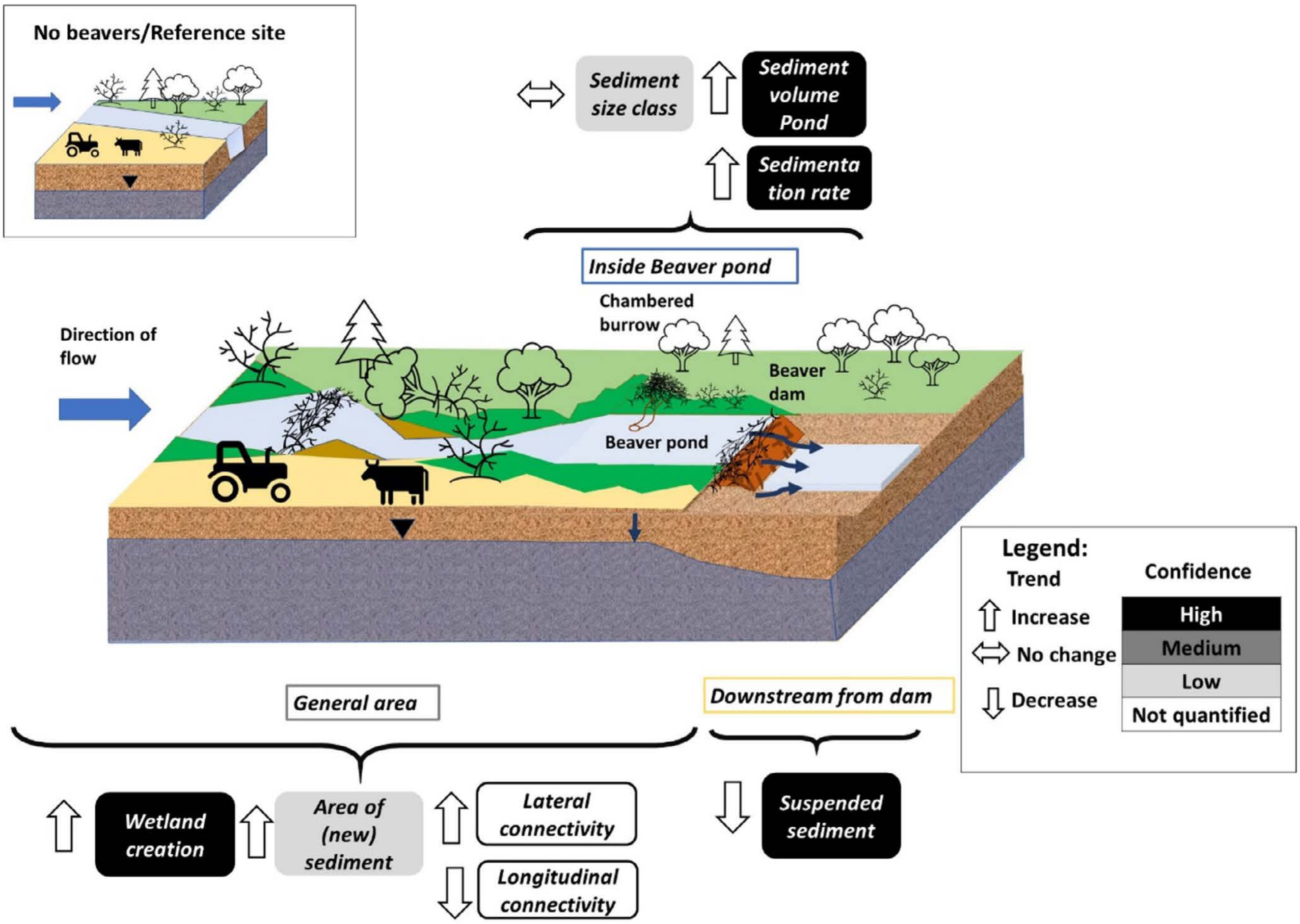

Figure 5. Conceptual overview of the levels of confidence in trends in change in geomorphology metrics due to beaver activity. For abbreviations and definitions of terms see Glossary .

to low confidence level effects is provided in Figure 5[7]. More detail on longitudinal and lateral connectivity is provided at the end of this section. However, as these aspects were not consistently reported in a quantitative way, it was harder to provide confidence ratings in the way done for the other metrics.

3.2.1 Trends with high confidence levels

Increase in sediment deposition inside the beaver pond (sediment volume and sedimentation rate) and decrease in suspended sediment downstream

Many studies have provided evidence of increasing sediment deposition behind beaver dams. Dam construction dissipates stream energy, creates a backwater effect, and drives floodplain inundation. This introduces changes in sediment transport resulting in an increased sedimentation rate and sediment volumes behind beaver dams. Given the increase in floodplain connectivity, it is worth noting that geomorphic change due to beaver activity is not limited to deposition inside the ponds but is often related to creating heterogeneous channel shapes behind the dam or dam sequence. Downstream of the beaver activity, there is a clear trend of reduced suspended sediment.

The total volume of additional sediment deposition depends on multiple factors, including the sediment availability upstream and the storage capacity of the beaver ponds. Butler and Malanson (2005) estimated sediment deposition could range between 11 and 5084 m^3, depending on pond size. For this they combined 10 years of fieldwork with continent-scale data of beaver pond sedimentation rate and volumes in the USA and Canada. Furthermore, for an urbanising catchment in the USA, Chang *et al.* (2021) found that the effects of wetlands, which were connected because of beaver activity, resulted in the largest decreases in total suspended solids, at least during high flows.

For a site in Devon, UK, Puttock *et al.* (2017, 2018) estimated that 78% of the suspended sediment coming from intense agriculture upstream was retained by the beaver dam sequence. However, an opposite trend was observed by Law *et al.* (2016) for an agricultural site near Blairgowrie in Scotland, where they measured a 5.8 times increase in suspended sediment downstream of a sequence of beaver dams. This contrasting result was probably related to several factors. The Scottish study site was on relatively degraded land, subject to restoration

7 The results of all individual analyses are given in Appendix 5.

efforts. Here beaver dams were constructed with poorly consolidated materials. There was also exposure of steep, sparsely vegetated banks and accumulation of sediment under low flows. Therefore, these results might not be applicable to many other parts in Scotland with healthier habitat status. Moreover, with longer duration of the beaver activity, banks stabilisation and wetland creation will reduce the export of suspended sediment downstream with time.

Increase in wetland creation

Beaver damming is strongly associated with wetland creation and maintenance. Hood and Bayley (2008) showed that beaver activity can be even more important than certain climatic variables (rainfall, air temperature, etc.) in maintaining open water areas. For Elk Island National Park (194 km^2), USA, the increase in wetland area was nine-fold with beaver presence than without. Wetland resilience increases with more connectivity between different wetland areas, and beavers can play an important role in this too (Hood and Larson, 2015). For some areas where extensive wetlands already existed, beaver activity did not result in more wetland creation (Little *et al.*, 2012). Nevertheless, Willby *et al.* (2018) showed that beaver activity can still enhance the existing wetland in such cases, by supporting more plant species than wetlands not engineered by beavers.

Evidence for wetland creation was reported from studies in USA, Canada and Europe. It was consistent for different catchment scales and land uses. Law *et al.* (2016) demonstrated that after nine years of beaver activity, the landscape had transformed into a comparatively species-rich habitat and with increased water storage. Syphard and Garcia (2001) showed that, even in a rapidly urbanising environment, beavers can maintain wetland habitat.

3.2.2 Trends with low confidence levels

Increase in new area of sediment

Although only a few studies were identified that explicitly quantified the area of newly deposited sediment due to beaver activity (e.g., Pollock *et al.*, 2007) they consistently suggested that channel widening and channel aggradation by beaver activity promotes areas of new sediment deposition. These areas become available for plants to establish.

Change in sediment size class

In her review, Gurnell (1998) outlines the sorting of bed sediment as a likely geomorphological effect of dam construction. There is evidence for relatively finer sediment within the body of the pond (Ruedemann and Schoonmaker, 1938; Giriat *et al.*, 2016) and coarsening of sediment downstream of dams (de Visscher *et al.,* 2014). However, within the small number of studies overall, there was also some contrasting evidence for the effect of beaver dams on the change in sediment size class. For example, Bigler *et al.* (2001) found no significant differences in sediment class size between areas upstream and downstream of or within-ponds in sequences of beaver dams. Contrasting results are likely to be related to site-specific differences in the availability and mobility of sediment.

3.2.3 Trends without confidence levels

Changes in connectivity within the stream and of the stream with the adjacent landscape

Beaver activity increases the flow of water and exchange of sediments between the stream channel and the adjacent land on the floodplain. Despite not quantified in a consistent manner, this effect is widely documented in the geomorphology literature as an increase in lateral connectivity or floodplain connectivity (Burchsted *et al.*, 2010; Wohl and Beckman, 2014; Wegener *et al.*, 2017). Confidence in the effects on connectivity is therefore not low. Generally, the increase in lateral connectivity is largest for small streams and for those streams that are not already well connected to the floodplain (Larsen *et al.*, 2021).

Dam building and the creation of heterogeneous flow patterns generally decrease longitudinal connectivity in beaver affected streams. This refers to connectivity within the stream (i.e., along the direction of flow), which may hinder the passage of fish (Kemp *et al.*, 2012; Malison and Halley, 2020). However, the effects on fish migration are particularly difficult to quantify as other factors can play a role, e.g., other natural and man-made barriers in the stream, year-to-year variations in streamflow. The changes in both lateral and longitudinal connectivity and flow patterns induced by beaver activity depend on the base landscape conditions, as discussed by Larsen *et al.* (2021).

3.3 Effects of beaver activity on water quantity

Figure 6 summarises the key effects with confidence levels of beaver activity on water quantity metrics. Behind beaver dams, water accumulates in ponds and wetlands, increasing water storage and local recharge. This also increases the water residence time. During high flow events, beaver dams can lower and delay peak flows. In most cases, this is because water is redirected onto the floodplain. The space available behind beaver dams to store water during these high flow events is typically small. This therefore also results in more out of bank flow and local flooding, which in turn allows greater infiltration and recharge of water on the floodplain. There is some

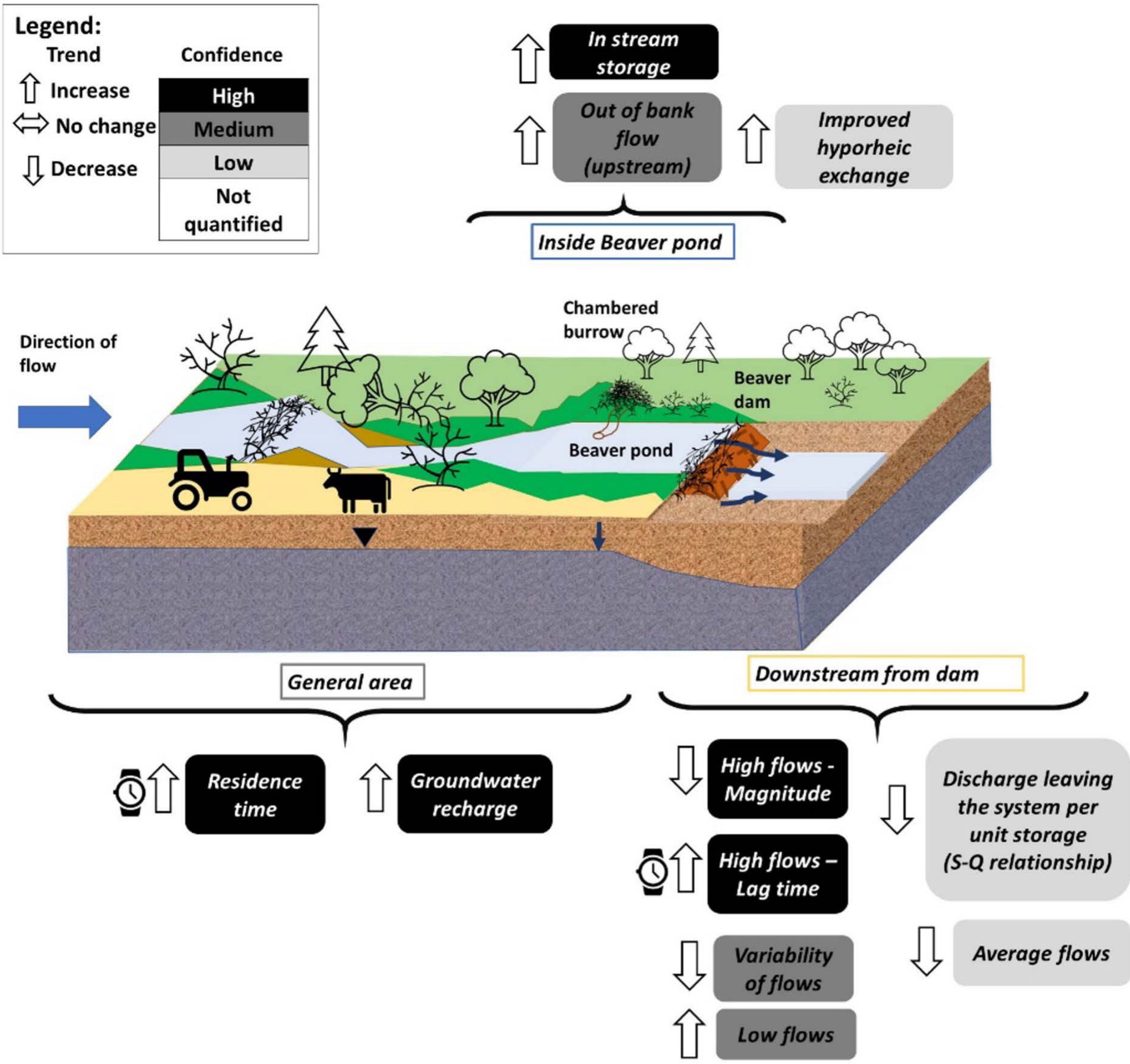

Figure 6. Conceptual overview of confidence of trends in change in physical processes related to water quantity due to beaver activity. For abbreviations and definitions of terms see Glossary .

evidence that beaver dams contribute to increase flows during dry periods and maintain water storage during periods of drought (Fairfax and Small, 2018; Fairfax and Whittle, 2020). Detailed descriptions of these water quantity processes are provided by Brazier *et al.*, (2021) and Larsen *et al.*, (2021).

Ten metrics related to the effect of beaver activity on water quantity were identified from a total of 112 sources of evidence[8].

3.3.1 Trends with high confidence levels

Decrease in high flows

Much evidence has shown that beaver dams can attenuate high flows, by decreasing the magnitude of flood peaks downstream of beaver dams and increasing their lag-time (Figure 6). In the UK, relevant research has been conducted both in England (Puttock *et al.*, 2017, 2018, 2021) and Scotland (van Biervliet *et al., in prep.*; Law *et al.*, 2016) with evidence coming from agricultural and forested environments. These studies were in lowland settings, but the flood attenuation effect of beaver activity has also been observed in upland settings in Europe (e.g., Nyssen *et al.*, 2011), Canada (Westbrook *et al.*, 2020) and the USA (Hillman, 1998). The spatial scale at which

8 An overview of the supporting analyses can be found in Appendix 5 and the spread of the evidence among different aspects is reported in Appendix 3.

beaver dams or beaver dam sequences have been shown to attenuate high flows is mainly at the local scale (0.1 km^2), yet some evidence is available at scales up to 10 km^2 (Nyssen *et al.*, 2011; Liao *et al.*, 2020; Neumayer *et al.*, 2020).

Given the pressing need to develop flood risk management in Scotland and the UK, the magnitude of beaver activity effects on high flows[9] is of importance. The evidence has a strong bias towards small scale catchments. In small catchments, Puttock *et al.* (2017) linked beaver activity to a 30% reduction of the peak discharge of 0.1 m^3/s was, while Beedle (1992) reported a 4% decrease of a 50-year flood event of 1.2 m^3/s. Most studies that studied the effect on peak flows were associated with a sequence of beaver dams. For the two studies where only one dam was involved, the magnitude effect ratio was small. For magnitude, as well as lag time, effect ratios were typically higher for forested catchments than for agricultural sites. However, the evidence for the forested sites also involved more mature and larger scale beaver activity. More evidence would be required to disentangle the relative roles of land use versus beaver activity extent on the effect ratio. A decreasing trend in the effect ratio of reductions in peak flow with catchment scale was found for studies that were all in agricultural sites and that also involved beaver activity of similar age. For the same set of studies, there was a small increase in the effect ratio for lag time with catchment scale, although all observed delays in lag time were relatively small.

Increase in water storage and residence time

Beaver activity increases both surface and subsurface water storage. In-stream storage increases as dams create ponds or raise the levels of existing lakes by impounding their outlets. In an upland area in USA, Butler and Malanson (1995) quantified ponded areas across a range of different beaver activities and observed these to be between 50 and 1710 m^2, depending on local characteristics. In Minnesota, Johnston and Naiman (1990) recorded a 1–13% increase in ponded areas between 1940 to 1986 as beaver presence grew to 1 colony/km^2. In the UK, Puttock *et al.* (2017) estimated that 13 beaver ponds could be holding up to 1000 m^3 of surface water in a hectare scale site.

Groundwater recharge increases locally due to the backwater effect created by dams; lateral flow which aids the recharge of riverbanks increases too. Together, these processes increase the water residence time in a system (Figure 6). Increased and sustained groundwater levels directly help maintain wetland and peatland areas (Pęczuła and Szczurowska, 2013; Karran, 2018). In an agricultural catchment in Germany, Smith *et al.* (2020) observed increased and more stable groundwater levels after beavers were reintroduced. In a Canadian agricultural setting, Hill and Duval (2009) also recorded an increase in water table of 0.8–1.2 m. Even after dam breaching, water tables remained 0.6–0.8 m higher than in the pre-beaver period. This attenuated the lowering of water tables during the summer. Similar effects on water tables have also been observed in forested areas, e.g., in USA (Dewey *et al.*, 2021) and Knapdale, Scotland (Willby *et al.*, 2014).

9 More details on the effect ratios are provided in Appendix 7.

3.3.2 Trends with medium confidence levels

Increase in out-of-bank flow (flooding upstream from dam)

Although less studies explicitly quantified the extent of flooding upstream of dams during high flow events, this phenomenon is a common effect of beaver activity (e.g., Fairfax and Small, 2018; Robinson *et al.*, 2020; Westbrook *et al.*, 2020) and of interest in modelling studies (Liao *et al.*, 2020; Neumayer *et al.*, 2020). The frequency, duration and magnitude of out-of-bank flow due to beaver activity depends on numerous factors, including slope, rainfall patterns and soil characteristics (Westbrook *et al.*, 2006; Hood and Bayley, 2008; Hill and Duval, 2009).

Decrease in flow variability

A decrease in the variability of flow is often observed downstream of beaver dams. In the UK, such changes have been observed at the small (0.1 km^2) scale both in eastern Scotland (van Biervliet *et al, in prep.*; Law *et al.*, 2016) and in England (Puttock *et al.*, 2021). In an upland area in Europe, Nyssen *et al.* (2011) also recorded an attenuation of flow variability overall, while the attenuation effect was lost in a forested Canadian catchment after beaver dams were removed (Green and Westbrook, 2009).

Increase in discharge during periods of low flow

Beaver damming and associated increase in surface and subsurface storage can lead to an increase in low flows. Woo and Waddington (1990) observed an increase discharge during periods of low flows and decreased flashiness in the stream discharge at their study site in Canada. In Europe, Nyssen *et al.* (2011) observed a 32% increase in the lowest flows (from 0.6 to 0.88 $m^3 s^{-1}$) after beaver reintroduction. In Tayside, Scotland, preliminary results from van Biervliet *et al.* (in prep) suggest that a beaver dam sequence increases the lowest 2% of the streamflow. Increases in discharge during periods of low flows have also been reported indirectly (e.g., Andersen *et al.*, 2011; Fairfax and Small, 2018) and often in association with other storage-discharge changes, such as increased in-stream and groundwater storage, which sustain flows during otherwise dry periods (Woo and Waddington, 1990; Hill and Duval, 2009; Nyssen *et al.*, 2011).

3.3.3 Trends with low confidence levels

Change in storage-discharge relationships, decrease in average flows and increase in hyporheic exchange

There are three water quantity metrics for which confidence in the evidence is relatively low. This is mostly because there is little evidence available for the individual metrics and not because the evidence is conflicting. In turn, this is the result of practical difficulties in observing processes directly. For example, measuring streamflow in beaver affected environments is difficult and associated with a high degree of uncertainty, especially for low flows. In isolation, there is low confidence in the change in storage-discharge relationships, decreases in average flows and increase in hyporheic exchange (i.e., vertical exchange between the water column, riverbed and underlying gravels of the hyporheic zone). However, the hydrological processes involved in these metrics are related to each other and the trends are therefore linked. Hence, together, the metrics indirectly provide more confidence for each of the individual metrics.

Beaver dams, and especially sequences of them, modify local storage-discharge relationships, by stabilising and decreasing the variability of flow (see previous sub-section). For instance, Wegener *et al.* (2017) in the USA, and Smith *et al.* (2020) in Germany both reported a decrease in discharge per unit storage.

Beaver dams introduce variations in the stream channel topography and with that affect hyporheic exchange locally (for detailed description of the process see Larsen *et al.* (2021)). Given the complexity of measuring hyporheic flow, only a few studies reported direct quantifiable evidence on this (White, 1990; Lautz *et al.*, 2006; Wang *et al.*, 2018). The total flux of water via this flow tends to be relatively small and concentrated around the dams. However the hyporheic exchange has implications for stream fauna, as it provides oxygenated water and nutrients, extending the habitat for invertebrates and providing refuge in periods of high flows (Perfect *et al.*, 2013). In flat landscapes, beaver dams may provide the only significant hyporheic exchange element, however the relative contribution of beaver dams would also depend on other factors, e.g., regional groundwater and surface water gradients (Larsen *et al.*, 2021).

3.4 Effect of beaver activity on water quality

Of all the beaver activity effects evaluated in this review, those on water quality are most site-specific, and often depend on background water quality status (e.g., the background concentrations of contaminants, but also pH, temperature, etc). Figure 7 summarises the general trends for water quality and the associated confidence levels. These effects are strongly related to geomorphological and water quantity changes. Beaver dam building shifts the flow regime from lotic (rapidly moving freshwater) to lentic (still or slowly moving freshwater) conditions (Gurnell, 1998; Larsen *et al.*, 2021). This is the result of decreased longitudinal connectivity, slowing flow and increasing water storage in the landscape. Nutrient, carbon and metal deposition, as for sediment, is enhanced behind the beaver dam. The trends in water quality changes downstream of beaver activity are generally the opposite of those in the beaver pond, but not consistently (Figure 7). This is complex because the increased wetness and primary production also alter biochemical cycling overall, e.g., via changing to more oxygen deprived (i.e., anoxic) conditions (Yavitt *et al.*, 1992; Giriat *et al.*, 2016; Cazzolla *et al.*, 2018). Dissolved oxygen (DO) thereby reduces behind the beaver dam and there are increasing trends in methane (CH_4) and carbon dioxide (CO_2) emissions. Finally, beaver activity regulates stream water temperature, although the effects vary with time and tend to be localised. The review by Larsen *et al.* (2021) provides extensive summaries of the effects of beaver activity on water quality; the meta-analysis by Ecke *et al.* (2017) compares the quantifiable effects on water quality of beaver dams with those of man-made dams.

Sixteen metrics related to the effect of beaver activity on water quality (Table 1). A total of 140 pieces of quantifiable evidence were identified[10]. The metrics include water quality effects within the beaver pond and those downstream of beaver activity[11]. The complexity of stream temperature effects meant these were inconsistently reported in the literature. It was therefore mostly not possible to assign confidence levels to specific trends, but the key evidence is summarised at the end of this section.

10 An overview of the spread of evidence across different aspects is reported in Appendix 3.

11 The results of all individual analysis are provided in Appendix 5.

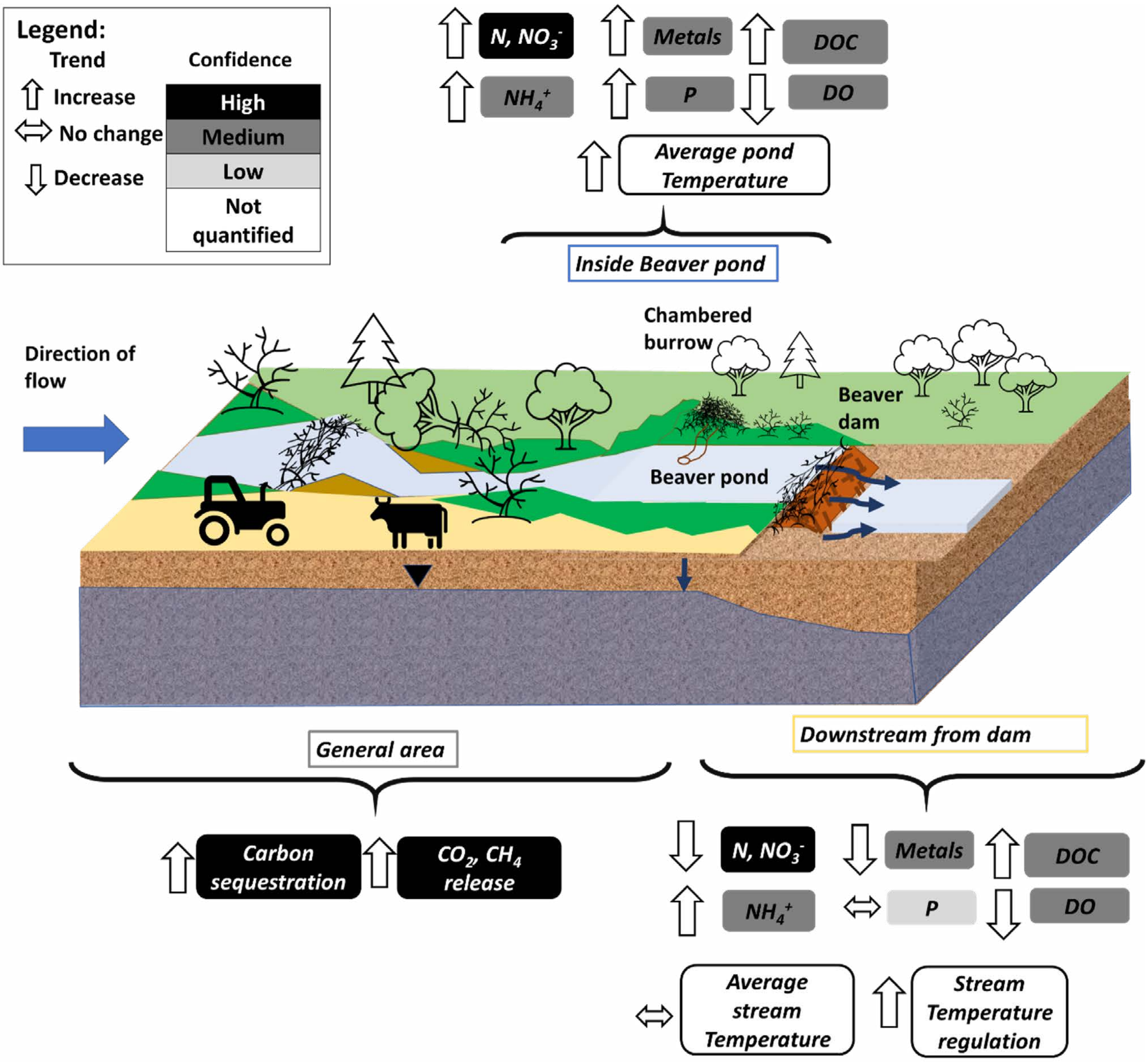

Figure 7. Conceptual overview of trends in change in water quality metrics due to beaver activity. Conceptual diagram adapted from Larsen et al. (2021). For abbreviations and definitions of terms see Glossary .

3.4.1 Trends with high confidence levels

Increase in Nitrogen (N) and Nitrate (NO_3^-) retention in the pond[12] and decrease in removal of Nitrogen from the stream

The evidence base for nitrogen retention in beaver ponds and the associated decreasing trends downstream is substantial and mostly consistent. Beaver engineered wetlands tend to remove nitrates (NO_3^-) and total nitrogen (N) from streamflow via two mechanisms. Firstly, by accumulating nitrogen in the sediment trapped behind dams. Secondly, through denitrification (via N_2 losses); this is an important ecosystem service provided by wetlands (Hantush *et al.*, 2013). The effects of beaver ponds on the retention and removal of N are related to N loads (i.e., are a function of water quantity and N concentration) and may vary seasonally (Robinson *et al.*, 2020; Larsen *et al.*, 2021).

Total nitrogen and nitrate increase upstream and decrease downstream of beaver activity has been extensively documented across spatial and temporal scales and mostly in forested and agricultural environments. The evidence for moorland areas is more limited (see Appendix 3). The evidence base includes agricultural environments in Scotland (Law *et al.*, 2016) and England (Puttock *et al.*, 2017, 2018). In Perthshire, Scotland, Law *et al.* (2016) demonstrated that a beaver dam sequence was associated with a 43% reduction of nitrogen downstream. Similarly, Puttock *et al.* (2017) documented a decrease in total organic nitrogen of 53% downstream of a beaver dam sequence in England. At this same site Puttock *et al.* (2018) estimated that the 13 beaver ponds in the

12 For effects on ammonium (NH4+) see sections 3.4.2 and 3.4.3 ‘Trends with medium and low confidence levels’.

system held 0.91 ± 0.15 tonnes of nitrogen within the accumulated sediment.

Given the significance of nitrate in the diffuse pollution of water resources in Scotland, variations in effect ratios were also explored (see Appendix 7). Effect ratios were highest for decreasing nitrate trends in ponds and downstream of beaver activity at agricultural sites. The largest effects were observed for sites with agricultural land use and this could be a function of these sites having higher background nitrate loads. However, there was also a bias towards more studies in agricultural sites. More studies in other environments are therefore needed to reduce uncertainty in the links between impacts and land use. There was also a tendency for the effect ratio to be larger with increasing extent of the beaver activity.

Increase in carbon sequestration

An increase in carbon (C) sequestration has been observed in beaver engineered habitats across countries, environment types and for a range of beaver activity extents. Long-term carbon storage may be enhanced by the sustained expansion of oxygen-poor conditions and consequently slow decomposition rates of dead wood (Naiman and Melillo, 1984). Carbon storage has been positively correlated to the level of flooding (Roulet *et al*., 1997; Minke *et al.*, 2020). The rate of carbon accumulation is also a function of the production and decay of organic matter and peat formation and typically changes over time. The mechanisms of carbon cycling and storage have been discussed exhaustively by Larsen *et al.* (2021). Their review emphasised the importance of the initial conditions, i.e., before beaver introduction to the habitat. The net change in carbon storage due to beaver activity is generally larger in C poor environments and smaller in environments where C storage is already high, e.g., well-preserved peatland.

In an agricultural landscape in England, Puttock *et al.* (2018) studied nutrient and sediment storage in a beaver engineered wetland. They estimated that 13 beaver ponds held 15.90 ± 2.50 tonnes of organic carbon within the accumulated sediment. This was at a site that drained only 0.2 km^2. For a mixed land use (agriculture and forestry) catchment draining 2.28 km^2 in the USA, Correll *et al.* (2000) estimated a 28% reduction in total organic carbon downstream of a single beaver dam. Johnston (2014) estimated that soil carbon storage in a carbon-rich boreal beaver meadow in Canada was twice as much as for a forest without beaver activity.

Increase in carbon dioxide and methane emissions

Increased emissions of carbon dioxide (CO_2) and methane (CH_4) in beaver impacted environments have been documented across the world. Due to the change to a standing water environment, paired with increased ponding and elevated groundwater tables, oxygen deprived conditions tend to increase in beaver impacted environments (Naiman *et al.*, 1994; Larsen *et al.*, 2021). Methane is then generated because of the carbon build up in the oxygen-poor environment (Hodkinson, 1975). A further effect is the slowing down of organic matter decomposition (Naiman *et al.*, 1986). Overall fluxes of carbon dioxide can also increase because more organic matter is available for decomposition in the beaver system (Yavitt and Fahey, 1994; Roulet *et al.*, 1997). In Eurasia, evidence comes from agricultural (Otyukova, 2009) and moorland (Vecherskiy *et al.*, 2011; Minke *et al.*, 2020) environments; examples from Canada include evidence at forested sites (Weyhenmeyer, 1999) and in USA from moorland areas (Dove *et al.*, 1999). A study by Naiman *et al.*, (1991) in a boreal forest site showed that annual fluxes of methane were 40 times larger in permanently wetted zones as compared to occasionally inundated meadow and forest sites. It is worth noting that there are more studies with methane measurements than with carbon dioxide in beaver ecosystems (e.g., Nummi *et al.*, 2018).

3.4.2 Trends with medium confidence levels

Increase in ammonium in beaver pond and downstream of beaver activity

The overall increased ammonium in ponds and downstream of beaver activity is related to the breakdown of organic matter in anoxic conditions, which increase with beaver activity. Some studies have shown that with increasing distance downstream, ammonium increases and nitrate decreases. This may partly be explained by plants directly taking up ammonium (Naiman and Melillo, 1984). However, this might also indicate that some ammonium is being re-oxidised to nitrate with stream water increasingly returning to more aerobic conditions (Larsen *et al.*, 2021). Nevertheless, generally, there is still an overall net reduction in nitrate owing to beaver activity as reported in section 3.4.1.

While there is high confidence for nitrate, fewer studies report the effects of beaver activity on ammonium (NH_4^+) and there are slightly more contradictory results. Again, the effects are variable in time (e.g., between seasons) and depend on location. In the pond behind the beaver dam, trends are mostly similar for ammonium and nitrate. Devito and Dillon (1993) reported an annual ammonium retention of 89%, while this was 51% for nitrate. Similarly, Naiman *et al.* (1994) reported an 295% increase in ammonium, while this was 208% for NO_3^-. One exception was provided by Vehkaoja *et al.* (2015), who found no significant differences between nitrogen cycling in beaver ponds and natural ponds in a boreal forest environment.

Increased storage of metals and contaminants in beaver ponds and decreased metal concentrations downstream of beaver activity

The capacity of beaver ponds and meadows to filter and trap heavy metals and contaminants within their sediment has been well documented, mostly for the USA, but there are some studies from Eurasia. Murray *et al.* (2021) estimated that beaver ponds could attenuate heavy metals (including barium, cadmium, lead) at a rate 2 to 4 times greater than a reference riffle reach in a lowland agricultural environment. Another study from the USA revealed that a former beaver pond (73,000 m^2) retained 80% of mining legacy uranium (Kaplan *et al.*, 2020). In that case, the beaver wetland was located 2 km downstream from the contamination source and significantly lowered concentrations downstream. The anoxic conditions in beaver ponds also facilitate storage of toxic methyl mercury (MeHg). This was observed by Painter *et al.* (2015) in a peatland in the Canadian Rockies and by Čiuldiene *et al.* (2020) in a forested environment in Lithuania. In a study by Naiman *et al.* (1994), an 82%–169% increase of calcium, magnesium, and iron was measured in soils affected by beaver impounding.

In some cases, the increased water levels and subsurface flow by beaver activity can also result in the mobilisation of contaminants that were stored in the soil. For beaver activity in an historical mining area, Briggs *et al.* (2019) described how the increased subsurface flow through contaminated soils resulted in increased heavy metal concentrations (including; arsenic, manganese and aluminium) downstream of the beaver activity. Compared to the upstream area unaffected by beaver activity, arsenic was five times higher, and manganese was 50–400 times higher in the beaver pond and in the stream downstream from the dam. In these examples, it is important to note that the site-specific conditions including geology and historical land use play an important role in the changes in heavy metals concentrations. Finally, if beaver ponds are drained and water tables lowered, metals otherwise retained in sediment may become remobilised due to switching from anaerobic to aerobic conditions (Ecke *et al.*, 2017).

Increase in dissolved organic carbon behind beaver ponds and downstream of beaver activity

Beaver activity is often linked with an increase in primary production (Hodkinson, 1975; Naiman *et al.*, 1986; Ecke *et al.*, 2017) and associated dissolved organic carbon. Fewer studies reporting on dissolved organic carbon in beaver ponds were found than those on the effects downstream.

Background dissolved organic carbon levels are important to understand the actual effect of beaver activity on dissolved organic carbon concentrations. Net increase tends to be larger in systems with low initial dissolved organic carbon values. Moreover, effects on dissolved organic carbon may also be vary between years and be different in the short term from long term. As an example from Europe, Vehkaoja *et al.* (2015) studied interconnected lakes in boreal Finland and found that in years when beavers impounded the lakes they had significantly higher dissolved organic carbon values than lakes that were not occupied by beavers, but only for the first three years of impoundment. After 4–6 years, dissolved organic carbon values went back to base levels and effects were not transferred to downstream lakes.

In agricultural settings in the UK, Puttock *et al.* (2017) measured a 38% increase in dissolved organic carbon downstream, and Law *et al.* (2016) estimated an increase of 50% downstream of a beaver dam sequence. In Germany, Smith *et al.* (2020) measured an approximately 50% increase in dissolved organic carbon in most agricultural streams with beavers. At the Scottish Beaver Trial in Knapdale, while some increase in dissolved organic carbon was detected in smaller lochs with raised water levels and high initial values of dissolved organic carbon, evidence was not sufficient to show this was due to beaver activity (Willby *et al.*, 2014). For forested areas, there were no consistent trends. For instance, Rodríguez *et al.* (2020) measured a decrease of up to 1.3 mg/L of dissolved organic carbon downstream of beaver dams, while Kalvīte *et al.* (2021) observed significantly lower dissolved organic carbon at beaver sites in comparison with drainage ditches without beaver activity.

In Scotland, where organic rich soils are often saturated, high levels of dissolved organic carbon in streamflow are a common water quality concern. Effect ratios in dissolved organic carbon across the evidence base were therefore also explored (see Appendix 7). Studies were relatively sparse and no consistent trends were observed with increase of spatial scale or extent of activity. However, the highest dissolved organic carbon increase effect ratios were observed downstream of beaver activity in agricultural environments. The greatest dissolved organic carbon decrease effect rations were observed downstream of beaver activity in forested sites.

Decrease in dissolved oxygen in beaver ponds and downstream of beaver activity

Dissolved oxygen (DO) tends to decrease in beaver ponds; this is often associated with elevated pond surface water temperature and increases in algae. Studies reporting changes in dissolved oxygen originate mostly from America, but there are some European examples (Otyukova, 2009; Levanoni *et al.*, 2015; Vehkaoja *et al.*, 2015). In agricultural settings, Hill and Duval (2009) measured 25–70% decreases in dissolved oxygen in riparian groundwater after beaver dam construction. In agreement, Otyukova (2009) estimated a decrease of up to 61% in dissolved oxygen for reaches where beaver dams appeared; highest dissolved oxygen reductions were associated with periods of most heating. In forested areas, Cirmo and Driscoll (1993) also measured a decrease in dissolved oxygen downstream of beaver activity (86% to 70%) downstream of a dam, depending on location in a sequence. The study by Andersen *et al.* (2011), conducted in a relatively dry ecosystem, was one of the very few where no consistent downstream reduction in dissolved oxygen was observed.

***Increased storage of phosphorus in sediment accumulated behind beaver dams*[13]**

Generally, the storage of phosphorus (P and phosphate (PO_4^{-3})) behind beaver dams tends to increase with increased sediment deposition, although some studies reported no significant change. This has resulted in medium confidence levels for this trend. Additionally, whether the ponds act as a sink or source may change seasonally. For instance, Murray *et al.* (2021) found that beaver ponds acted as significant sources of dissolved inorganic phosphorus in spring (61% source) and as a sink in summer (7% sink). They also suggested that beaver ponds can act as important sinks for total phosphorus in the first few years and after that become a weak source of dissolved inorganic phosphorus. For a moorland environment, Devito and Dillon (1993) estimated that total phosphorus annual retention was 4% and that seasonal trends in phosphorus retention were inversely correlated with runoff. Retention was associated with low streamflow (and increased biotic assimilation); loss was observed during high winter flows. Robinson *et al.* (2020) compared the retention of phosphorus by beaver ponds in agricultural and forested environments in Switzerland to explore the role of land use. However, they found that higher retention in the forested site in summer was related more to a flatter landscape at the forested site, rather than a function of land use.

3.4.3 Trends with low confidence levels

No consistent pattern in downstream export of phosphorus

The pattern of phosphorus export downstream of beaver dams is the least consistent, as similar numbers of studies reported a decrease (n = 8) and no significant change (n = 7), while two studies reported a relative increase. The lack of consistency relates to the fact that phosphorus cycling is one of the most complex nutrient cycles (Withers and Jarvie, 2008; Wu *et al.*, 2021). The effect of beaver engineered systems on phosphorus cycling depends on multiple factors and is therefore best evaluated locally.

Scientific evidence for phosphorus trends in the UK comes both from agricultural areas (Law *et al.*, 2016 in Perthshire, Scotland; Puttock *et al.*, 2017, in England) and forested areas (Scottish Beaver Trial in Knapdale; Willby *et al.*, 2014). In the agricultural environments, Law *et al.* (2016) observed a 49% decrease in phosphate downstream of a sequence of beaver dams, while up to a 72% decrease was measured by Puttock *et al.* (2017). In Knapdale, there were some changes in total phosphorus when comparing concentrations prior to and during the beaver trial, yet the researchers concluded that there was insufficient evidence to suggest that those changes were related directly to beaver activity. In other agricultural environments across Eurasia, beaver ponds were also found to have a limited effect on reducing total phosphorus downstream (Katsman *et al.*, 2020; Smith *et al.*, 2020).

3.4.4 Trends without confidence levels

Effect of beaver activity on stream temperature

The change from running to standing water conditions and the increase of open water areas in beaver dam systems also affects water temperature, both within ponds behind beaver dams as well as downstream of beaver activity (Larsen *et al.*, 2021). Sixteen studies that reported quantifiable evidence on water temperature were examined for this review. However, the effects were not consistently reported, and it was therefore not possible to allocate confidence levels to the trends.

Generally, average temperature in beaver ponds appears to be higher (Naiman *et al.*, 1994; BłČdzki *et al.*, 2011). There is also a local increase in stream temperature downstream of beaver dams (Ecke *et al.*, 2017; Zaidel *et al.*, 2021). However, the change is relatively small, especially when compared to the effect on other variables (Ecke *et al.*, 2017), and effects diminish quickly with increasing distance downstream (Lowry, 1993; Smith *et al.*, 2018). Results are again site-specific. Zaidel *et al.* (2021) found the largest increase in temperature for cold water streams and at sites where beaver effects involved the greatest relative widening of the stream channel. The increased heterogeneity of channel geomorphology and associated changes in spatial flow patterns usually results in increased spatial heterogeneity in water temperatures (Smith *et al.*, 2018; Majerova *et al.*, 2020). Overall, streams with short dams in forested sites have the smallest effects on temperature downstream of the dam (Zaidel *et al.*, 2021). In deeper beaver ponds, a distinction should also be made between changes in the bottom and top temperature of the pond (Majerova *et al.*, 2020).

13 For effects on phosphorus downstream of beaver activity, see section '3.4.3 Trends with low confidence levels'.

The most common effect of beaver dams is the attenuation of water temperature fluctuation (Bouwes *et al.*, 2016; Weber *et al.*, 2017; Majerova *et al.*, 2020). For example, downstream of a beaver dam sequence in a forested reach, (Weber *et al.*, 2017) observed 2.5ºC decrease in maximum, and a 1.5ºC increase in the minimum stream temperature. In an agricultural catchment in Russia, Otyukova (2009) found temperature increases in spring and autumn, but decreases in the dry summer period. In Germany, Smith *et al.* (2020) reported a slight increase in mean annual stream temperature downstream of beaver dams, and significant increases in stream temperature in the spring, summer and autumn (although specific values were not reported).

3.5 Workshop and other expert engagement outcomes

The authors presented preliminary results during a virtual workshop (see Appendix 6) with 13 experts, including members of the steering group. Two sessions were held to discuss issues around knowledge gaps in beaver activity effects for ecosystem services in Scotland, scalability, and approaches for addressing knowledge gaps. These and individual discussions with four of the (other) experts were used for the following section.

4 Discussion

4.1 Ecosystem services provided by beavers – advantages and limitations for water management challenges in Scotland

Most of the evidence of beaver activity effects on the physical functioning of streams and rivers points to positive contributions to ecosystem services. The literature review revealed that there is a relatively high level of confidence that beaver activity results in wetland creation and the 'filtering' of suspended sediment, nutrients and contaminants. In addition, high flows are typically lowered and delayed, while recharge, water storage and residence times increase. Beaver activity can therefore contribute to water purification, water supply, the moderation of extreme events, nutrient cycling and riverbank restoration (Table 1; see also Thompson *et al*., 2021).

Some beaver activity effects have benefits as well as disbenefits for ecosystem services. Firstly, beaver activity is simultaneously paired with greenhouse gas emissions and sequestration. There is high confidence in the evidence that impounded areas contribute to emissions of methane and carbon, but also store carbon (Figure 7; Hodkinson, 1975; Johnston, 2014). Beaver activity also influences peat formation, which further modifies greenhouse gas dynamics (Nummi *et al.*, 2018). Offsets are highly variable and poorly understood because calculating the net biogeochemical effects of beaver activity is challenging. The dominant processes involved in greenhouse gas budgets may vary as a function of water table levels and spatial and temporal variations in beaver activity (Lazar *et al.*, 2015; Vehkaoja *et al.*, 2015; Nummi *et al.*, 2018). Some have also speculated that emission rates slow as beaver systems age (Ecke *et al.*, 2017). More research is needed with continuous flux measurements across different beaver systems to better understand the effect of beaver activity on carbon budgets (Nummi *et al*., 2018). Nevertheless, it is worth noting that greenhouse gas emissions associated with the effects of beaver activity are in the order of 0.001% of total methane emissions of aquatic systems (Larsen *et al*., 2021).

The role of beaver activity in flooding differs strongly between the area behind a beaver dam (increase) and downstream of it (decrease). Behind a beaver dam, wetland is created and out of bank flow is more extensive and occurs more regularly. To accommodate this land must be 'sacrificed', which can cause local conflict (Campbell *et al.*, 2012; Gaywood *et al.*, 2015; Auster *et al.*, 2020; Coz and Young, 2020; NatureScot, 2021b). On the other hand, there is clear evidence that beaver dam building can slow and reduce high flow events. This has the potential to mitigate floods downstream of beaver dams. However, the measured effects are typically small in magnitude (e.g., Beedle, 1992; Nyssen *et al.*, 2011; Puttock *et al.*, 2017) and the evidence has been collected mainly from small catchments. There are knowledge gaps on the combined effects of beaver activity in multiple headwaters (see also the discussion in section 4.2.2 below on scaling). It is unlikely that beaver activity alone can address large scale downstream flooding (Kelmanson *et al.*, 2019; Ellis *et al.*, 2021), but there is potential for it to be part of a suite of beneficial measures (Burgess-Gamble *et al.*, 2017; Hewett *et al.*, 2020).

The reduction of longitudinal connectivity has been associated with potential problems for fish migration (Sigourney *et a*l., 2006; Taylor *et al*., 2010). Scottish river basin management planning does involve investments in removal of artificial barriers to fish migration elsewhere. This review focused only on the geomorphological trends associated with beaver activity. However, recent work has suggested that salmonid migration may not be significantly affected by beaver activity (Bryant, 1983; Mitchell and Cunjak, 2007; Ecke *et al.*, 2017; Malison, 2019; Malison and Halley, 2020). However, fish movement is site-specific, and the effect of beaver dam building depends on both dam morphology and location, as well as river flow regimes. In places with potential negative effects on fish migration, others have suggested that these could be mitigated with levellers. Levellers are devices that decrease the difference in water levels between pond and downstream (Machus and Wilson, 2018), although in practice this does require monitoring and resourcing. Recent work in Scotland on the effect of beavers on brown trout showed that beaver presence promoted higher abundances of larger fish size classes (Needham *et al.*, 2021). In a large scale study in USA Pollock *et al.*, (2004) showed that significant decrease in smolt production potential was related to loss of beaver ponds, which are key slow-water features for the salmonids. Beaver ponds may also increase low flows in summer, which indirectly benefits fish passability. For more detailed evidence on the effect of beavers on fish in England and Wales, see work by Malison (2019) and The Beaver Salmonid Working Group (BSWG, 2015).

There is also some debate surrounding increases in average stream temperature and how this increase might adversely affect in-stream habitat (Collen and Gibson, 2000). This review revealed that, overall, these effects are very local. Moreover, maximum temperatures are most critical for in-stream ecological habitat (e.g., McRae and Edwards, 1994), and beaver activity has been linked to decreasing these. This suggests that beaver activity has the potential to contribute to mitigating increases in maximum stream water temperatures under climate change. It is worth reiterating that beaver activity effects on temperature are also spatially variable (Weber *et al.*, 2017). Overall, they tend to create more heterogeneity in spatial temperature profiles (with depth within the pond and horizontally across the river channel). However, it was beyond the scope of this study to evaluate the effects on in-stream ecology directly. Examples that address those relationships include reviews by Collen and Gibson (2000) and Kemp *et al.* (2012). Gaywood *et al*. (2015) provide a comprehensive review of the effects of beaver activity on ecology in Scotland.

This study focused mainly on the effects of intact and evolving beaver dam systems. However, dam breaching is part of the evolution of beaver systems (Westbrook *et al.*, 2006; Nyssen *et al.*, 2011). Dam breaching can have detrimental effects. Examples include: exacerbating flood events (Hillman, 1998; Butler and Malanson, 2005); the associated flushing of sediment (Wilcox, 2010; Kalvīte *et al.*, 2021) and contaminants (Ecke *et al.*, 2017) contained therein. The effect downstream of unexpected or unmanaged dam breaches with high concentrations of sediment or contaminants, could potentially be harmful. However, the relative impact of these effects depends on the timing of the dam breaching (Stoll and Westbrook, 2020; Westbrook *et al.*, 2020) as well as the extent of breaching (Nyssen *et al.*, 2011). Furthermore, textbox 1 highlights some of the impacts of other beaver activities, including: borrowing, channel digging, felling and lodge building. In addition, there could be problems if beavers interact directly with infrastructure. The issues arising in those situations are typically local and isolated; but could potentially become more frequent where beavers advance closer to urbanised areas.

4.2 Addressing knowledge gaps

4.2.1 Scaling

The most fundamental outstanding question relates to scale. Most evidence has been recorded at the local scale, for catchment areas up to about 1 km^2 (Figure 4); however, policy and practice are generally interested in the larger catchment scale impacts for many water-related ecosystem services (e.g., decrease flood risk, improve water quality for bathing waters, water supply, etc.). Scaling was a core discussion topic during the expert workshop (Appendix 6). Maintaining ecological flows, flood risk management and increasing or securing water supply were rated by experts as among the most relevant ecosystem services provided or maintained by beaver activity. However, in agreement with the evidence review, these were also considered the least well understood, in particular, for catchment scales of 10 km^2 and higher. For example, large volumes of available storage in catchments are needed to manage extreme flood events (Wilkinson *et al.*, 2019). The evidence base has shown that the available storage behind a beaver dam is relatively small in that context, although storage on the floodplain can be greater.

Similar to other natural flood management approaches, questions remain about how the effects scale to large catchment areas and for extreme events (Kelmanson *et al.*, 2019). Nevertheless, beaver activity could contribute to flood risk management, alongside other natural and traditional approaches. For example, much work is being done on Natural Flood Management in the UK and 65 case studies are presented in the Environment Agency's Working with Natural Processes Evidence Directory (see Burgess-Gamble *et al.*, 2017). A few of these studies also involve beaver activity. As part of designing such flood management strategies, beavers should also be acknowledged for the other wider services they deliver, even though these too will have uncertainty at larger scales. There are limits to the habitat of beavers, related to food availability or landscape suitability (Gurnell, 1998; Gurnell *et al.*, 2009; Graham *et al.*, 2020). For example, streams wider than 6m are unlikely to be dammed (Stringer *et al.*, 2018). For such streams draining larger catchment scales, the knowledge gaps are mainly around the aggregated effects of multiple beaver systems in numerous headwaters. Distributed beaver activity across larger catchments becomes a realistic scenario with increasing beaver expansion. However, the effects of these do not scale linearly (i.e., they cannot simply be summed up) and there is a need to also consider disbenefits that might occur, such as synchronisation of flood peaks (Lane, 2017). Disentangling the effects of beaver activity from other impacts (e.g., variations in land use and management, soil properties, and other physiographical characteristics) also becomes more challenging with increasing scale.

4.2.2 Summary of other knowledge gaps

Of the metrics examined, confidence levels were relatively low for beaver activity effects on the full range of the flow regime (in particular, low flows); interactions of surface and groundwater, and the overall storage-discharge relationships (Figure 6). This was mainly related to the low number of studies that provided evidence. Positive trends in storage and how this relates to flows during dry periods are critical for addressing water scarcity and other ecosystem services (e.g., maintaining flows for in-stream ecology). The effect of beaver dam building on flows across the full range of stream discharge, but especially low flows and subsurface connectivity, therefore, needs to be further investigated.

Other key knowledge gaps are related to the role of study site-specifics, e.g., the aspects that were considered in section 3.1. Much of the literature was site-specific and the issue of transferability of effects is challenging. This was most striking for the effect on water quality of phosphorus cycling, for which the evidence base provides low confidence. In fact, most of the trends with medium confidence levels are due to conflicting evidence (see section 3). For the effects of beaver activity on physical processes, there is a bias towards studies that collected evidence in forested environments, mostly at small scales and in North America. The role of site-specific effects was most apparent when evaluating variations in the magnitude (effect ratio) of effects, so that studies in Scotland will be particularly valuable to gain more insights into the magnitude of the trend effects.

4.2.3 The role of modelling and beaver dam analogues

Long-term (years) and large-scale (over >10km^2) monitoring studies are needed to address knowledge gaps and statistically assess the effects of beaver activity on catchment scale water management issues. In the absence of these studies, modelling tools can have an important role. Modelling is often used to explore how knowledge on local effects translates to effects at the catchment scale. It can also be useful for exploring transferability of knowledge to different land use or under climate scenarios. However, only a very limited number of modelling studies explored the effects of beaver dams on the physical functioning of river systems (examples are Liao *et al.*, 2020 and Neumayer *et al.*, 2020). For Scotland, modelling studies have so far explored the suitability of dam creation in Scottish river sections (Stringer *et al.*, 2018; Graham *et al.*, 2020). However, studies that use models to explore the effects beaver activities are lacking. This may, in part, be because modelling the effect of beaver activity on physical processes is complex and challenging. It is vital that model structures are appropriate, informed with empirical evidence, and parameterised correctly to avoid high levels of uncertainty (Moges *et al.*, 2021). Addy and Wilkinson (2019) reviewed modelling tools that could be used for representing natural and artificial in-channel large wood in hydraulic and hydrological models. They highlighted that knowledge on appropriate representation of wood in rivers in models is lacking; a message also reflected in the limited beaver modelling studies available. A review on modelling tools has not been conducted for beaver dams, but the principles set out by Addy and Wilkinson (2019) could be applicable here. The most common approach to modelling large wood is by altering channel roughness to represent flow resistance. The expert consultation also stated that hydraulic modelling of beaver dam functioning is challenging as it requires a 3-D approach (Appendix 6). Upcoming work by van Biervliet *et al.* (in prep) is exploring the use of a coupled hydrological/hydraulic approach (MIKE 11 and MIKE SHE) to investigate the effects of beaver activity on catchment hydrology in Scotland.

There is also the question whether knowledge gaps could be addressed by studying beaver dam analogues (BDAs) such as leaky barriers. In the UK, these involve large woody debris or flow restrictors implemented mainly as a strategy for natural flood management (Burgess-Gamble *et al.*, 2017), while riparian woodlands establish. In North America, they have also been installed for a range of other purposes (e.g., Lautz *et al.*, 2019; Orr *et al.*, 2020; Wade *et al.*, 2020). The design of many of these incorporates features common in beaver dams, e.g., increased storage behind the dam – see Dodd *et al.* (2016) and Burgess-Gamble *et al.* (2017). Discussions during the expert workshop highlighted that these BDAs do not fully mimic the functioning of beaver dams (see also Westbrook and Cooper, 2021). BDAs were rated somewhat useful for achieving lateral connectivity and wetland creation, regulating flow and regulating out of bank flooding. They were considered much less effective for achieving carbon sequestration, regulating stream temperature and nutrient cycling. It would, therefore, be inappropriate to study BDAs to address knowledge gaps on the effects of beaver activities. However, even though BDAs cannot provide the full range of ecosystem services that are provided by beavers, they might be applied alongside or to support beaver activity. BDAs could also provide solutions in very degraded environments which cannot support beavers (Castro *et al.*, 2018).

4.3 Study limitations

This study aimed to provide an independent overview of the effects of beavers on physical processes related to geomorphology, water quantity and water quality. The focus was on those studies that provided quantitative evidence. However, certain measures and processes (e.g., subsurface storage, recharge) are difficult to observe directly, which may have resulted in relatively low confidence levels. Where it was not possible to fully evaluate the physical effects of beaver activity, key observations were summarised although without confidence levels. This involved the effects on longitudinal and lateral connectivity and stream water temperature. This does not necessarily mean that confidence in the evidence is low.

For the confidence levels, an approach was implemented whereby the levels depended on both the available amount of evidence and the level of consensus in the results. Thresholds involved those considered appropriate for the total amount of evidence collected. The confidence levels are, therefore, relative to each other. Furthermore, these confidence levels should be considered alongside any bias in the study site specifics, e.g., the aspects as presented in Figure 4 and Appendix 3. This is a common issue with nature-based solutions when trying to assess the impact of a particular ecosystem service (Burgess-Gamble *et al.*, 2017).

The extensive literature search was conducted in the English language. Whilst this should capture most scientific literature globally, it is possible that there could be grey literature produced in different languages. This is mostly applicable to the European grey literature studies, where it is possible a technical report may have been conducted by a national environmental authority, e.g., beaver studies in Germany, Poland, etc. As scientific peer reviewed literature is considered the standard for evidence, this limitation should have limited impacts on the study.

4.4 Outlook and recommendations

These are the main recommendations and areas for future work based on this review:

- Scaling and magnitude of effects

More research is required to address the fundamental knowledge gaps in the scaling of beaver activity effects. This is a common message for nature-based solutions in general (see Wilkinson *et al.*, 2019). There is a need to better understand how beaver activity effects on ecosystem services change with increasing spatial and temporal scales. This refers both to the trends (e.g., increase vs decrease in hydrological and geomorphological factors) as well as the magnitude of effects. To consider beaver activities as part of wider nature-based catchment solutions, it is also important to know the aggregated effect of widespread beaver activities across multiple headwaters within larger catchments. Addressing these gaps requires integrated monitoring and modelling approaches over larger catchment scales (>10 km^2) and time. In an ideal situation, this would involve sites for which background hydrological and geomorphological data exist.

- Monitoring

In addition to the monitoring requirements for scaling, data from a wider range of landscapes are also required to understand the role of site-specificity better. In summary, there is a need for more long-term experimental work in Scotland, agricultural and moorland environments and at larger scales. In most cases, experimental data on the full range of flow variability and the relationships with water storage are also lacking. Overall, monitoring the effects of beaver activity on hydrology and geomorphology, as well as ecology, would allow for a more holistic understanding of the interlinked effects.

- Modelling

While additional datasets need time to develop, modelling can provide insights into beaver activity effects at larger scales and in environments that are underrepresented in the evidence base. Modelling could also help to test hypotheses on geomorphological and hydrological processes that are difficult to observe directly, e.g., surface and subsurface water storage and flow interactions. However, many modelling tools have limitations and further exploration of how best to integrate beaver dams into modelling approaches is needed (Addy and Wilkinson, 2019). It is imperative that these models are informed and validated by empirical evidence.

- Beavers as part of riparian management for multiple ecosystem services

Beavers have the potential to make a valuable contribution to a wide range of ecosystem services. Despite the knowledge gaps on scaling, confidence levels for multiple positive contributions to ecosystem services at the local scale are high. It is recommended that beaver activity becomes part of riparian management appraisal, alongside other management strategies. This could, for example, link with the ongoing Scottish Riverwoods initiative (see https://scottishwildlifetrust.org.uk/our-work/our-projects/riverwoods/). Given the services they provide, beaver presence may also be covered under existing payments for ecosystem services schemes (Kuhfuss *et al.*, 2018).

- Engagement with wider sector

Despite the potential to make a positive contribution to a wide range of ecosystem services, beaver activities will also have local adverse effects, including some loss of land currently used for other management purposes. It is in these places, where trade-offs between services need to be made, that most conflicts will exist. Improved dialogue with landowners and wider societal players is recommended. This needs to involve a consideration of: (i) wider ecological and socio-economic aspects of beaver reintroduction and expansion, as well as; (ii) mechanisms that ensure those negatively affected are appropriately involved and compensated.

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