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Legacy effects of loss of beavers in the continental United States

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Abstract

Through their modifications of channels and floodplains, beavers are a premier example of ecosystem engineers. Historical and stratigraphic records suggest that hundreds of millions of beavers once modified small to medium rivers throughout the northern hemisphere. Where beavers actively modify the channel and floodplain with dams, ponds, and canals, their activities increase habitat abundance and diversity, biodiversity, nutrient uptake, attenuation of downstream fluxes of water and sediment, and resilience of the river corridor to disturbances. Loss of beavers through commercial trapping and habitat modification occurred simultaneously with other human modifications of uplands and river corridors. The cumulative effects of these human modifications have been to greatly reduce the ecosystem services provided by rivers. Contemporary efforts to re-introduce beavers in North America and Eurasia and to mimic the effects of beaver engineering with beaver dam analogues and Stage 0 restoration represent a good start, but fundamental questions remain about the extent of such restoration efforts needed to create and maintain significant increases in riverine functions.

1. Beavers as ecosystem engineers

An ecosystem engineer is a plant or animal that creates, significantly modifies, maintains, or destroys a habitat (Jones et al. 1994). Beavers (Castor canadensis in North America, C. fiber in Eurasia) are the most commonly cited example of ecosystem engineers because of their intensive modification of river corridors. River corridor here refers to the active channel, adjacent floodplain, and underlying hyporheic zone (Harvey and Gooseff 2015). Beavers build dams of wood and sediment across small channels (typically at gradients less than 6%), secondary or abandoned channels on floodplains, and hillside seeps or springs, creating a stepped longitudinal pattern of ponded water and dams. Beavers also dig narrow canals (Grudzinski et al. 2020) across the floodplain and, where the valley bottom is sufficiently wide, the combination of canals and overbank flows exacerbated by dams commonly leads to an anastomosing channel planform in which multiple channels branch from the main channel and then rejoin it downstream (John and Klein 2004, Polvi and Wohl 2012) (figure 1). Where habitat is sufficient to support more than one colony of beavers, the river corridor becomes spatially heterogeneous, with multiple channels, dams, and ponds in varying stages of being filled with sediment. This spatially complex river corridor is referred to as a beaver-meadow complex (Ruedemann and Schoonmaker 1938, Ives 1942, Polvi and Wohl 2012). The diversity of terrestrial, riparian, and aquatic habitats present in the beaver meadow supports a high level of biodiversity for organisms from plants (Wright et al. 2002, Bartel et al. 2010) and aquatic and terrestrial insects (Clifford et al. 1993, Law et al. 2016) through fish (Smith and Mather 2013), amphibians (Popescu and Gibbs 2009, Hessack et al. 2015), reptiles, birds (Aznar and Desrochers 2008), and mammals (Rosell et al. 2005, Windels 2017).

In addition to enhancing the ecosystem services of habitat abundance and diversity and biodiversity, beaver meadows strongly influence connectivity within river corridors. Longitudinal connectivity typically declines (Burchsted et al. 2010) because of the presence of dams and ponds, and enhanced magnitude, duration, and extent of overbank flow (Westbrook et al. 2006, 2011), all of which attenuate downstream fluxes of water, sediment, solutes, and particulate organic matter (Naiman et al. 1994, Nyssen et al. 2011, Wegener et al. 2017). Beaver meadows thus provide ecosystem services such as flood-peak attenuation. The retention of fine
Figure 1. A beaver meadow along North St. Vrain Creek in Rocky Mountain National Park, Colorado. The drier conifer forests on adjacent hillslopes in the foreground and rear of this view surround the wet river corridor modified by beavers.

sediment (Butler and Malanson 1995, Kramer et al 2012) and dissolved and particulate nutrients facilitates biological processing of nutrients and associated denitrification (Naiman and Melillo 1984, Naiman et al 1994, Correll et al 2000, Klotz 2010, Lazar et al 2015). Beaver-modifications can also increase sequestration of organic carbon in floodplain sediment (Naiman et al 1987, Wohl 2013a, Johnston 2014, Laurel and Wohl 2019).

Lateral and vertical connectivity commonly increase in river corridors with beaver dams. The dams enhance overbank flows (Westbrook et al 2006) and associated hyporheic (Lautz et al 2006, Janzen and Westbrook 2011, Briggs et al 2013) and groundwater recharge (Johnston 2017). Subsurface water storage may in turn enhance downstream base flows (Nyssen et al 2011, Majerova et al 2015, Wegener et al 2017). By attenuating peak flows and enhancing surface and subsurface water storage within a river corridor, beaver ecosystem engineering can enhance the resilience of the river corridor to floods, drought, and wildfire (Pollock et al 2003, Westbrook et al 2006, Hood and Bayley 2008, Arkle and Pilliod 2015, Duncombe 2019, Silverman et al 2019, Fairfax and Whittle 2020). Table 1 summarizes the physical effects of beaver ecosystem engineering.

2. Historical distribution and population density of beavers in the continental United States

Little is known of beaver population density prior to European contact and establishment of a commercial fur trade in North America. The most commonly cited estimate of 60–400 million beavers in North America (e.g. Naiman et al 1988, Baker and Hill 2003, Bailey et al 2019) comes from Seton’s 1928 book Lives of Game Animals. Seton’s estimate was based on extrapolation from population estimates of 10–60 beavers to the square mile (4–23 beavers km\(^{-2}\)) in the Adirondack Mountains of New York, the shores of Lake Superior, the area formerly known as Cochetopa National Forest in Colorado, and Algonquin Park in Ontario. The area of the contiguous United States is 41% of the area of the area within North America capable of providing adequate beaver habitat, so the estimate above equates to a range of 25–164 million beavers in the contiguous United States.

The historical distribution of beavers in North America is better constrained than their population density. Beavers were historically present from northern Mexico up to the southern fringe of the tundra on the Arctic coastal plain in Alaska and northern Canada. The only areas within the continental United States that do not appear to have had beavers were the southern tip of Florida and the arid Great Basin (Pollock et al 2017). (Perennial rivers in other parts of the arid southwestern U.S. hosted beaver populations that were exploited by 19th century fur trappers; Rea 1983, Carrillo et al 2009.)

Within this huge geographic range, beavers were present in all portions of drainage networks. Although the animals typically only dam smaller streams, they dig dens in the banks of larger rivers and they commonly dam secondary or floodplain channels, as well as hillslope seeps and springs along larger rivers.

In suitable habitat, beavers establish about 1 colony per km of river with, on average, 5–6 animals per colony (Olson and Hubert 1994). Small to moderately sized perennial channels with wide valley bottoms (>45 m) and gradient <6% are generally considered prime beaver habitat (Allen 1982, Baker and Hill 2003), but beavers are remarkably adaptable.
(Johnston 2012). Beavers can build dams across rivers up to 15% gradient (Wohl 2013a), although the relatively narrow valley bottoms of steep channels prevent the development of extensive wet meadows and the abandoned dams and ponds present in lower gradient valleys. Beavers are thus less effective ecosystem engineers in steep channels and beaver population density is lower in steep river corridors. Ephemeral streams that flow only briefly after precipitation do not provide sufficient beaver habitat, but beavers can dam intermittent streams (Baker and Hill 2003, Griffin 2004).

Both commercial records from the fur trades (Carlos and Lewis 1993, Kay 1994, Dolin 2010) and the first written descriptions of diverse regions of the continental United States suggest that it is difficult to imagine what river corridors throughout the country once looked like. The great majority of small to medium-sized rivers did not have a single, freely flowing channel. Instead, most streams and smaller rivers branched repeatedly around large logjams and beaver dams and had a stepped morphology with large areas of ponded water separated by short drops, as well as extensive floodplain wetlands beyond the active channels (e.g. Sedell and Froggatt 1984, Collins et al 2012, Wohl 2014).

### 3. Effects of reduced beaver populations on riverine wetlands and water quality

When beavers leave a river corridor because of trapping or hunting by humans, extreme competition for favored woody riparian species from cattle or native ungulates (Beschta and Ripple 2009), or natural feedbacks including limited food supply (Hartman 1994, Parker and Rosell 2012), much of the spatial heterogeneity described above disappears. As beaver dams are breached and removed, the anastomosing channel planform is likely to metamorphose to a single channel (Green and Westbrook 2009, Polvi and Wohl 2013). This concentration of flow, combined with loss of woody riparian vegetation that thrives with the high riparian water table promoted by beaver dams, can result in incision of the channel and lowering of the riparian water table. The river corridor can stabilize in the form of an elk grassland (Wolf et al 2007, Besdcha and Ripple 2009). An elk grassland represents a simpler morphology with greater longitudinal connectivity but less lateral and vertical connectivity and less attenuation and retention of downstream fluxes. In other words, loss of beavers and their engineering results in substantial loss of riparian wetlands and associated declines in habitat abundance and diversity (Kay 1994), biodiversity, nutrient uptake, and storage of water, sediment, carbon, and nutrients (Naiman et al 1986, Muskopf 2007, Green and Westbrook 2009) (figure 2).

Although there is no published estimate of the quantity of beaver-created floodplain wetlands that have been lost as a result of human alterations, there are estimates of total wetland loss. The area covered by wetlands in the continental United States, including floodplain wetlands, has declined substantially since European settlement of North America. Dahl (1990) estimated that wetlands constituted roughly 9% of the land surface of the continental US at the time of European colonization. Approximately half of these wetlands have now been converted to agriculture, urban areas, and other uses (NRC 1995) and the proportion of wetland loss is much higher in some areas of the United States (Brinson and Malvarez 2002, Blann et al 2009).

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### Table 1. Physical and biogeochemical effects of beaver ecosystem engineering.

| Observed effects | Reference |
|------------------|-----------|
| Enhanced surface water storage | Hood and Bayley (2008), Green and Westbrook (2009) |
| Increased hyporheic exchange | Lautz et al (2006), Janzen and Westbrook (2011), Briggs et al (2013) |
| Enhanced downstream base flow | Nysson et al (2011), Majeroa et al (2015), Wegener et al (2017) |
| Enhanced overbank flow | Westbrook et al (2006) |
| Attenuation of small to moderate peak flows | Burns and Mcdonnell (1998), Nysson et al (2011) |
| Retention of sediment and streambed aggradation | Butler and Malanson (1994), Kramer et al (2012) |
| Retention of particulate organic matter | Naiman et al (1994), Westbrook et al (2011) |
| Enhanced denitrification | Naiman et al (1994), Corell et al (2000), Klotz (2010), Lazar et al (2015) |
| Increased floodplain soil organic carbon concentrations | Johnston (2014), Laurel and Wohl (2019) |
| Formation of multithread channel planform | John and Klein (2004) |
| Enhanced resilience to drought and wildfire | Hood and Bayley (2008), Fairfax and Small (2018), Fairfax and Whittle (2020) |
| Increased methane emissions | Wohl and Waddington (1990), Burns and Mcdonnell (1998) |
| Increased methylmercury concentrations in streams | Whitfield et al (2015), Levani et al (2015) |
Quantifying the legacy effects associated with loss of beaver engineering on a particular stream or river network is very difficult because of the other changes that typically accompanied loss of beaver populations during the 18th and 19th centuries, including upland deforestation (Marsh 1864, James 2019), floodplain drainage and deforestation (Blann et al. 2009, Wohl 2013b), removal of instream large wood (Sedell and Froggatt 1984, Montgomery et al. 2003, Wohl 2014), channelization (Shields et al. 1995), and construction of mill dams (Walters and Merritts 2008) and levees (Wohl et al. 2017). The cumulative effects of these human-induced changes overlap significantly: loss of habitat abundance and diversity (Gregory and Bisson 1997); declining biodiversity and abundance (Kwak 1988, Ricciardi and Rasmussen 1999); reduced attenuation and retention of downstream fluxes, including floods (Woltemade and Potter 1994, Lawrence et al. 2019); reduced carbon sequestration (Walters and Merritts 2008, Hanberry et al. 2015); and impaired surface and groundwater quality (Yates and Sheridan 1983, Harris and Gosselink 1990, Forshey and Stanley 2005, Schramm et al. 2009, Scott et al. 2014, Schilling et al. 2015).

In many regions, the cumulative effects of these historical land uses and modification of river corridors are so substantial that contemporary resource managers are skeptical that beavers ever inhabited portions of stream networks (A. Parola, U. of Louisville, pers. comm., Feb. 2019). Careful examination of river corridor stratigraphy, including buried seed banks and plant remains, however, can reveal the evidence of buried beaver dams (James and Lanman 2012, Kramer et al. 2012), hydric soils, and wetland plants in portions of a river network that have no indication of past beaver engineering at the surface. Place names can also suggest the historical presence of beavers: every state except Hawaii has at least one Beaver Creek, as well as other place names that record the former presence of beavers.

4. Mitigating legacy effects of loss of beavers

Recognition that beaver ecosystem engineering along a river corridor can enhance diverse ecosystem services dates to at least the late 19th century (e.g. Morgan 1868, Mills 1913). Efforts to actively reintroduce beavers to parts of their former range occurred during the 1930s, when the U.S. Soil Conservation Service used beavers to limit channel incision (Schefter 1938). Beaver reintroduction continued during the succeeding decades of the 20th century (e.g. Grasse 1951, Brayton 1984, Albert and Trimble 2000), but seems to have accelerated at the start of the 21st century (Pollock et al. 2014). Beavers have now been reintroduced to some of their former habitat throughout the continental United States and in 27 European countries (Wohl 2019).

Where lack of existing suitable habitat, food supply, or some other constraint limits the ability for beavers to survive, river management also employs simulated beaver dams. Although referred to via a variety of terms, these human-built structures are most commonly known as beaver dam analogues (BDAs). BDAs can be built to closely resemble real beaver dams, with a structural core composed of wood pieces inserted upright into the streambed and smaller branches woven through the uprights (figure 3). BDAs can also take the form of large logs piled atop one another parallel to the streambed and anchored into the banks. Some projects involve one or a small number of BDAs (Scamardo and Wohl 2020), whereas others install more than a hundred structures along stream lengths of hundreds to thousands of meters (Bouwes et al. 2016).
Figure 3. An example of a beaver dam analogue (BDA) installed along Fish Creek in Estes Park, Colorado. This structure incorporated beaver-chewed wood obtained from nearby active beaver colonies.

Typically, BDAs are installed with the intent to (a) cause local streambed aggradation that can mitigate channel incision and enhance channel-floodplain connectivity, (b) raise the riparian water table and facilitate reestablishment of native riparian vegetation, and (c) restore habitat that will eventually facilitate colonization of the site by beavers (Pollock et al. 2014, Lautz et al. 2019). In other words, BDAs are intended to reverse the effects illustrated in figure 2. Depending on the details of the site and the design and maintenance of the structures, BDAs may or may not have the desired effects.

Beavers can build more than a dozen dams along a relatively small stream in one season and the animals continually maintain their dams and shift water among different ponds in a beaver meadow. As dams enhance overbank flows or are flanked by bank erosion, beavers extend the dam, sometimes more than a hundred meters across the floodplain. BDAs, in contrast, commonly extend only across the active channel (although they are sometimes designed with the expectation that bank erosion will move the main channel beyond the BDA) and humans are seldom as fast and nimble as beavers in reacting to changes in the geomorphology of the river corridor. Projects installing tens of BDAs in sequence along a channel have been relatively rare (although they are becoming more common; Bouwes et al. 2016), whereas beavers will build numerous dams along a channel with suitable habitat. The existence of sequential dams limits the hydraulic forces exerted on most of the dams and enhances the potential for reach-scale sediment storage in the channel and overbank flows onto the floodplain.

In reviewing the use of BDAs in the western United States, Pilliod et al. (2018) noted that, in common with other stream restoration practices, implementation of BDAs has outpaced research on the efficiency and best practices of this restoration method. Very few studies of quantitative monitoring following BDA installation have been published (table 2) and, in their inventory of 97 beaver-related restoration projects, Pilliod et al. (2018) found that few projects included post-implementation monitoring. The intention of installing BDAs is that the structures will create the same effects as real beaver dams (e.g. Pollock et al. 2014), but such effects cannot be automatically assumed. In particular, beavers maintain their own dams or build new dams, but the level of human intervention necessary to maintain BDAs over many decades is largely unknown and will vary greatly between sites.

BDAs can also be used as the central focus or one component of Stage 0 restoration. Stage 0 restoration is named in reference to a stage of the Cluer and Thorne (2014) channel evolution model. In this model, a Stage 0 channel has an anastomosing planform and the active channels are highly connected to the adjacent floodplain. In addition to BDAs, Stage 0 restoration can involve removing sediment from the floodplain and adding abundant large wood to the channel (e.g. Powers et al. 2019). Regardless of the methods used, some forms of Stage 0 restoration essentially seek to recreate the conditions present in a beaver meadow.

Where conditions permit, reintroduction of beavers is likely to be more successful than BDAs in creating desired changes in river corridors. Guidelines for beaver reintroduction (Pollock et al. 2017) and software that can be used to evaluate habitat suitability (Macfarlane et al. 2017, Dittbrenner et al. 2018, Kornse and Wohl 2020) can assist with these efforts. Extensive modification of river corridors throughout the temperate latitudes limits the remaining areas...
suitable for beaver reintroduction, however, and we do not yet have the empirical data or numerical modeling capability to quantitatively predict the extent of beaver reoccupation necessary to create desired levels of change in river ecosystem services (Bernhardt and Palmer 2011). Under the circumstances, careful measurements and monitoring of both beaver reintroduction and BDA sites (Pilliod et al 2018, Lautz et al 2019, Scamardo and Wohl 2020) can help to improve our predictive ability regarding the effects of these management practices on river corridors. Such monitoring is likely to reveal the types of feedbacks and complex interactions that have limited aspen and willow recovery in elk grasslands in Yellowstone National Park (Kauffman et al 2010). Reintroduction of gray wolves (Canis lupus) to the park has reduced elk (Cervus canadensis) riparian herbivory and allowed willow communities and beavers to return to some river corridors, but other factors such as limited water availability have hindered willow recovery in some sites (e.g. Tercek et al 2010). The relatively well-studied example of this national park indicates that response of river corridor ecosystems to reduction of stressors limiting beaver presence may not follow a simple, rapid, or easily predictable trajectory.

5. Questions of scale and context

Given the nearly ubiquitous reduction in functional floodplain extent, loss of floodplain wetlands, and severe reductions in beaver populations, important questions relevant to mitigating legacy effects associated with loss of beavers include how to (a) estimate the scale of effects that might be associated with beaver reintroduction or mimicry using BDAs, (b) prioritize sites for beaver-related restoration within a watershed, and (c) use existing case studies, which are limited in number and place-based, to infer potential regional differences in the response to beaver reintroduction or mimicry.

With respect to scale, studies of a single beaver dam-pond pair on a channel indicate that the associated sediment storage (Butler and Malanson 1995), peak flow attenuation (Burns and Mcdonnell 1998), and nutrient uptake can be impressive but limited (Correll et al 2000), as might be expected. Either a series of dams and ponds along a single channel, or a beaver-meadow complex of multiple ponds and anastomosing channels where the valley bottom is sufficiently wide, create greater attenuation of downstream fluxes (Jin et al 2009, Kramer et al 2012, Puttock et al 2018) and greater habitat abundance and diversity (Rosell et al 2005). Lazar et al (2015) found that beaver pond denitrification rates depended on pond age and the presence of emergent macrophyte vegetation versus open water, implying that a beaver-meadow complex with ponds of varying age would maintain higher denitrification rates through time than a single pond in which denitrification rate declines through time.

As with other forms of floodplain attenuation of peak flows (Woltemade and Potter 1994), small to moderate floods may be more effectively attenuated by beaver dams and ponds (Neumayer et al 2011, Nyssen et al 2011), whereas exceptional floods remain relatively unaffected. Analogously, even a beaver-meadow complex may not be able to compensate for substantial, catchment-scale increases in nutrient flux (Bernhardt and Palmer 2011).

The manner in which the beneficial effects of beaver engineering increase in relation to the spatial extent and diversity of this engineering is not well quantified, however. Consequently, we do not know whether increasing the spatial extent of beaver engineering creates linear or nonlinear responses.

### Table 2. Effects observed following installation of beaver dam analogs (BDAs).

| Location                      | Observed effects                                                                 | Reference                  |
|-------------------------------|----------------------------------------------------------------------------------|----------------------------|
| Bridge Creek, OR, USA; dr A   | Significant increases in density, survival, & production of juvenile steelhead   | Bouwes et al (2016)        |
| 710 km²; 121 BDAs installed   | (Oncorhynchus mykiss); increase in quantity & complexity of steelhead habitat    |                            |
| 2009–2012                     |                                                                                   |                            |
| Bridge Creek, OR, USA         | Moderation of diel water temperature cycles during periods of low surface flow by | Weber et al (2017)         |
|                               | increasing water storage & enhancing surface-subsurface water exchange            |                            |
| South Fork, OR, USA; dr A     | Increased groundwater levels at and upstream of BDAs & laterally into floodplain; | Orr et al (2020)           |
| 2500 km²; monitoring 1–2 years| increased willow growth; sediment aggradation at structures                        |                            |
| after 5 BDAs installed        |                                                                                   |                            |
| Fish Creek, CO, USA; dr A     | 1 years after installation, sediment storage increased, but no effect on          | Scamardo and Wohl (2020)   |
| 4 km²; 8 BDAs along 0.3 km in  | groundwater levels                                                                |                            |
| 2017                          |                                                                                   |                            |
| Campbell Creek, CO, USA; dr A |                                                                                   |                            |
| 8 km²; 17 BDAs along 0.7 km in|                                                                                   |                            |
| 2017                          |                                                                                   |                            |

dr A indicates drainage area.
With respect to site prioritization, choosing portions of a watershed with evidence of former beaver occupation is likely to optimize the survival of reintroduced beavers and enhance the effects of BDAs. The remnants of old dams commonly appear as vegetated berms and upstream ponds filled with distinctive vegetation communities relative to adjacent areas of the valley bottom. Other indicators of past beaver damming include tighter-than-average meander bends where an old beaver-dam berm deflects a channel and beaver-gnawed stumps (Kornse and Wohl 2020). Abundant evidence of past beaver occupation can suggest that site conditions were at one time conducive to beaver, although a drop in floodplain water table and/or reduction in woody riparian vegetation such as willows (Salix spp.) might now limit beaver survival. Formerly occupied sites may retain a seed bank or root stock of wetland and riparian species that can enhance vegetation recovery following beaver reintroduction or construction of BDAs (A. Parola, U. of Louisville, pers. comm., Feb. 2019, D. Merritts, Franklin and Marshall College, pers. comm., Apr. 2017).

Choosing areas formerly occupied by beavers may also minimize potential negative effects of beaver-pond inundation. Among these negative effects, methylmercury concentrations in streams increase following pioneer inundation but exhibit negligible change when previously inundated surfaces are re-submerged (Levanoni et al. 2015).

Site prioritization can also focus on the desired scale of beaver ecosystem engineering. Laterally confined headwater channels can support single or sequential dam-pond pairs, but development of a beaver-meadow complex requires a valley bottom several times wider than the active channel. Alternatively, a wide floodplain associated with a moderate to large river can support extensive beaver engineering. In both of these scenarios, the presence of a wide valley bottom will attenuate downstream fluxes if the channel and floodplain are hydrologically connected, but attenuation is likely to be enhanced by the spatial heterogeneity created by beaver modifications (Appling et al. 2014, Helton et al. 2014, Laurel and Wohl 2019). At present, however, we do not have sufficient data to evaluate the beneficial effects of beaver activities on small mainstream channels versus the floodplains of larger rivers.

With respect to the applicability of case studies to diverse geographic regions, the limited information available supports three preliminary inferences. The first is that local, site-specific details can strongly influence the effects of beaver activities or BDA installation. In drylands, for example, observations of increased aquifer recharge during overbank flows (e.g. Cartwright et al. 2019) suggest that the increased surface water storage associated with beaver dams and ponds is likely to form an important source of floodplain aquifer recharge, although this increased recharge may support greater transpiration losses from riparian vegetation (e.g. Fairfax and Small 2018). In contrast, beaver ponds may primarily increase evaporation in river corridors in which an impermeable layer limits infiltration (e.g. Woo and Waddington 1990). Beaver-created inundation can significantly increase stream methylmercury concentrations, but only for areas that were not previously inundated (Levanoni et al. 2015). BDAs can raise floodplain water tables (Orr et al. 2020), but may have no effect on water table in losing reaches or where local conditions limit infiltration from the channel (Scamardo and Wohl 2020). Individual studies have highlighted the increase in gaseous emission of carbon from beaver ponds (e.g. Whitfield et al. 2015) and the increase in soil organic carbon concentration in beaver meadows (e.g. Wohl 2013a, Johnston 2014, Laurel and Wohl 2019), but we do not know the relative importance of each of these effects in diverse settings.

The second inference from published case studies is that we need more comprehensive quantification of the effects of beaver modifications on river-corridor budgets for materials such as water and carbon. Beaver modifications can increase water storage in a reach of river corridor via ponding and hyporheic and groundwater recharge, but they can decrease water storage via increased evaporation, transpiration, and downwelling in a losing reach. Analogously, beaver modifications can increase carbon loss via methane emissions (Whitfield et al. 2015) but can also increase carbon sequestration via greater floodplain primary productivity (Silverman et al. 2019), retention of dissolved and particulate organic matter (Naiman et al. 1994), and greater concentration of organic carbon in saturated, reducing floodplain soils (Wohl et al. 2012, Wohl 2013a, Johnston 2014, Laurel and Wohl 2019). Investigators have quantified the effects of beavers on one or more components of a water or carbon budget at the reach scale, but not their effects on the entire budget.

A third inference from published case studies is that we cannot yet infer scaling effects. One beaver dam-pond pair cannot effectively attenuate a large peak flow. But can a beaver-meadow complex with multiple dams, anastomosing channel planform, and dense riparian vegetation effectively attenuate a peak flow that greatly exceeds the annual average? Or, can one beaver meadow or several beaver meadows significantly increase watershed-scale denitrification? The ability to answer such questions could significantly improve the effectiveness of ongoing efforts to reintroduce beavers and to mimic beaver modifications.

Beaver-related restoration has been described as cheap and cheerful (Camp 2015) because it can be less expensive than other commonly used forms of river restoration. Better constraining the effectiveness of beaver-related restoration in diverse settings, however, will help to avoid unrealistic expectations that
beavers provide a panacea for all of the human-induced changes in river corridors.

6. Conclusions

Beavers once maintained diverse, abundant, and highly retentive riverine wetlands across large portions of North America and Eurasia. River corridors engineered by beavers host high biodiversity, nutrient uptake, and attenuation of downstream fluxes of water and sediment. Along with other modifications of uplands and river corridors, the massive loss of beaver populations in the Northern Hemisphere has substantially reduced the ability of river corridors to provide ecosystem services that sustain human and biotic communities. As recognition grows of the beneficial effects of beaver ecosystem engineering, there are increasing efforts to reintroduce beavers to their former habitat and to mimic the effects of beavers using approaches such as BDAs and Stage 0 restoration. Fundamental questions remain, however, regarding the effectiveness of these methods in different settings and, in particular, the extent of restoration needed to significantly restore desirable processes, given the nearly complete transformation by humans of uplands and river corridors throughout the temperate latitudes.

Beaver reintroduction and mimicry can have contrasting effects in different portions of a watershed, different valley geometries, and different geographic regions and beavers alone cannot reverse the negative effects of centuries of human-induced modification of catchments and river corridors (e.g. Mitsch et al 2005, Marshall et al 2013). Beaver reintroduction and mimicry can be an important part of a multi-pronged watershed restoration effort, however, and the science of beaver-related river restoration can now be most effectively advanced by careful, quantitative studies of the magnitude and duration of changes in river corridors following beaver reintroduction and mimicry.

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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