ANNUAL REVIEWS

Annual Review of Ecology, Evolution, and Systematics

The Ecology and Evolution of Beavers: Ecosystem Engineers That Ameliorate Climate Change

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Annu. Rev. Ecol. Evol. Syst. 2024. 55:323–45

First published as a Review in Advance on August 9, 2024

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-102722-122317

Keywords

beaver, climate change, ecosystem engineer, resilience, wetlands, *Castor*

Abstract

Beavers, *Castor canadensis* in North America and *Castor fiber* in Eurasia, are widely referred to as nature's engineers due to their ability to rapidly transform diverse landscapes into dynamic wetland ecosystems. Few other organisms exhibit the same level of control over local geomorphic, hydrologic, and ecological conditions. Though freshwater ecosystems are particularly vulnerable to changing climate, beavers and their wetland homes have persisted throughout the Northern Hemisphere during numerous prior periods of climatic change. Some research suggests that the need to create stable, climate-buffered habitats at high latitudes during the Miocene directly led to the evolution of dam construction. As we follow an unprecedented trajectory of anthropogenic warming, we have the unique opportunity to describe how beaver ecosystem engineering ameliorates climate change today. Here, we review how beavers create and maintain local hydroclimatic stability and influence larger-scale biophysical ecosystem processes in the context of past, present, and future climate change.

1. INTRODUCTION

The past century of rapid climate change has significantly disrupted physical and ecological processes worldwide, with little evidence of such change stopping or slowing in the near future (IPCC 2023). Drought and wildfire are increasingly intense and frequent, infrastructure is strained by shifting precipitation regimes, and multiple species go extinct or are forced to shift their range each year. Despite this alarming trend, at least one creature appears capable of engineering its way out of peril: the beaver.

Beavers are powerful ecosystem engineers capable of transforming a myriad of different landscape types across biomes into their preferred wetland habitat and then maintaining it (Brazier et al. 2021). The construction and maintenance of wetlands is particularly valuable under a changing climate. Wetlands are widely recognized as critical natural infrastructure due to their enhanced nutrient processing capabilities; high levels of biodiversity; and ability to modulate streamflow, store carbon and freshwater, and reduce erosion (Erwin 2008). However, the majority of naturally occurring wetlands have been lost or impaired in the Northern Hemisphere since 1700, with the loss ranging from 35% to >90%, depending on location (Krueper 1993). Beavers are unique in their ability to both create and maintain wetland ecosystems, including during prior periods of intense climate change in the Holocene and Pleistocene (Dittbrenner et al. 2018, Persico & Meyer 2009, Rybczynski 2007). Today, scientists have had the opportunity to observe and quantify the influence that beavers have on biophysical processes in the environment and how that affects their ability to immediately insulate themselves from the stressors of climate change as well as ameliorate its effects on much larger spatiotemporal scales.

There are two extant species of beaver today, both natively occurring in the Northern Hemisphere: North American beaver (*Castor canadensis*) and Eurasian beaver (*Castor fiber*) (Larsen et al. 2021). North American beaver and Eurasian beaver have differing numbers of chromosomes (40 and 48, respectively) (Lavrov & Orlov 1973) and minor morphological differences but are quite similar in their activities (Larsen et al. 2021). Given the considerable overlap in their evolutionary history and the ecology, behaviors, and mechanisms through which they modify environmental processes, both species are discussed jointly as beavers in this review, unless stated otherwise.

2. EVOLUTION OF BEAVER ECOSYSTEM ENGINEERING

2.1. Fundamentals of Ecosystem Engineering

Ecosystem engineers, broadly defined, are organisms that can significantly alter the environment to better suit their own needs. While there are ongoing discussions about what constitutes ecosystem engineering and whether it is redundant with the related concept of keystone species, consensus has emerged around the concept of physical ecosystem engineering. Physical ecosystem engineering was recently defined as "organismally caused, structurally mediated changes in the distribution, abundance, and composition of energy and materials in the abiotic environment arising independent or irrespective of changes due to assimilation and dissimilation," (Jones & Gutiérrez 2007, p. 6) or more simply, when living organisms control abiotic resources and processes independently of larger-scale environmental forcings and cycles. Ecosystem engineers are autogenic or allogenic (Jones et al. 1994). Autogenic ecosystem engineers alter physical processes via their own physical structure, e.g., oyster reefs disrupting wave dynamics and altering sediment transport mechanics (Grabowski & Peterson 2007). Allogenic ecosystem engineers alter physical processes through their behaviors, e.g., prairie dogs digging extensive burrow networks that create conduits for water and heat throughout the subsurface (Dickman 1999).

Allogenic ecosystem engineering by animals is often accomplished through one or more of the following general behaviors: clast transport, mound building, nest building, vegetation removal, burrowing, digging, food caching, trampling, wallowing, and geophagy (Butler 1995). Many ecosystem engineering behaviors are undertaken by animals for purposes unrelated to abiotic process alteration, e.g., earthworms moving through soil are simply trying to navigate the landscape (Singh et al. 2016). There is no intentionality on the worm's part with regards to altering soil porosity and overlying forest litter composition, and the consequences of that bioturbation may or may not ultimately be beneficial to the worm. Some ecosystem engineering behaviors are intended to modify a physical process, but that intentionality does not extend to the full suite of processes that are influenced. For example, a salmon creating a redd excavates small depressions in a streambed with her body and tail, then fills it with coarse-grained gravels to alter the streamflow to ensure consistent, highly oxygenated water flows over her eggs without being powerful enough to scour them away. In the short term and on small spatial scales, the salmon has engineered the abiotic environment specifically to better suit her evolutionary needs. While individually small, these small bedform changes in aggregate across populations of salmon result in long-term shifts in stream sediment dynamics and morphology that have secondary effects throughout the greater ecosystem that are disconnected from the salmon (Schindler et al. 2003). Beavers are allogenic ecosystem engineers that engage in multiple ecosystem engineering behaviors that, in combination, alter numerous abiotic processes and initiate or amplify several biophysical feedback loops (Rosell et al. 2005). Unlike the earthworm, most of the beaver's ecosystem engineering behaviors are intentional forcings on abiotic processes—beavers' evolutionary success as a species is highly dependent on its ability to control physical environments (Rybczynski 2007).

2.2. Evolution of Ecosystem Engineering in Beavers

Modern beavers are often referred to as nature's engineers due to their ecosystem engineering prowess. Castoridae, the family that modern beavers belong to, originated in the Northern Hemisphere during the Eocene (56–33.9 Mya) and has contained numerous varieties of beaver ecosystem engineers over the millennia (Rybczynski 2007) (**Figure 1**). However, not all extinct species of beaver could modify their physical environments as profoundly as the two modern species of beaver can. While modern beavers dig, burrow, cut trees, and build dams—all of which radically change the physical environment—most prior species of extinct beavers engaged in fewer forms of ecosystem engineering, primarily digging and burrowing. For example, *Paleocastor*, a small extinct beaver in North America, famously dug large spiral-shaped dens, colloquially referred to as devil's corkscrews, downward into the earth (Martin & Bennett 1977). As with many extinct species, the abundance and geographic distribution of *Paleocastor* is poorly understood, making it difficult to estimate the scale of influence their ecosystem engineering had on larger-scale environmental processes and conditions. Given the similarities to ecosystem engineering done by modern prairie dogs and gophers, it is reasonable to assume that *Paleocastor*'s digging played a measurable role in changing soil porosity as well as subsurface hydrologic connectivity and heat exchange. However, in the absence of other ecosystem engineering behaviors, it is unlikely that these proto-beavers were as disproportionately influential in the landscape as modern beavers are.

Tree cutting likely evolved 25 Mya in the Arctic, based on a combination of fossil beaver-cut wood and morphological and behavioral evidence associated with both *Dipoides* and *Castor* (Rybczynski 2007). Dam building may have evolved contemporaneously in a common ancestor shared by modern beavers, *Castor*, and other likely tree-cutting beaver taxa (*Dipoides*, *Steneofiber*, *Castoroides*), or it may have evolved only approximately 7.5 Mya in *Castor* when *C. fiber* and *C. canadensis*—both known dam builders—diverged (Plint et al. 2020). Of the other known tree-cutting beavers, *Dipoides* was best suited to also potentially build dams; it was two thirds the size of the modern beaver, large enough to move logs around the landscape, and had woody material in

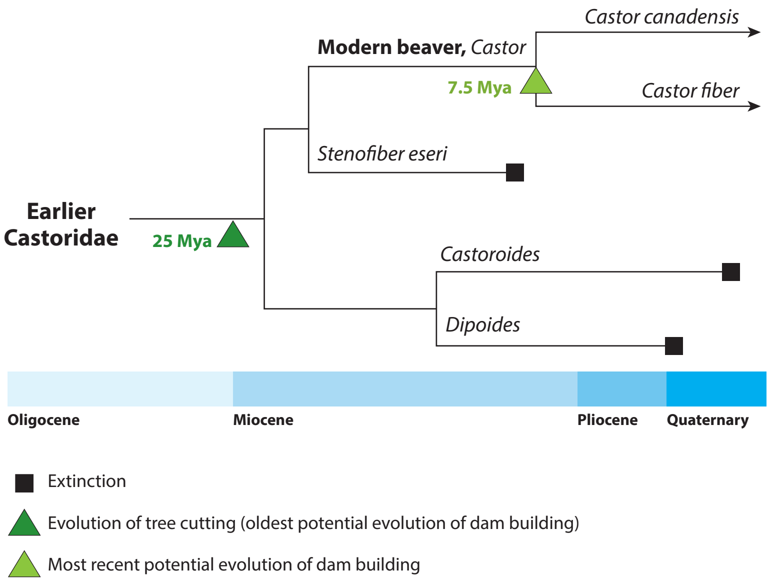

Figure 1

A simplified phylogenic tree for known tree-cutting beavers in Castoridae. Black boxes mark extinctions, the dark-green triangle marks the evolution of tree cutting, and the light-green triangle marks the most recent possible evolution of dam building. Note that time is not linearly scaled in this simplified tree, with expansion of the Pliocene and Quaternary to show detail. Figure adapted from Plint et al. (2020, figure 8).

its diet (Plint et al. 2020). *Stenofiber eseri* was much smaller bodied (approximately 1 kg) and would have struggled to move large woody material. Though *Castoroides* was very large (100–150 kg or more) and capable of moving heavy objects, analyses of its diet indicate that they primarily consumed herbaceous material—not woody material like modern *Castor* (Plint et al. 2020, Rybczynski 2007). In contrast, multiple Indigenous peoples from the Great Lakes region in what is now the United States and Canada lived alongside *Castoroides* in the late Pleistocene and early Holocene and have stories of it building dams (Beck 1972). Further research is needed to confidently determine precisely when dam building behavior first evolved and which fossil beavers engaged in it on a meaningful scale.

The Early Miocene is characterized by an onset of hard winters after a period of relative warmth in which the Arctic was forested (Matthews Jr. & Ovenden 1990, Whitlock & Dawson 1990). This shift from mild to harsh winter conditions drove many Arctic mammals to shift their range southward, otherwise adapt, or go extinct. Fossil evidence suggests that early castorids did not leave higher latitudes when winters became colder and food resources became more scarce (Rybczynski 2007). Instead, this climate shift prompted the evolution of tree cutting and food caching, and potentially, dam construction behaviors. Tree cutting allowed early beavers to harvest material for food during warm summers and caching allowed them to save it for access during hard winters.

Dam construction by modern beavers creates ponds and increases the depth of water. Deeper water is important in locations with prolonged winter ice cover on water bodies, as it provides an under-ice, accessible storage location for their food (Brazier et al. 2021, Busher 1996). It logically follows that dam construction would have been advantageous to early castorids at high latitudes as well, but it is unknown whether it was a requirement for their survival. Isotopic analysis of the diet of three northern-dwelling beaver species—*Castor* (modern beaver) and two extinct beavers from a separate evolutionary branch of Castoridae, *Dipoides* and *Castoroides*—to assess behavioral overlap between the various taxa determined that *Dipoides* had a similar diet to modern *Castor*, composed of both herbaceous aquatic plants and woody materials, while the Pleistocene megabeaver *Castoroides* subsisted almost exclusively on herbaceous aquatic plants (Plint et al. 2020). So, while both *Castor* and *Dipoides* were clearly taking advantage of an earlier behavioral evolution and cutting trees for food, paleoecologists posit that it is unlikely for dam building to have evolved twice independently on two separate branches of Castoridae. Given our current understanding of Castoridae phylogeny, this implies that *Castor* were dam builders, but *Dipoides* were not. It is worth noting that relatively high uncertainty remains around the position of the megabeavers (*Procastoroides*, *Castoroides*, and *Trogontherium*) within the phylogenetic tree (Rybczynski 2007), which is of consequence when determining the temporal and species origins of dam building. Regardless, the two species of modern beaver, *C. canadensis* and *C. fiber*, are both dam builders that diverged 7.5 Mya, so the evolution of dam building must be at least as old. Subsequent discussion of beavers in this review is restricted to the modern dam-building beavers, *C. canadensis* and *C. fiber*.

3. MODERN BEAVER RANGE AND ABUNDANCE

3.1. Beaver Social Structure

Beavers form monogamous pairs and live in family units, called colonies (Busher 2007). Every member of a beaver colony helps to maintain the wetland habitat, and the scale of the work done each day is beyond what an individual beaver is capable of, so being part of a colony is necessary for long-term beaver survival (Johnston 2017). A typical beaver colony is composed of the breeding adult pair, several juvenile offspring between 1 and 3 years old, and a litter of at least one young-of-the-year called a kit (Baker & Hill 2003), though other family arrangements including the beaver equivalent of aunts, uncles, cousins, and grandparents have been observed in places where family fragmentation by natural predation or human trapping is high (McTaggart & Nelson 2003). Beavers are generally territorial with other beavers from outside of their family group, and when living in a river corridor, they try to maintain an average territory size of 1–2 km of stream length (Graf et al. 2016, Mayer et al. 2017), though much higher and lower colony densities have been observed. Beavers that dwell in lakes do not have as clearly defined linear territories and instead are distributed spatially along the length of the shoreline. Previous observations identified territory sizes of lake-dwelling beavers to be ∼0.2 colonies per kilometer of shoreline; however, just as with stream-dwelling beavers, there is likely considerable variability depending on resource availability (Bashinskiy 2020). Beaver territories abut one another in systems that are at or near their beaver-holding capacity, resulting in many continuous kilometers of beaver-engineered wetlands (Naiman et al. 1988).

3.2. Beaver Habitat Selection

Beavers are considered habitat generalists, though that stems more from their ability to convert many different landscape types into their preferred wetland habitat rather than an innate ability to thrive in a broad range of environmental settings. Even so, beavers have certain physical and ecological requirements that must be met either through the base environmental conditions or through their ability to engineer them. Beavers are a semiaquatic freshwater rodent and as such need access to fresh or brackish water and terrestrial habitat (Brazier et al. 2021). Beavers routinely occupy lakes, wetlands, streams, deltas, estuaries, and rivers and ideally have a minimum water depth of 1 m near their lodge or den (Larsen et al. 2021). Dams are often built specifically to increase water depth but are not always necessary in larger rivers or existing water bodies like lakes or open water wetlands (Bashinskiy 2020). They exhibit a strong preference for living in perennial water sources but are known to tolerate ephemeral streams, provided they can store enough water in their ponds to maintain sufficient water depth year round (Gibson & Olden 2014, Norman et al. 2022). When living in river corridors, low gradients (less than 5°) and broad valley bottoms are preferred, but beavers have been observed damming high gradient streams (up to 25°) in narrow, steep-walled valleys (Macfarlane et al. 2017). Suitable riparian vegetation must be abundant and regenerate quickly enough for them to meet their caloric needs year after year (Naiman et al. 1986, Baker & Hill 2003). If it is reduced to a point where that is no longer the case, then a beaver colony moves as a unit to find new habitat (Polvi & Wohl 2012, Ronnquist & Westbrook 2021, Westbrook et al. 2011), though beaver dams can persist for over 100 years relatively unchanged (Johnston 2015). Beavers typically prefer to live immediately adjacent to their preferred food resources—deciduous trees such as aspen, willow, and birch, as well as forbs and grasses (Haarberg & Rosell 2006). Their foraging behavior is consistent with central place foraging theory (Jenkins 1980), but they are known to excavate and travel significant distances along their canal networks or the stream network to access food if necessary (Abbott et al. 2012, Grudzinski et al. 2020), as is the case for beavers that live above the tree line in mountain regions. Digging is an important part of a beaver's ability to manipulate the physical environment, so it follows that malleable soils that hold their shape after excavation are preferred over sandy or cobbly ones. Yet, when necessary, beavers live in gravel pits and sandy estuaries (Bylak et al. 2024, Jung & Staniforth 2010).

Though it makes creating accurate habitat suitability models for beaver challenging, the fact that beavers routinely adapt to and survive in nonideal conditions speaks to the extent of their ecosystem engineering abilities. Furthermore, beavers are a highly mobile species that can respond quickly to shifts in climate and the geography of resources (Tape et al. 2018), with individual beavers capable of traveling 80 km or more during a single dispersal event in search of more suitable habitat (Halley et al. 2012). Sedimentological pollen and macrofossil analyses show that during the Pleistocene and Holocene, beavers arrived in landscapes shortly after deglaciation or ice sheet retreat and remained in the ecosystem relatively continuously, provided climate conditions supported the growth of one or more of their preferred food species (Boudreau et al. 2005, Garrison 1967). Looking forward, we can expect the same behavior; as changing climate leads to new suitable habitat in previously frozen landscapes (thermokarst), beavers will rapidly colonize it (Tape et al. 2022). And as formerly suitable habitat aridifies and the abundance of preferred food species is reduced, beaver populations are likely to decrease in those places (Stoll & Westbrook 2020).

3.3. Distribution of Beavers in the Recent Past

Climate conditions and the distribution of freshwater and ecological resources determine where beavers can live in the Northern Hemisphere, but the most impactful influence on actual beaver population counts and distribution in recent history has been from humans. Beaver fur and castoreum, an oily substance secreted by the castor sacs on a beaver, were prized in Europe and Asia, which drove hunting and trapping of *C. fiber* to the point of near extinction at various points over the last 2,000 years (Ott 2003, Wien 1990). European colonists arriving in North America in the 1500s quickly learned that beavers were common, though it was *C. canadensis* rather than *C. fiber*, and by the 1600s, the European–American fur trade was well developed (Innis & Ray 1999). European demand for beaver fur drove westward settlement in North America and is inextricably intertwined with the forced relocation (to reserves) and genocide of Indigenous peoples (Hood 2011). By the mid-1800s, beaver populations had crashed from a peak of 100–400 million beavers prior to the fur trade to approximately 100,000 in North America in a restricted range (Naiman et al. 1988). While the peak beaver population in Eurasia prior to the fur trade is unknown, it is estimated that <2,000 beavers in fragmented regions remained by the mid-1800s (Halley et al. 2021). Through a combination of luck, reasonably high reproductive rates, conservation efforts, and changing fashion trends, beaver populations began rebounding in the 1900s, and reestablishment throughout their historic range in Eurasia and North America is ongoing (Baker & Hill 2003).

The tendency of beavers to live in river corridors, combined with the rapid nature of their extirpation throughout the Northern Hemisphere, has made reconstructing their historic range difficult. Though fossil preservation is fairly common on river floodplains, these environments are also some of the most heavily disturbed by agriculture and human infrastructure development, which can make finding intact, in situ beaver fossils difficult, particularly in places where beavers were present but not particularly abundant. Fossil, historical, and observational evidence collected to date determined that beavers were historically present in the following modern countries: Canada, Mexico, and the United States in North America (Larsen et al. 2021) and Austria, Belarus, Belgium, Bosnia, Bulgaria, China, Croatia, Czech Republic, Denmark, England, Estonia, Finland, France, Germany, Hungary, Italy, Iran, Iraq, Kazakhstan, Latvia, Liechtenstein, Lithuania, Luxembourg, Moldova, Mongolia, Netherlands, Norway, Poland, Portugal, Romania, Russia, Scotland, Serbia, Slovenia, Slovakia, Spain, Sweden, Switzerland, Syria, Türkiye, Ukraine, and Wales in Eurasia (Halley et al. 2021). Understanding their historic northern range is particularly salient as beavers rapidly recolonize the Arctic. Sedimentological and fossil wood evidence from Alaska, Yukon, and Northwest Territories indicates that beavers were present in much of the Arctic 10,000–6,000 years ago during a warm period in the early Holocene (McCulloch & Hopkins 1966, Robinson et al. 2007), but whether they were present in the Arctic more recently is currently unknown.

3.4. Distribution of Beavers Today

At present, beavers live in Mexico, the United States, and Canada in North America. The southernmost range of beavers in North America extends to 25° north (coinciding with Monterrey, Mexico), and the northernmost range extends to approximately 70° north (into the Arctic circle). The current population of beavers in North America is estimated to be between 10 and 30 million individuals and is widespread across the continent (Wohl 2021); however, no large-scale beaver monitoring efforts exist, so a high degree of uncertainty remains for both absolute population count and precise geographic distribution (Whitfield et al. 2015). Beavers at their southernmost range in Mexico appear limited by access to both perennial water resources and suitable food species, while beavers at their northernmost range in Canada and Alaska are limited primarily by access to suitable food species. Beavers' presence in the Arctic today is associated with widespread shrubification and thermokarst (landforms emerging after permafrost thaw) associated with anthropogenic global warming (Tape et al. 2018). There is no published research on the southern extent of beavers during prior cold periods or glacial maxima, so the true southern limit of the species is unknown.

The range of beavers in Europe and Asia today is similar latitudinally to that in North America, though it is more substantially influenced by conservation, rewilding, and wildlife management decisions than the beaver distribution in North America. The population of beavers in Eurasia is estimated to be approximately 1.5 million individuals today (Halley et al. 2012, 2021). Strategic reintroductions have been conducted many times over the last century—sometimes for fur resources and sometimes for ecological restoration (Andersen et al. 2023, Auster et al. 2020)—leading to their reestablishment in much of their known historic range, with the exception of Portugal, the southern Balkans, and the Tigris–Euphrates basin. As in North America, beavers were historically present in the Arctic, but the true southern limit of the species is understudied and unknown.

4. MODERN BEAVER ECOSYSTEM ENGINEERING

Modern beavers are perhaps the most powerful present-day ecosystem engineers in terms of their ability to control the environment at spatial and temporal scales well beyond the scale of individual organisms (Brazier et al. 2021). They are accurately described as a disturbance regime (Westbrook 2021), similar to wildfire (Fairfax et al. 2024). It should be noted, however, that just as wildfire is a natural and necessary part of the ecosystems in which it occurs, the beaver disturbance regime is also a natural and necessary part of the ecosystems in which they evolved. Centuries of beaver suppression via trapping led to novel geomorphic, hydrologic, and ecological conditions that are distinct from those present for thousands of years prior to beaver extirpation (Scamardo et al. 2022; Wohl 2011, 2021). As beavers return to their historic habitats and expand their range northward to freshly available habitat, the resulting landscape modifications are likely to be pronounced and notably different from what we have become accustomed to over the last couple of centuries.

Beaver ecosystem engineering is achieved through three main behaviors: tree cutting or foraging, canal digging or excavation, and dam building (**Figure 2**). The three domains of beaver ecosystem engineering—digging, cutting, and building—have individually measurable influences on the abiotic conditions and processes in the beaver's local environment (Rosell et al. 2005). Yet beavers do not engage in these behaviors individually. The interplay between these forms of ecosystem engineering leads to multiple self-reinforcing positive feedback loops that strengthen the beaver's ability to create wetlands buffered locally against the stressors of climate change (Dittbrenner et al. 2018, Pollock et al. 2014). Owing to the full suite of beaver ecosystem engineering behaviors, beaver wetlands are ecologically, hydrologically, and geomorphically unique and complex wetland types capable of modifying numerous biophysical processes (Larsen et al. 2021). And while individual beaver colonies can create locally climate-resistant landscapes through their ecosystem engineering activities, populations of beavers are capable of ameliorating climate

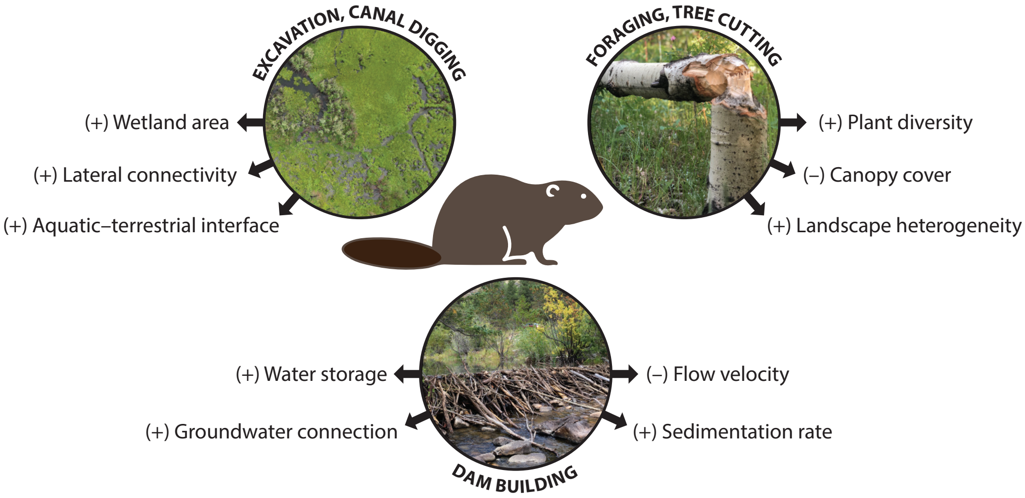

Figure 2

Conceptual diagram of beavers' three main ecosystem engineering behaviors: excavation, tree cutting, and dam building, as well as the resulting increase (+) or decrease (−) in key abiotic and biotic processes for wetland development and climate resilience.

change on much larger spatiotemporal scales that affect a multitude of other species, including humans (Baldwin 2015, 2017; Dittbrenner et al. 2018; Jordan & Fairfax 2022).

4.1. Digging and Excavation

Beavers engage in multiple forms of digging and excavation behavior. They dig burrows into the banks of rivers and lakes, excavate fine sediments from the bottom of their ponds (Larsen et al. 2021), and dig canals radiating outward from their primary aquatic habitat (lake, pond, or river) across the adjacent floodplain, valley bottom, or landscape (Grudzinski et al. 2020). Beaver bank dens can extend 3 meters or more laterally into the streambank or lakeshore, functioning as a conduit for heat exchange and potentially increasing erosion rates, similar to muskrat and otter burrows (Meentemeyer et al. 1998). Excavation of fine sediments from the pond bottom is a form of bioturbation that keeps the aquatic–terrestrial interface well mixed and with higher porosity than is found in most other wetland types (Briggs et al. 2013, Janzen & Westbrook 2011). This increases the rate at which water can flow from the surface into the subsurface hydrologic system and thus is not only a modification of sediment dynamics but also an important control on biogeochemical processing, carbon storage, and nutrient cycling within the beaver pond (Wang et al. 2018). The excavated fine sediments are typically used either as cement in their lodge and dam construction (Larsen et al. 2021, Rosell et al. 2005) or as the base of scent mounts along the riverbank or lakeshore that mark the beaver's territory (Rosell et al. 1998). In addition, the canals that beavers dig are the primary means by which beavers safely navigate, forage, and transport trees across the terrestrial landscape that surrounds their ponds. These canals are typically narrow (<1 m wide) but vary in depth (<1 m to 2 m) and can meander many meters (tens to hundreds of meters) across the landscape, sometimes connecting upstream and downstream river environments and likely functioning hydrologically and geomorphically like a small river anabranch (Grudzinski et al. 2020). The canals that beavers excavate greatly increase the area of the terrestrial–aquatic interface, enhance lateral aquatic connectivity and sometimes longitudinal aquatic connectivity in river corridors, and greatly expand the beaver's area of influence and ultimate wetland habitat creation (Abbott et al. 2012, Anderson et al. 2015, Grudzinski et al. 2020).

4.2. Tree Cutting

Beavers cut trees for food and building material (Plint et al. 2020, Westbrook & England 2022). A beaver's diet is composed primarily of herbaceous material (forbs, grasses, weeds, etc.) and cambium—the sugary layer between the outer bark and inner wood of hardwood trees (Busher 1996, Jenkins 1980). Many of the trees that coevolved with beaver over the millennia have developed defense mechanisms to prevent overexploitation and allow for rapid regeneration post cutting. Willows, for example, are able to clone from cuttings and put out new roots even in challenging environments (Jones et al. 2009, Radtke et al. 2012). Then, when beavers cut willow and use the branches in the construction of their dams and lodges, those cuttings can asexually produce new willow growth directly on top of the beaver's structures. This both reinforces the beaver's infrastructure and acts as a way for willow to reproduce across the landscape. Cottonwoods, along with other riparian hardwoods, are well adapted to periodic cutting and are capable of resprouting many new shoots from their stumps after being chewed (Bailey & Whitham 2006). This ultimately leads to denser, more productive riparian forests, albeit with less tall canopy cover than in older, undisturbed forests (Jones et al. 2009). Beaver-cut trees left on the landscape act as physical roughness elements during high-flow events (Wohl 2011, 2015; Wohl et al. 2018), and beaver-cut trees cached in their ponds form massive woody tangles that reduce flow velocity and increase the physical complexity of the aquatic environment (Busher 1996, Slough 1978). Beavers travel significant distances from their home ponds (tens to thousands of meters, depending on topography, aquatic connectivity, and the presence of predators) to access their preferred food species, resulting in broad areas of significant ecosystem engineering influence. In many environmental contexts, tree cutting by beavers leads to greater plant diversity, smaller ecological patch sizes, and greater landscape heterogeneity (Markle et al. 2022). By periodically felling large trees in a distributed pattern across their territory, beavers open up small areas of canopy and create space for a variety of understory vegetation species in those gaps (Westbrook 2021).

4.3. Dam Building

Dam building is the most unique and possibly the most consequential form of ecosystem engineering a beaver engages in. The primary functions of a beaver dam are to slow flow velocity, create deep water environments, and store surface water (Gurnell 1998). As a consequence of obstructing streamflow and thereby slowing water velocity, beaver dams also massively alter sediment dynamics, increase sedimentation rates within the beaver pond and on stream banks, and increase connectivity to groundwater and hyporheic flow paths (Butler & Malanson 1995, Puttock et al. 2018, Scamardo & Wohl 2020). Beaver dams are constructed from cut trees, other vegetative material like cattails and reeds when available, mud, and stones (Rosell et al. 2005). It is not uncommon for beavers to include anthropogenic materials in their dams as well. Beaver dams vary dramatically in size, ranging in height from a fraction of a meter to over 5 m tall and ranging in length from 1 m to 850 m long (Hafen et al. 2020). Extremely long or tall beaver dams are uncommon; a typical beaver dam is approximately 1 m tall and tens to low hundreds of meters in length (Larsen et al. 2021). Variability in dam construction style and dimensions stems from the broad range of environments and physical settings that beavers live in—mountains, lowlands, coasts, deserts, forests, prairie, peatlands, tundra, etc. Beaver colonies do not usually build just one dam. The largest dam they build creates the pond in which they build their lodge or bank den and is referred to as the primary dam (Hafen et al. 2020). Beavers build several additional dams, referred to as secondary dams, upstream and downstream of the primary dam, or on the floodplain, to further increase the wetland habitat area and improve hydrologic stability during precipitation extremes, e.g., drought and flood (Brazier et al. 2021).

4.4. Site Abandonment and Recolonization

In the absence of predation or disease, beavers occupy and engineer a site until it becomes more challenging to survive in place than it is to leave and engineer a new site. This typically occurs when there is a loss of food resources or excessive sedimentation reducing water depth in the ponds (Ives 1942). Upon abandonment, beaver dams begin to degrade, vegetation regrows, and canals fill in with sediment. Over time, the site is restored to high-quality beaver habitat, and beavers recolonize and engineer it again (Ruedemann & Schoonmaker 1938). The cyclic nature of beaver occupancy, engineering, and abandonment sustains wet meadow and riparian forest ecosystems that provide long-term, high-quality beaver habitat and can persist hundreds to thousands of years (Laurel & Wohl 2018; Polvi & Wohl 2012; Wohl 2013, 2021). Thus, beaver ecosystem engineering today may influence the success and survival of beavers occupying the same site for many years in the future.

5. CLIMATE CHANGE AMELIORATION BY BEAVERS

Broadly speaking, there are two strategies for addressing climate change: mitigation and adaptation. Climate mitigation is the suite of actions taken to slow or stop the trajectory of climate change, often involving greenhouse gas sequestration or the reversal of runaway warming feedback loops. Climate adaptation is focused on reducing damage from the impacts of climate change that have already come to fruition and figuring out how to thrive in the current and probable future state of the planet. Most climate change amelioration efforts require humans to engage in specific policies and actions, e.g., converting lawns to natural vegetation to reduce water use, decommissioning coal power plants to decrease greenhouse gas emissions, or building seawalls to protect coastal infrastructure. There is growing interest in another form of climate change amelioration: bolstering nature-based solutions or natural infrastructure (Cohen-Shacham et al. 2016, Norman et al. 2022).

Nature-based solutions emphasize natural processes and protecting, sustainably managing, and restoring ecosystems offering these processes in a way that addresses climate change while also providing human well-being and biodiversity benefits (Seddon et al. 2020). Beavers and their ecosystem engineering are gaining momentum as a nature-based solution to ameliorate the effects of climate change on aquatic ecosystems and water resources in North America, Europe, and Asia. Recent studies have highlighted the substantial climate-related ecosystem services provided by beavers including greenhouse gas sequestration, flood attenuation, drought and fire mitigation, improved water quality, and increased biodiversity. As climate changes, the contrast sharpens between impaired or degraded landscapes and landscapes that have been restored through beaver ecosystem engineering, highlighting their increasing value in the future (Jordan & Fairfax 2022).

5.1. Innate Greenhouse Gas Dynamics

Beaver wetlands, like all other types of wetlands, have complicated greenhouse gas dynamics. The frequent cutting of trees induces new growth and the conversion of carbon dioxide to biomass but also increases the amount of dead vegetation and organic carbon that, when broken down by decomposers, releases carbon dioxide and methane. Beavers significantly alter streamflow velocity and the inundated extent of their wetlands through modest modifications to their dam or canal networks. The slow-water environment, anoxic sediments in deep pools, hydrogeomorphic heterogeneity, and frequent fluctuations in the aquatic–terrestrial interface area result in both the release and sequestration of greenhouse gasses (Smufer et al. 2023). There is a significant body of research indicating that the soils around both active and inactive beaver ponds have very high rates of carbon sequestration compared to alternative riverine states that do not have beaver—1,150–1,400 Mg C/ha in active beaver meadows and 300–400 Mg C/ha in relict beaver meadows versus 40–100 Mg C/ha in dry grassland soils (Laurel & Wohl 2018, Wohl 2013). This suggests that the construction of beaver wetlands was historically a notable net sink for carbon within river corridors.

All wetlands produce methane—approximately 20–30% of global methane emissions come from wetlands—and beaver wetlands are no exception (Clark et al. 2023, Whitfield et al. 2015). Methane is a more potent greenhouse gas than carbon dioxide, so concerns about the effect that restoring beaver populations would have on its production are understandable. However, the entire carbon cycle is important to consider when evaluating methane emissions from beaver ponds, as they can function as both a source and a sink of different gases. While there is abundant research describing increased methane emissions in and around beaver ponds, the temporal dynamics of those emissions—particularly in relation to carbon sequestration mechanisms—are still largely unquantified. One study found that beaver ponds in Arctic tundra ecosystems contain lower abundances of methane-producing bacteria, archaea, and fungi than were found in tundra lakes and streams that did not have beavers present, suggesting that those beaver wetlands have a lower capacity for methane production than other hydrologic features (Shannon et al. 2023).

5.2. Flood Attenuation

When a beaver builds its dam, one of the main goals is to cause localized flooding. So, in that sense, beavers exacerbate flooding. However, on larger spatial scales, beaver wetlands are uniquely capable of attenuating flood waves and reducing downstream damage and erosion (Puttock et al. 2021, Westbrook et al. 2020). An analysis of >1,000 storm events in the UK found that beaver dams can attenuate flood flows by up to 60% (Puttock et al. 2021). In Canada, 68% of beaver complexes persisted after an extreme rainstorm in which nearly 2 meters of rain fell over 4 days (Westbrook et al. 2020). Beaver dams are semipermeable flow obstructions: Water moves through them, under them, around them, and over the top of them (Ronnquist & Westbrook 2021). Maintaining a deep pond, even during high flows, is key to a beaver's safety, and as such, they are quite good at building sturdy structures. Often anchored at the base with heavy stones, tree stumps, or branches wedged into the streambed, beaver dams are capable of withstanding significant flood events with minimal damage and are usually just overtopped when the surface water storage capacity of the wetland is reached. Additionally, beavers build secondary dams upstream and downstream of their primary dam to aid in their control of the water within their territory. Although the partial breach or complete failure of beaver dams can cause catastrophic flooding downstream (Hillman 1998), there are typically more dams downstream that continue dispersing the flood wave (Westbrook et al. 2020).

The canals that beavers dig also play a key role in flood attenuation. Each canal is a conduit for surplus water, efficiently routing it out of the main channel and onto the floodplain and into stream banks. Once on the floodplain, that water encounters physical roughness from the dense riparian vegetation and abundant dead wood that surround beaver ponds and is also provided the time and space to seep into spongy floodplain soils. In systems without beaver, flood waters swiftly move through the river corridor and cause substantial erosion. In systems with beaver, flood waters are slowed, spread out, and stored in surface water, soil water, and groundwater reservoirs (Westbrook et al. 2006). For example, in Washington, USA, beaver impoundments stored 243 cubic meters of surface water per 100 m of stream, and 2.4 times as much groundwater per unit surface water storage (Dittbrenner et al. 2022). In a Canadian peatland, the water table was 12.8 cm higher and twice as stable within a 150-m radius around beaver dams in comparison to areas without beavers (Karran et al. 2018). In current conditions, this is a valuable way to adapt to climate change–exacerbated flood events and store the excess water for later ecosystem use. It may also help stabilize the timing of water delivery in future climate scenarios in which snow-dominated systems shift toward being more rain-dominated systems and the capacity for winter water storage in snowpack is diminished.

5.3. Drought Resistance

Beavers strongly prefer perennial water environments, as they are much more vulnerable to predation and heat-related illness on land than in the water. Through the construction of dams and canals that capture water during high flow or precipitation events, as described above, beavers are able to store enough water to locally buffer their wetland habitat against drought. This effect has been observed in both arid shrubland and wet boreal ecosystems. In one study, beaver-engineered river corridors in Nevada, USA, maintained plant productivity throughout the summer similar to irrigated agricultural lands during a 3-year drought period, while riparian areas without beaver began wilting as soon as winter precipitation ended (Fairfax & Small 2018). Another study found that beaver-engineered wetlands in Canada maintained wetland habitat and surface water area during drought more effectively than wetlands that were not associated with beavers—beaver-dammed areas had a ninefold increase in open water area compared to areas without beavers during the same drought period (Hood & Bayley 2008). Sedimentological studies and a sedimentary ancient DNA study in the Greater Yellowstone Ecosystem determined that beavers were continuously present in the watershed and maintained wetland habitat even during extended periods of drought 100 or more years long (Baker et al. 2023, Persico & Meyer 2009).

Increased water storage capacity and residence times are the most likely physical mechanisms contributing to drought resistance, both of which increase with the scale of beaver ecosystem engineering. Larger, more complex beaver wetlands have more storage capacity and delay water delivery longer than smaller, less developed ones (Puttock et al. 2017). Thus, they also have greater capacity to reroute water to longer subsurface flow paths and therefore buffer the wetland habitat and downstream environment against drought—provided they have been present long enough to have captured excess water during previous high-flow events.

5.4. Fire Resistance

Wildfires are a necessary disturbance in most ecosystems. Some species are completely dependent on periodic fire as part of their reproductive strategies, e.g., serotinous pine cones found on jack and lodgepole pines, among others. Over time, these ecosystems and landscapes develop a natural fire regime that can be described as the intensity and frequency of wildfire necessary to maintain existing environmental conditions and processes. Increasingly intense and frequent droughts, combined with centuries of misguided forest management and fire suppression, have resulted in many places experiencing fires that are far more intense and destructive than would normally be part of the fire regime. One of the most unique effects of beaver ecosystem engineering is their ability to create fire-resistant landscape patches—one study determined that in the American West, beaver-dammed riparian corridors burned about three times less intensely than riparian corridors without beavers (Fairfax & Whittle 2020). The fire-resistance of beaver wetlands persists even during massively destructive megafire events that burn areas larger than 100,000 acres (Fairfax et al. 2024, Fairfax & Whittle 2020, Markle et al. 2022). A recent study found that during megafires, 40% of nonriverine area, 60% of river corridor without beaver activity, and 89% of beaver-dammed area can be classified as fire refugia (Fairfax et al. 2024).

The mechanisms for fire resistance in beaver wetlands come from two aspects of their ecosystem engineering: (*a*) Their ability to slow, spread, and store water during high-flow events contributes to drought resistance, increased soil moisture, and high water content in nearby vegetation that reduces flammability (Fairfax et al. 2024, Fairfax & Whittle 2020), and (*b*) tree cutting by beavers results in smaller burnable patch sizes and more diverse vegetation mosaics in terms of plant species, canopy heights, and age classes (Markle et al. 2022). The more variable fuel configuration in beaver wetlands impedes fire progression and results in lower severity burning (Markle et al. 2022). As a result, beaver wetlands frequently function as fire refugia, areas of low severity burning or unburnt habitat in which plants and animals can safely wait while more destructive fire propagates across the landscape (Fairfax & Whittle 2020). In some instances, multiple beaver wetlands in sequence function as firebreaks that have been observed to limit the spread of wildfire in a given direction (Fairfax et al. 2024). It has been posited that other aspects of beaver ecosystem engineering may contribute to their pronounced fire resistance. For example, the deposition of wood shavings during tree cutting and deposition of excavated fine sediments from the pond bottom onto the floodplains may help trap moisture in the soil. While logically sound, the scientific research on beavers and wildfire is nascent, and no data yet exist on these hypotheses.

In some contexts, beavers benefit from infrequent fire, and complete fire resistance would be undesirable. For example, in dense coniferous forests, wildfire opens the canopy and allows herbaceous plants and fast-growing hardwoods like aspen and willow to establish. These species are preferred food sources, and once beavers occupy those postfire landscapes they contribute to the maintenance of open canopy and conditions favorable to hardwoods over conifers via their ecosystem engineering and wetland habitat maintenance. The widespread logging and subsequent fire activity in northern Minnesota and Wisconsin in the late 1800s to early 1900s is frequently credited as creating favorable conditions for beaver populations to rebound after their prior extirpation during the fur trade (Johnston 2017). Frequent fire, however, does not appear to be generally beneficial for beavers. A study on controlled burns in Canada found that beavers generally opted to leave a stream if fires were burning every year, as it would preclude regeneration of the woody materials needed by beavers (Hood et al. 2007).

5.5. Water Quality

Beavers impact water quality in two key areas: temperature and nutrient load. The majority of research is in agreement that beaver wetlands are a mosaic of water temperatures, with relatively cold water found in deep pools and near groundwater and hyporheic springs and relatively warm water found on the pond surface and along shallow depth margins (Majerova et al. 2015, Weber et al. 2017). Thus, there are parts of a beaver wetland that are beneficial to temperature-sensitive species and can function as thermal refugia, as well as parts where the water temperature likely exceeds the thermal tolerance of many coldwater fishes. The bulk of recent research on this topic has come from the American West, and it generally indicates neutral or net temperature decreases across beaver wetlands (Dittbrenner et al. 2022, Majerova et al. 2015, Weber et al. 2017). One study found that beaver damming resulted in an average temperature decrease of 2.3°C with individual sites ranging from 0.3°C to 6.0°C of cooling (Dittbrenner et al. 2022), another study found a decrease in maximum daily temperature of 2.6°C and an increase in minimum daily temperature of 1.6°C (Weber et al. 2017), while yet another found an average temperature decrease of 1.47°C (Bouwes et al. 2016). Though significant variability in findings and measurement methodologies is apparent, this trend of stream cooling has led many researchers to describe beavers as beneficial to coldwater fishes. There is very little research on beavers and water temperature in the rest of North America, Europe, and Asia. A recent study from Minnesota found that beaver ponds had a neutral effect on stream temperature during normal climate conditions but provided valuable thermal refugia for coldwater trout during summer drought conditions via increased connection to cold groundwater aquifers and thermal buffering along the water column in deep pools (Behar 2020).

Warmer winters and increased runoff from urban and agricultural areas has led to higher loads of potent nutrients, particularly nitrates and phosphates, in freshwater ecosystems. Surplus nitrates and phosphates cause eutrophication, which can also occur naturally in stagnant water environments—including some wetlands. Beaver impacts on nutrient cycling are relatively well-studied, with most data finding that their wetlands often, but not always, reduce nutrient loads (Law et al. 2017, Lazar et al. 2015, Murray et al. 2023). One study found that beaver dams were more influential in determining nitrate removal rates at climatic hydrologic extremes, with beaver-dammed reaches having 44.2% higher nitrate removal rates relative to seasonal extremes alone (Dewey et al. 2022). Another found that beaver ponds can reduce watershed nitrate loading in agricultural watersheds by 5–45% (Lazar et al. 2015). Nitrates are removed biogeochemically through microbial denitrification processes and are greatest in magnitude in parts of the pond with high sediment storage and deposition rates (Murray et al. 2023). Phosphates are removed mechanically, binding to fine sediments that flow into the beaver ponds then settling to the pond bottom where they are buried, and sometimes excavated and removed from the aquatic system, by beavers (Muskopf 2007).

5.6. Biodiversity

Approximately 40% of threatened or endangered species in North America live in or otherwise depend on having access to wetland habitats (Niering 1988). An estimated 80% of all terrestrial vertebrates and 95% of terrestrial vertebrates in the western United States rely on riparian ecosystems at some point in their lifecycle (Krueper 1993). Increased global temperatures have necessitated rapid shifts in the distributional range of many species. Many species simply cannot keep up with these changes and, if unable to otherwise adapt to the change, dwindle in population. Further, the increased frequency and intensity of natural disasters like drought, flood, and fire have resulted in local extirpation of species and widespread population declines in more sensitive organisms. Widespread wetland draining and land use changes in the last two centuries have compounded the biodiversity loss driven by climate change.

While beavers are not able to stop the current northward shift of many species or ecosystems, they do help reverse habitat loss by creating relatively stable wetland and riparian ecosystems that are resistant to flood, drought, and fire. The mosaic of hydrologic, ecologic, and geomorphic conditions within beaver wetlands provides a broad range of niches favorable for numerous species (Andersen et al. 2023; Fedyń et al. 2023; Jordan & Fairfax 2022; Law et al. 2016, 2017). A wide variety of plants, insects, amphibians, fish, mammals, and birds all benefit from living in beaver ponds. Greater species richness exists in beaver-modified environments, and abundance is generally increased as well (Wright et al. 2002). While no individual ecosystem engineering behavior is directly responsible for bolstering biodiversity within beaver wetlands, in ensemble, they provide numerous unique advantageous conditions for a variety of plants and animals that would otherwise not occur (Law et al. 2019). It is for this reason that beavers are considered a keystone species, as well as an ecosystem engineer. As significant anthropogenically driven wetland habitat loss persists across the beaver's native range, the higher biodiversity within beaver wetlands is generally considered a positive effect (Law et al. 2017). Several freshwater threatened and endangered species benefit from beaver-created habitat as well, including steelhead (*Oncorhynchus mykiss*) (Bouwes et al. 2016), Oregon spotted frogs (*Rana pretiosa*) (Rowe et al. 2024), Columbia spotted frogs (*Rana luteiventris*) (Arkle & Pilliod 2015), and water voles (*Arvicola amphibius*) (Puttock et al. 2023).

6. THE FUTURE OF BEAVER CONSERVATION AND SCIENCE

6.1. Factors Influencing the Distribution and Abundance of Beavers in the Future

Climate change and human intervention will each strongly influence where and in what quantity beavers exist in the future. As evidenced by prior periods of rapid environmental change, shifting hydrologic regimes, temperatures, and ecologies alone are not going to lead to beaver extirpation or extinction. Beavers adapt quickly to climatic stressors, both by engineering more stable local habitats and through range shifts when the scale of climatic change exceeds their ability to modify local conditions in their favor (e.g., the advance of continental ice sheets). For the vast majority of the 7.5-million-year evolutionary history of dam-building beavers, they lived and worked wherever the biophysical conditions were acceptable. The advent of human interest in beavers and human-built environments changed that. As was clearly demonstrated during the fur trade era, excessive hunting and trapping is a very real threat to beaver survival. Beavers are still trapped today, albeit in much smaller numbers, and are also routinely lethally managed during human–wildlife conflicts where beaver ecosystem engineering and wetland development is perceived as a threat to human infrastructure or productivity. Beavers routinely cut down trees that we find valuable for personal or economic reasons and flood our roads, fields, and housing developments—these are real challenges that are often still addressed through lethal management (Auster et al. 2020, Rosell & Campbell-Palmer 2022).

Our influence on their distribution and abundance is not solely detrimental, though. Beaver conservation, reintroduction, and rewilding are all being undertaken presently across their native range—in some cases for the benefit of the beavers and in some cases for our own benefit. We have developed ways to regain some control of their ecosystem engineering. Strategic fencing and installing pipes through beaver dams limit beavers' ability to flood the landscape and fell trees (Rosell & Campbell-Palmer 2022). Their potential role as a partner in the struggle to manage a changing climate has not gone unnoticed, though many questions remain about how, where, and when to include beavers in our climate change mitigation and adaptation efforts.

6.2. Remaining Questions and Recent Advances in Beaver Science

Our current understanding of beavers and the ways in which they control biophysical processes at both small and large spatiotemporal scales is vastly greater than it was 50 years ago. However, it remains extremely limited in ways that hinder our ability to confidently, ethically, and effectively live alongside and manage beaver populations in the future as climate changes. Significant uncertainty remains around the precise distribution of beavers prior to the fur trade, and there is disagreement about what the appropriate range for modern management should be. Unlike many other keystone species, beaver populations are not widely monitored. Most states, territories, and countries, particularly those in North America, do not know what their current beaver population is and whether it is above or below what it could be given existing habitat availability and historic precedent. And while our improved understanding of how beavers modify the physical environment has enabled scientific reconstructions of historically beaver-influenced landscapes, it remains unknown how the environmental feedback loops beavers initiate or contribute to via their ecosystem engineering are altered by direct and indirect anthropogenic influences.

Fortunately, recent technological advances in beaver science hold promise for rapidly progressing our understanding of their role in climate change adaptation and mitigation. The use of remote sensing, drones, and artificial intelligence has dramatically increased the spatial scale of beaver research (Fairfax & Small 2018, Fairfax et al. 2023, Puttock et al. 2015, Tape et al. 2022). Many beaver dams and canals are readily visible in high-resolution aerial and satellite imagery. Through increased availability of such imagery and the development of image-recognition algorithms, censusing beaver infrastructure and monitoring changes in its condition and distribution over time is faster and easier now than it has ever been. By considering watershed-scale and larger distributions of beavers, scientists are better able to quantitatively describe the impacts of population-level beaver ecosystem engineering as well as its interactions with other large-scale environmental processes and disturbances, including drought, wildfire, flooding, and nutrient cycling. The use of genomic technologies like environmental DNA (eDNA), ancient DNA (aDNA), and sedimentary ancient DNA (sedaDNA) provides novel insights into ecosystem composition, biological diversity, and—in the case of sedaDNA—high-resolution reconstruction of environmental conditions over time in direct relation to the presence or absence of beaver (Baker et al. 2023, Campbell-Palmer et al. 2020, Harper et al. 2019). Further, eDNA, aDNA, and sedaDNA are tools to more precisely determine the present and historic range and dynamics of the range shifts of beavers with spatiotemporal specificity that was previously not possible.

Creative uses of existing research methodologies are providing new insights into the physical, ecological, and climate amelioration impacts that beavers have in a landscape. Dendrochronology, pollen records, isotope geochemistry, and diatomic analyses conducted in areas of known modern beaver influence contribute to our understanding of the fingerprint of beavers in the landscape, which can then be traced back through time (Boudreau et al. 2005, Labrecque-Foy et al. 2020, Plint et al. 2020). Connecting Western science with Indigenous science and knowledge more thoughtfully has led to a recent uptick in valuable knowledge coproduction and a deeper understanding of how beavers influenced North American landscapes in particular (Albert & Trimble 2000, Blackfeet Nation 2018). All of these emerging technologies and interdisciplinary approaches, in combination with traditional field investigations, modeling, and laboratory analyses, are likely to provide insight into, if not complete answers for, the most pressing lingering questions discussed above.

7. CONCLUSIONS

Beavers evolved a unique set of ecosystem engineering behaviors that not only help insulate individual beaver colonies from the effects of climate change but also—at larger spatial and population scales—ameliorate the deleterious effects of climate-exacerbated natural disasters and biodiversity collapse. Beavers, however, are not entirely immune to climate change. They shift their range when ecosystems change and places become more or less hospitable habitat, as is currently being observed in thawing Arctic permafrost landscapes. Beavers are in many ways a natural disturbance regime, much like wildfire. And just as most landscapes have a natural fire regime that helps maintain balance and resilience in the ecosystem, they also have a natural beaver regime, although we do not currently have a strong understanding of what that is in many places.

While our current scientific understanding of the magnitude and spatiotemporal distribution of beaver influence in historic landscapes is limited, recent research suggests that the impacts of beaver ecosystem engineering are becoming increasingly pronounced as the planet warms and their population continues to rebound from the fur trade era, regardless of whether those impacts align with human interests. Given beavers' track record of thriving during prior periods of intense climate change and their disproportionately large role in controlling biophysical processes in freshwater environments, beaver management should be approached thoughtfully and through a systems-level perspective. Whether the goal is to remove beavers from a landscape or area, conserve beavers in place, or actively restore beaver populations where they have been long absent, managing beavers does not just affect those animals—it may alter the trajectory of the entire ecosystem and large-scale biophysical processes.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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