American beaver (*Castor canadensis)* and freshwater climate resiliency in Washington State

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Suggested citation:
Burgher, J., Hoza, J., Piovia-Scott, J. 2023. American beaver (*Castor canadensis*) and freshwater climate resiliency in Washington State. Prepared for the Washington Department of Fish and Wildlife.

Executive Summary

Stream and riparian ecosystems provide critical resources and services for the residents of Washington state but are increasingly threatened by climate change. Climate change is projected to increase stream temperatures, reduce summer streamflows, and increase wet-season flood events. These changes are expected to have negative consequences for many species, including protected species of salmon, trout, and amphibians.

Beavers were once abundant in North America. Though they were hunted nearly to extinction in the 18th and 19th centuries, populations have since recovered in many areas. Beaver-related restoration, which includes beaver reintroduction and the construction of structures that mimic beaver dams, seeks to facilitate the ongoing recovery of beavers and harness (or mimic) their engineering capabilities to restore and improve freshwater systems. Beaver-related restoration has gained popularity in recent years as a nature-based approach to facilitating climate resilience in stream and riparian ecosystems.

Both beaver reintroduction and the construction of beaver dam analogues are increasing in Washington State. However, there is a paucity of scientific information on the impacts of these forms of beaver-related restoration. This report synthesizes available scientific information on beaver-related restoration and climate resilience for streams in Washington state, summarizing the state of the science, highlighting knowledge gaps, and identifying challenges.

There is substantial evidence that beaver-related restoration, via beaver translocation and the construction of beaver dam analogues, has the potential to increase the climate resiliency of Washington's stream and riparian ecosystems (summarized in Table 1). By reducing summer water temperatures, increasing summer flows, and enhancing floodplain habitat, beavers and beaver-related restoration can benefit species of conservation concern, including trout, salmon, and amphibians. In addition, beaver-related restoration can ameliorate the negative impacts of high-flow events, create fire-resistant habitat patches in fire-prone landscapes, and foster heterogeneous mosaics of habitat that enhance the watershed-level biodiversity of aquatic and riparian ecosystems. However, these benefits are only likely to accrue under certain conditions, and there is a gap between our understanding of the aspirational potential of beaver-related restoration (what it ***can*** accomplish) and the realized benefits of restoration actions (what it ***does*** accomplish).

While the scientific literature on beaver-related restoration is developing rapidly, there are important limitations in our understanding. For example, most studies of beaver-related restoration are still relatively limited in spatial and temporal scope. In addition, key aspects of restoration practice are not well understood -- many translocated beavers do not establish; beaver dam analogs must be colonized by beavers or maintained by humans to persist, but it is not clear how frequently this happens. Finally, key drivers of variation in the effects of beavers and beaver-related restoration are poorly understood, including regional gradients in climate and land use.

Contents

1 Introduction

Stream and riparian ecosystems provide critical natural and cultural resources and services for the residents of Washington state. These ecosystems are increasingly threatened by climate change, which is driving dramatic shifts in their hydrology and will have major impacts on the organisms inhabiting them (Gates et al., 2022; Shirk et al., 2021). Because of this, ongoing stream and riparian restoration often aims to foster climate resilience. Restoration practices have increasingly focused on nature-based solutions, and one of the most prominent nature-based restoration practices in streams is beaver-related restoration (Nash et al., 2021; Pilliod et al., 2018). Beaver-related restoration (BRR), which includes beaver reintroduction and the construction of structures that mimic beaver dams, has gained popularity in recent years as a low-cost, process-based restoration practice that has the potential to enhance climate resilience. The recognition of this potential has led many states in the western United States to update policies on beaver relocation and depredation, with California being the most notable recent example. However, despite the increasing attention garnered by BRR in public discourse (e.g., Goldfarb, 2018; Sherrif, 2021) and the rapid increase in BRR projects, both in Washington and throughout western North America, there is a paucity of scientific information on the relationship between BRR and climate resilience. In part due to this scarcity of information, a comprehensive assessment of scientific evidence on the impacts of BRR that incorporates confidence and uncertainty is often missing from discussions of BRR implementation and related policy development. This report synthesizes available scientific information on BRR and climate resilience that is relevant for streams in Washington state, summarizing the “state of the science”, highlighting knowledge gaps, and identifying challenges.

The report includes background information, the “state of the science”, and synthesis and conclusions. The background portion of the report provides important contextual information. We first outline the projected impacts of climate change on small and medium streams in Washington and define climate resiliency for these ecosystems (Section 2). We then provide general information about beaver natural history and a detailed description of BRR and its implementation in Washington (Section 3). The “state of the science” sections of the report (Sections 4-8) describe our methods and provide detailed descriptions of the impacts of beavers and beaver dam analogs on abiotic and biotic components of aquatic ecosystems, with a focus on results relevant to Washington state. Finally, the synthesis and conclusion (Section 9) summarizes key findings and highlights important knowledge gaps.

2 Streams, climate change, and climate resilience

2.1 Impacts of climate change on Washington stream ecosystems

Climate change is projected to have profound impacts on Washington watersheds and the organisms that occupy them. These impacts have been the subject of multiple recent synthetic reports (e.g., Gates et al., 2022; Shirk et al., 2021). In this section we provide a brief overview of these projected impacts with a focus on small and medium streams and associated wetlands and riparian areas, where most BRR activities occur.

Stream hydrology and water temperature

Climate change is projected to have dramatic impacts on seasonal patterns of streamflow, including increased winter stream flows, earlier spring peaks in flow, and reduced summer flows (Chegwidden et al., 2019; Elsner et al., 2010; Hamlet et al., 2013; Pytlak et al., 2018; Vano et al., 2015). The dominant drivers of these changes are declines in winter snowpack and an increasing proportion of precipitation that falls as rain, rather than snow. Consequently, increased winter streamflows, earlier spring peaks in flow, and reduced summer flows are projected to be most dramatic in watersheds that historically experienced a mix of rain and snow (denoted by some authors as “transitional”) which generally occur at higher elevations on the west slope of the Cascade Range and in the Olympic Mountains, and in most areas east of the Cascade crest. These changes in hydrology due to reduced snowfall and snowpack are projected to be enhanced by changes in the seasonality of precipitation, with increases in rainy season precipitation and decreases in summer precipitation.

The largest proportional reductions in summer low flows are projected to occur at mid to high elevations in the Cascade Range and in the Olympic Mountains due to reduced snowpack and relatively high summer soil moisture levels (Hamlet et al., 2013; Pytlak et al., 2018; Tohver et al., 2014). Where soil moisture remains relatively high in summer, higher temperatures can drive increased water loss through evapotranspiration, whereas in drier areas east of the Cascade crest soil moisture levels are already very low in late summer, limiting additional losses. Reductions in summer flow may lead to complete dewatering of aquatic habitats in some cases, especially in the upper reaches of watersheds. For example, the presence of surface water in central Cascade Range headwater streams (including the southwest Washington Cascades) is projected to diminish (Olson & Burton, 2019), and montane wetlands in the Cascades and Olympics are projected to have shorter hydroperiods and increased probability of drying (Lee et al., 2015). Decreases in summer low flows are likely to be exacerbated by human withdrawals for irrigation and domestic use. Small and medium streams are most likely to be impacted by groundwater withdrawals (rather than surface water withdrawals) (Gates et al. 2022).

Wet season high-flow events (e.g., floods, spates) are projected to increase in frequency and magnitude (Chegwidden et al., 2020; Hamlet et al., 2013; Mantua et al., 2010; Queen et al., 2021; Tohver et al., 2014), due to an increased frequency of high precipitation events (e.g, Warner et al., 2015) and rising snowlines. Increases in high-flow events are expected to be most pronounced in transitional basins, where both of these mechanisms will act in concert. In addition, increases in the magnitude of maximum flows are expected to be more pronounced in smaller, higher-elevation catchments (Chegwidden et al., 2020; Tohver et al., 2014), which may make these changes more relevant for BRR.

Maximum stream temperatures are expected to increase throughout Washington as air temperatures increase and summer streamflows decrease (Mantua et al., 2010). The largest increases are projected for lower elevations in eastern Washington (e.g., Columbia Plateau), with smaller increases in western Washington and at higher elevations in eastern Washington (Isaak et al., 2017, Shirk et al. 2021). For forested streams in the Pacific Northwest, temperatures in colder streams are generally less sensitive to increasing air temperature than warmer streams, likely due to the stabilizing influence of groundwater inputs, fog (in coastal areas), and snowmelt (in basins with snowpack) (Luce et al., 2014). Consistent with this latter mechanism, watersheds that transition from snow-dominated to rain-dominated, such as the upper Snoqualmie River Basin, may be particularly vulnerable to increases in summer peak temperatures due to decreased summer flows and diminished cooling from snowmelt (Lee et al., 2020; Yan et al., 2021). Increased stream temperatures may also be exacerbated by groundwater withdrawals for human use (Gates et al., 2022).

Climate-driven increases in the size and frequency of wildfires (Halofsky et al., 2020) may also drive shifts in stream hydrology and temperature. Fires can decrease shading by removing riparian vegetation; increase runoff; and enhance sediment, debris, and nutrients inputs from riparian and upland habitats (Bixby et al., 2015). However, fire effects on water temperature are quite variable (Koontz et al., 2018) and the spatial and temporal scale of fire-related effects is likely to be more local and short-term compared to the broader impacts of changing climatic conditions (e.g., Holsinger et al., 2014; Isaak et al., 2010).

Fish and wildlife

Changes in stream temperature and hydrology are expected to diminish habitat quality and connectivity, with particularly dramatic consequences for cold-adapted native stream species including trout, salmon, and lamprey (Shirk et al., 2021). Species and populations that spend extended periods of time in stream habitats (e.g., state or federally listed species such as steelhead [*Oncorhynchus mykiss*], coho [*O. Kisutch*], sockeye [*O. Nerka*], and some chinook salmon [*O. Tshawytscha*]; bull trout [*Salvelinus confluentus*]; lamprey genus [*Entosphenus & Lampetra*]) are likely to be vulnerable to reduced streamflows and increased temperatures in summer (e.g., Falke et al., 2015; Mantua et al., 2010; Wang et al., 2020). This can directly lead to mortality if critical thermal tolerances are exceeded, and also reduce fitness via sublethal mechanisms such as enhancing susceptibility to disease, impeding migration (Whitney et al., 2016). In addition, species and populations whose early life stages occupy streams during the wet season, especially in transitional basins (e.g., pink [*O. Gorbuscha*], chum [*O. keta*; listed as threatened by USFWS], chinook, sockeye, and coho salmon; bull trout; lamprey) may be affected by the increased frequency and magnitude of high-flow events (Goode et al., 2013; Mantua et al., 2010; Sharma et al., 2016). Finally, climate-driven changes to the biological components of ecosystems, such as algal blooms, changes in riparian vegetation, phenological mismatches with prey species, and invasive species encroachment may further impact fish.

Changes in stream hydrology and temperature are also likely to influence other wildlife species. For example, a number of at-risk amphibians inhabit streams, most of which are cold-adapted (e.g., candidates for state listing such as Cascade torrent salamander [*Rhyacotriton cascadae*; includes], and Rocky Mountain tailed frog [*Ascaphus montanus*]) and likely to be vulnerable to increased stream temperatures and the loss of surface water (Olson & Burton, 2019; Thurman et al., 2022). In addition, pond and wetland-breeding amphibians (e.g., Cascades frog [*Rana cascadae*], Columbia spotted frog [*Rana luteiventris*; candidate for state listing]) are also likely to be threatened by reduced hydroperiods, especially where the presence of introduced fish populations (which can predate upon and compete with amphibians) excludes amphibians from permanent water habitats that are less vulnerable to climate change (Ryan et al., 2014). Many other stream-associated aquatic and riparian wildlife species are likely to be impacted by the influence of climate change on these habitats. These include aquatic macroinvertebrates (e.g., Richards et al., 2018; White et al., 2018), birds that rely on aquatic and riparian habitats, including Species of Greatest Conservation Need such as Barrow's Goldeneye (*Bucephala islandica*) and Harlequin Duck (*Histrionicus histrionicus)* (2015 SWAP Ch. 5), and mammals that rely on aquatic and riparian habitats, such as moose (*Alces alces)* and mink (*Mustela vison)* (2015 SWAP Ch. 5).

2.2 Defining climate resiliency for Washington stream and riparian ecosystems

Climate resilience can be defined as the capacity for an ecosystem to adjust and adapt to changing climatic conditions while preserving desired functions and services (Grantham et al., 2019; Walker et al., 2004). While ecological resilience was traditionally considered in terms of an ecosystem's capacity to return to an equilibrium state, contemporary notions of resilience in freshwater ecosystems emphasize their dynamic nature and the potential to exist in multiple stable states (Angeler et al., 2014; Pelletier et al., 2020). Thus, when considering climate resilience in freshwater systems it is important to focus on attributes that confer adaptability and the maintenance of key functions and services, rather than specific ecosystem states. There are five main attributes commonly associated with climate resiliency in freshwater systems.

Connectivity

Freshwater ecosystems are characterized by the movement and exchange of water and associated transfers of energy, chemical constituents, and organisms (Pringle, 2001). Connectivity is critical in maintaining abiotic and biotic processes that promote function and resilience in these systems. Connectivity occurs across four dimensions in stream and riparian systems: longitudinal (upstream-downstream linkages), lateral (aquatic-terrestrial linkages), vertical (hyporheic exchange), and temporal (seasonal linkages) (Grantham et al., 2019). Across these four dimensions, connectivity in freshwater systems promotes biotic resilience because it facilitates recolonization post disturbance, maintains capacity for aquatic population dispersal and genetic flow, maintains access to varied habitats and refugia, and may facilitate range shifts for organisms threatened by climate change (Grantham et al., 2019; Pelletier et al., 2020; Timpane-Padgham et al., 2017).

Habitat heterogeneity

Spatial heterogeneity can enhance both biodiversity and connectivity, provide variety and redundancy of habitats at the watershed scale, increase the likelihood of the presence of refugia habitat, and buffer ecosystems from catastrophic change (Grantham et al., 2019; Pelletier et al., 2020; Timpane-Padgham et al., 2017). Temporal heterogeneity refers to the dynamic nature of freshwater systems and can maintain selective pressures and flexible species adaptations (Grantham et al., 2019; Timpane-Padgham et al., 2017).

Biodiversity

Diversity is often assumed to enhance resiliency because it can increase the likelihood that an ecological community includes species that can withstand, adapt to, or recover from climate-associated changes. Additionally, higher biodiversity increases the likelihood that species with similar functional traits co-occur such that if one disappears another can functionally replace them, often called the insurance hypothesis. Furthermore, the maintenance of at-risk or protected species is often a key facet of climate resilience for many stakeholders.

Natural disturbance regimes

The presence of natural disturbance regimes can maintain resiliency by influencing the spatiotemporal variability of habitats, promoting connectivity, and building biotic capacity to adapt to and/or resist environmental changes. Systems with histories of disturbance can contain species that have evolved plasticity and flexibility related to spatiotemporal variation in conditions, and are thus resilient (Grantham et al., 2019; Pelletier et al., 2020; Timpane-Padgham et al., 2017). It is important to note that the impacts of disturbance regimes on resiliency may be positive or negative depending on the timing, frequency, and magnitude of the disturbance event but disturbance regimes consistent with historical patterns, such as seasonal floods, are generally considered beneficial to resiliency in freshwater systems.

Social-ecological linkages

Freshwater ecosystem climate resilience can be enhanced by linkages between social and ecological systems through the recognition of the ecosystem services provided by freshwater ecosystems. For example, incorporating perspectives from a diverse suite of partners and stakeholders into freshwater system management can increase resiliency by promoting stewardship of natural and cultural resources (Pelletier et al., 2020).

3 Beavers and beaver-related restoration

3.1 Beaver natural history

Beavers are large semi-aquatic rodents that usually occupy small to medium sized low-gradient perennial streams occurring in unconfined valleys (Pollock et al., 2023). They live in extended-family colonies, consisting of two parents and typically two young of the year and two young of the previous year. Young disperse from the colony around their second year, and this dispersal represents the primary way beaver populations expand. Beavers are territorial and defend their home range from other beavers, often maintaining uninhabited space between colonies (Baker & Hill 2003; Naiman et al., 1988). The density of beaver populations can vary in space and time and are heavily influenced by geomorphology and abiotic factors. Beavers exhibit an array of engineering behaviors that modify habitats to suit their needs and these behaviors can have widespread impacts on both biotic and abiotic components of their ecosystems. Their engineering behaviors include iconic ones, such as damming and tree falling, but also include vegetative browsing, lodge building, burrowing, and canal digging. The impacts of these behaviors on stream and riparian ecosystems will be considered in detail in the next section of the report.

3.2 Historic and contemporary beaver distribution and abundance

Historically, American beavers (*Castor canadensis)* were widely distributed and abundant across North America. There were estimated to be 60-400 million beavers in North America at the time of European contact (Baker & Hill, 2003; Naiman et al., 1988; Wohl, 2021). Beavers were found in most biomes from coast to coast, excluding dry desert areas of Nevada and California, the tip of Florida, and the arctic (Pollock et al., 2023). Populations declined drastically due to overharvesting in the 18th and 19th century, driven by demand for beaver pelts, westward expansion of European colonizers, and land use competition from human agriculture and development. Only small populations of American beaver remained at the end of the 19th century. While some populations have partially or fully recovered, habitat loss, degradation, and increasing conflict with human land use has reduced overall availability of suitable habitat and distributions often remain patchy. There were estimated to be 6-12 million beavers in North America at the end of the 20th century (Baker & Hill, 2003; Halley & Rosell, 2002; Naiman et al., 1988; Rosell et al., 2005).

While beaver populations in North America have recovered in many areas, detailed data on beaver abundance and distribution are often lacking at the state and regional level. As a furbearer, beavers are typically managed at the state level as a game animal, with regulated harvest producing annual harvest data for state fish and wildlife agencies. This lethal harvest data has generally been applied for population estimation by determining average number of individuals in beaver colonies and applying this index to other population estimation techniques, such as the use of aerial photography to estimate active colony density (Hay, 1958; Johnston & Windels, 2015; Novak, 1977; Swafford et al., 2003). However, the dynamic nature of site abandonment and colonization, and the fact that some beavers don't engage in behaviors that are apparent from aerial surveys (e.g., damming), make it challenging to generate robust estimates of abundance and distribution with these methods. Comprehensive knowledge of contemporary distributions of beaver populations across the western US and within Washington state are generally limited.

3.3 History of beaver-related restoration

Beaver reintroduction efforts in North America date back to the early 1900's and were implemented across the United States, often accompanied by trapping bans. Reintroductions and trapping prohibitions continued throughout the 20th century, until reintroductions and natural population growth and spread increased beaver populations to the point that trapping bans were lifted to better manage these growing beaver populations (Pollock et al., 2023; Wohl, 2021). Many of these early reintroductions focused primarily on restoring beaver populations, though recognition of beaver engineering potential for restoring stream processes and reversing stream incision was also a driver in some cases. Over the past two decades, increasing understanding of beavers' ecosystem engineering capabilities and their hydrologic legacy on the landscape has garnered interest in their potential role in maintaining freshwater ecosystem function and fostering climate resilience (Fairfax & Small, 2018; Hood & Bayley, 2008; Hood & Larson, 2015; Jordan & Fairfax, 2022; Law et al., 2017; Willby et al., 2018). As a result, in many regions of the US and Europe, freshwater restoration increasingly involves applications of beaver mimicry or beaver reintroductions to enhance the resilience of freshwater systems and reestablish important freshwater ecosystem processes (Jordan & Fairfax, 2022; Law et al., 2019; Pilliod et al., 2018; Willby et al., 2018).

3.4 Beaver-related restoration: methods and application

Beaver related restoration (BRR) refers to a suite of process-based restoration approaches that seek to harness or mimic the engineering capabilities of beavers to restore and improve degraded freshwater systems. BRR is generally comprised of three main techniques: beaver reintroduction, beaver mimicry, and habitat restoration to naturally attract beavers. All three of the approaches are considered relatively low cost, broadly applicable restoration strategies that are often implemented simultaneously or in sequence to achieve a wide variety of restoration goals. Many commonly cited goals for freshwater restoration projects overlap considerably with the benefits that can be provided by beaver engineering or mimicry;for example, beaver activity can improve water quality, create in-stream habitat, stabilize banks, reverse stream incision, and modify flow (Bernhardt et al., 2005; Pollock et al., 2004). Indeed, motivations for the use of BRR often include multiple goals, such as relocation of conflict beavers, increasing water storage on the landscape, controlling sediment, restoring riparian vegetation, and improving fish and wildlife habitat (Pilliod et al. 2018, Pollock et al., 2023).

Beaver reintroduction

Beaver reintroductions or translocations intentionally place beavers into historically occupied or degraded systems, usually in the hope of achieving restoration goals with minimal additional human assistance. Potential release sites are typically scored using a habitat suitability index and on-the-ground surveys (Pilliod et al., 2018, Pollock et al., 2023). A variety of tools have been developed to assess site suitability, including the Beaver Intrinsic Potential model (Dittbrenner et al., 2018) and the Beaver Restoration Assessment Tool (McFarlane et al., 2017). However, the successful establishment of reintroduced beavers is challenging, and reintroduction sites may be limited by suitable habitat in many areas.

A growing body of literature on beaver reintroductions addresses mortality rates, dispersal, and disease among translocated beavers (Roug et al., 2022; Campbell-Palmer et al., 2021; Epps et al., 2021). In most cases, survival appears to be <50%. For example, Petro et al. (2015) reported survival rates of 47% for translocated beavers over 16 weeks post-release, and McKinstry and Anderson (2002) reported 43% survival over one year after release. Life stage plays a role in translocation survival probabilities, with adults having higher rates of survival compared to subadults (Doden et al., 2022; McKinstry & Anderson, 2002; Nolet & Baveco, 1996). Disease may be a leading cause of death among relocated beavers in Europe (Nolet et al., 1997), and while parasite and infectious disease loads were generally low and all beavers appeared healthy, some beavers screened before translocation in northern Utah state tested positive for diseases such as *Leptospirosis spp., Giardia spp., and Toxoplasma spp.* (Roug et al., 2022). In practice, multiple relocations to a single site are often required to successfully establish beavers within a targeted restoration site.

Beaver dam analogues and beaver mimicry

This restoration approach typically involves the installation of artificial structures that mimic beaver dams, often called beaver dam analogues (BDAs) if they completely span the channel. Beaver mimicry may also include other varieties of instream structure such as post-assisted log structures (PALs) and wicker weaves that may or may not span the entire stream channel. Shahverdian et al. (2019) defines beaver dam analogues as "permeable, channel-spanning structure[s] with a constant crest elevation, constructed with a mixture of woody debris and fill material to form a pond and mimic a natural beaver dam." BDAs are distinct from PALS, which mimic and promote the processes of wood accumulation, but do not impound water to form ponds. Both BDAs and PALS may alternatively be called beaver dam support (BDS) structures (Pollock et al., 2012) or beaver mimicry structures (BMS) (Askam et al., 2022). BDAs are typically semi-porous to water and sediment and are created from biodegradable materials like those used by beavers. In heavily degraded and incised streams, these structures are often necessary predecessors to natural or assisted beaver recolonization to provide suitable habitat and anchor points for beaver-built dams (Nash et al., 2021, Pilliod et al., 2018, Pollock et al., 2023). Additionally, these structures represent a BRR tool that can be applied in areas where active beavers may lead to conflicts or issues with other land-use needs. However, just like natural beaver dams these structures are temporary and require maintenance, and the primary goal in many cases is to attract beavers that will maintain these structures in the absence of human intervention (Davee et al., 2019).

While instream structures constructed from biodegradable materials, including large woody debris, have been used for stream restoration for decades, BDAs began gaining recognition after the watershed scale installation of BDAs in the Bridge Creek Intensively Monitored Watershed, located in a relatively arid sagebrush and juniper steppe environment in north-central Oregon (Pollock et al., 2012). Initiated in 2009, more than 80 BDAs and BDA-like structures were installed across 32km of Bridge Creek, with subsequent years of intensive monitoring of hydrologic and biologic outcomes generating peer-reviewed articles that have led broader interest in BDA installation for restoration purposes. Most commonly, single BDAs or small series of 4-5 BDAs are installed in treatment reaches across the western United States due to the relative financial and logistic simplicity of such small-scale restoration. However, there is growing recognition that BDA function and longevity can be enhanced with increasing numbers of structures installed (Shahverdian et al., 2019). Research on best configuration and structure types for different hydrologic, biologic, and geomorphologic outcomes is ongoing and BDA installation is accelerating across the western United States (Pilliod et al., 2018).

Habitat restoration

This restoration approach typically involves alteration of land-use practices and active restoration of riparian vegetation to provide conditions suitable for beavers. In practice, this takes the form of reducing grazing competition from native and non-native herbivores in riparian areas, primarily using riparian fencing and/or limiting access to riparian areas to reduce competition from cows. Additionally, where riparian vegetation is sparse or unsuitable, active planting of easily propagated species that are preferred by beavers, such as willow and cottonwood, can be used to increase habitat suitability. These approaches are often applied in conjunction with beaver mimicry to improve habitat and naturally attract and encourage beaver colonization and dam construction (Nash et al., 2021, Pilliod et al., 2018, Pollock et al., 2023). To our knowledge there has been little peer-reviewed literature on this topic. In addition, habitat restoration is usually implemented in concert with other approaches, so in our report we only consider this form of BRR in the context of the other methods.

3.5 Beaver-related restoration in Washington State

In Washington State, long-running beaver translocation projects like the Methow Beaver Project, which started in 2008, are currently operating alongside newer beaver translocation projects. As of 2017, legislative changes have allowed for the expansion of relocation and reintroduction efforts statewide (RCW 77.32.585). State-wide data from the Washington Department of Fish and Wildlife (WDFW) shows that, since 2018, the number of permitted projects has fluctuated with an annual average of four projects collectively relocating 20-30 beavers each year. Additional relocations have come from tribal projects across the state, where individual projects may relocate up to 30-60 beavers per year (Sarah Garrison WDFW personal comm. & Molly Alves Tulalip Tribe personal comm.). Considering this increasing interest and implementation, WDFW began a statewide beaver translocation pilot program in 2019 to provide training and permitting for relocation projects. Additional goals of the pilot program are to gather data to establish standardized best practices and monitoring methods as increasing numbers of beavers are moved in Washington State.

Beaver translocation across Washington and the greater Pacific Northwest has been conducted across a gradient of landownership including federal, state, and private lands; each landowner type has unique potential for conflict with beavers, and the type of conflict varies depending on a rural to urban gradient. In rural areas, Federal and state landowners such as the Forest Service or Washington State Department of Transportation often conflict with beaver activity that floods roads, including gravel roads in National Forests and paved highways used by commuters. As well as sharing complaints over flooded roads, private agricultural groups in rural areas frequently conflict with beavers that dam irrigation canals, chew down crop trees, or even eat fruit products (Payne & Peterson 1986; Wigley & Garner 1987). In more urban areas, state or city landowners often conflict with beavers that alter park infrastructure or interfere with landscape design (Bailey et al. 2019). Urban private landowners may experience unwanted flooding or tree damage at private residences. Regardless of landowner or conflict type, the first management strategy attempted is often lethal beaver control, despite WDFW's beaver pilot program, which seeks to increase live relocation and in-place management strategies over lethal management. However, targeted education and outreach programs can be effective in supporting non-lethal management, and landowners have been shown to understand both drawbacks and benefits of beavers (Charnley et al. 2020).

Beaver relocation projects in Washington are expected to explore conflict resolution and in-place beaver management options prior to relocation (WDFW, 2023). For example, landowners may be consulted as to what real issues the beavers are causing (sometimes there are none), pond-leveling devices may be used to avoid flooding, or trees can be protected from beaver chew (Babik & Meyer, 2015). The first step in conflict resolution is often to determine whether the beaver is causing real or only perceived problems. Landowners often have preconceived notions that beavers will cause major flooding, destroy landscapes, or, in agricultural settings, damage infrastructure (Charnley et al., 2020). However, these concerns are not always well-founded, and beavers may be able to coexist with humans without intervention. At other times, these concerns are valid, and intervention is needed. Interventions need not be so extreme as relocation, though, which may just create vacant habitat that another beaver will quickly move into, creating a cycle of removals with no resolution (Wheaton, 2013). If landowners are not open to coexistence, lethal management or live relocation are the only remaining options. Live relocation is preferred since beavers remain on the landscape in some capacity, even if not in their original location.

BDAs have been increasingly applied as a stream restoration tool across the state, with many beaver relocation projects also undertaking BDA installation (Davee et al., 2019). These restoration projects are often intended to improve beaver habitat in the hopes of facilitating natural colonization or preparing sites for future reintroduction. However, BDAs are also used as a restoration tool in and of themselves, without a specific goal of preparing habitat for beaver. BDA-based restoration includes small-scale installations (4-5 structures) on specific stream reaches, though growing efforts for watershed scale BDA restoration projects (>100 structures) is increasing in the Okanagan-Wenatchee region (Michael Dello Russo, Trout Unlimited and Mark Ingman, Cascadia Conservation District personal communication). There is a general lack of data on the implementation of habitat restoration aspects of BRR (e.g., riparian vegetation planting or fencing of riparian habitats to exclude grazing cattle) across Washington.

4 Methods

4.1 Literature review and synthesis

We used a quasi-systematic approach to comprehensively search literature from Washington state and more broadly understand the state of the knowledge on BRR impacts on abiotic and biotic variables. Our approach included searches of the scientific literature using various combinations of BRR related search terms in Google Scholar and Web of Science. These results were supplemented with additional sources derived from papers we discovered in our initial searches, including several reviews of beaver ecosystem engineering (Brazier et al., 2020; Collen & Gibson, 2000; Jordan & Fairfax, 2022; Larsen et al., 2021; Rosell et al., 2005); we added additional sources through conversations with experts in the field and restoration practitioners.

Sources were included in our confidence assessments based on regional applicability; we compiled all available studies conducted in Washington or in ecoregions similar to those found in Washington. Applicable ecoregions include areas throughout the American West and parts of British Columbia, Canada as described by the US EPA (2022). According to EPA level 1 ecoregions, Washington state consists of marine west coast forests (lower elevations in western Washington), northwestern forested mountains (Cascade Range, Rocky Mountains, Okanogan Highlands, Olympic Mountains, and Blue Mountains), and North American deserts (Columbia River Basin) (US EPA, 2022). Each of these ecoregions is shared with other states in the American West and British Columbia, so studies conducted in any of these ecoregions were considered in our assessments of confidence for each variable that beavers influence, and Table 1 indicates the regions of Washington that confidence scores apply to. However, it is important to note that Washington's true climatic diversity is not adequately captured by solely three ecoregions as described above. For example, there is a definitive divide between the wetter montane areas west of the Cascade crest and drier montane areas east of the Cascade crest (see EPA Level 3 ecoregions, EPA 2022). While this distinction has potential repercussions for beaver influence, there are very few studies conducted west of the Cascade crest, so all montane areas of the state have been lumped for the purposes of our confidence assessments.

We broke down our findings into separate sections on the effects of beavers on abiotic and biotic components of ecosystems and the effects of beaver mimicry on abiotic and biotic components of ecosystems. Little research has directly assessed the ecosystem effects of translocated beavers (Dittbrenner et al., 2022; Gaywood, 2018; Petro et al., 2015). Given the lack of studies on biological and physical impacts of beaver relocations on ecosystems, we focus on describing the effects of established, non-translocated beaver as a representation of the potential impacts of beaver reintroduction. Beaver-mimicry includes a wide variety of process-based methods. Here, we focus on beaver dam analogues (BDAs), which are widely implemented and are the most well-studied form of beaver-mimicry. Because of a lack of literature, we do not evaluate post-assisted log structures or other small-scale debris jams that are frequently paired with or incorporated into BDA and beaver translocation projects. BDA installations are also frequently paired with beaver translocations to the same sites or are colonized by beavers. While this is often a goal of BRR, it can make it difficult to parse the effects of beavers and BDAs on ecosystems.

4.2 Assessment of evidence

We used two categorical assessment strategies to characterize (1) the validity of evidence and (2) the level of agreement within the literature on specific abiotic and biotic variables. Next, we combined the validity and agreement levels to assign a level of confidence for each variable of interest. Calibrated language was used to describe our confidence in each variable based on the IPCC's fifth assessment report (Mastrandrea et al., 2010) and the 2015 Washington State Wildlife Action Plan (SWAP, 2015). Our language and categories are detailed below.

Validity

Confidence in the validity of a finding was based on the type of evidence, replication within the study, and the applicability of the study to Washington ecosystems. Studies were considered individually, and the body of literature was assigned to a category for the validity of evidence for a specific variable of interest (e.g., beaver impacts on water temperature).

- Terms for categorizing validity of evidence are *'limited', 'medium',* or *'robust'*.
- The number of studies investigating a specific variable of interest were incorporated into assigning the validity of evidence, with thresholds based on SWAP confidence criteria (2015 SWAP). These sources were only considered if they came from ecoregions that could be applied to regions of Washington state.
- Individual study quality was assessed using the following criteria.
    - *Type of evidence*; based on type of study (experimental or observational) with experimental studies considered higher quality of evidence.
    - *Replication*; based on the level of replication with case studies representing *lower quality* evidence and replicated studies higher quality evidence.
    - *Applicability*; based on region where study was conducted and applicability to Washington ecoregions, with Pacific Northwest studies considered higher quality.

Degree of agreement

Degree of agreement for each variable was based on whether studies found the same directions of effect (e.g., beaver engineering warms water downstream vs. cools water downstream). Each study was assessed for the direction of influence on each variable, and then the level of agreement across the body of literature was assigned.

- Terms for categorizing the level of agreement are *'low'*, *'medium'*, or *'high'* and assigned using the following criteria.
    - *High*: Greater than 75% of studies agree on the direction of effect.
    - *Medium:* Greater than 50% but less than 75% of studies agree on the direction of effect.
    - *Low*: Less than 50% of studies agree on the direction of effect.

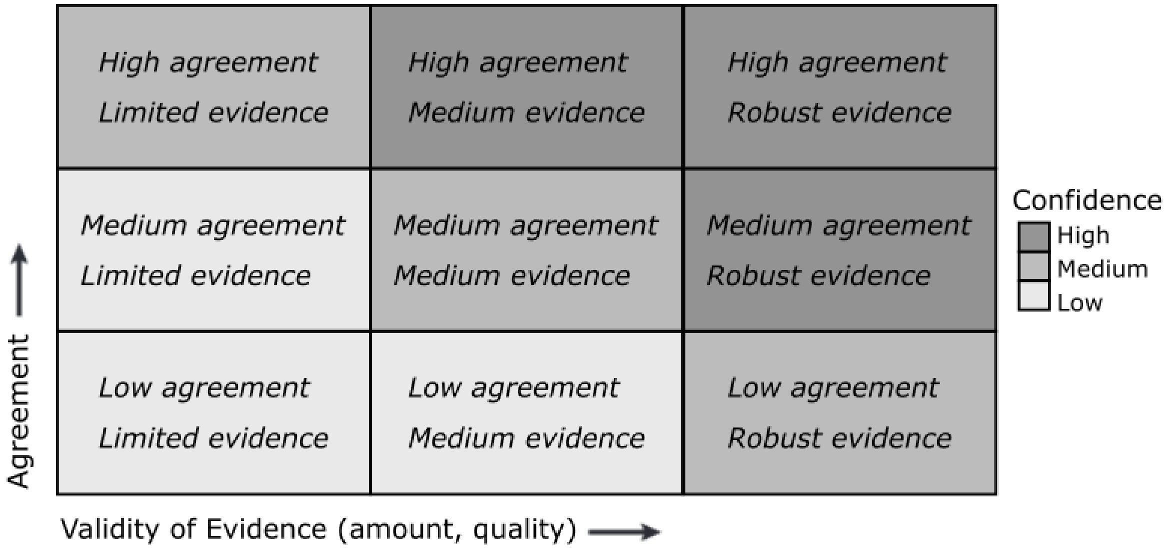

Figure 1. Agreement among sources and evidence available were used to determine confidence. Confidence increases as agreement and evidence increase, with the highest confidence associated with high agreement and robust evidence (top right corner) and the lowest confidence associated with low agreement and limited evidence (bottom left corner). Figure adapted from Mastrandrea et al., 2010.

Confidence

Our confidence was qualitatively assigned to *'low', 'medium',* or *'high'* based on a combination of the validity of evidence and degree of agreement (Figure 1; Mastrandrea et al., 2010). This approach was adapted from the more detailed IPCC categories in accordance with the WDFW 2015 SWAP. Robust evidence (multiple, independent, well-executed studies) or high agreement (consistent outcomes) resulted in the highest confidence in the evidence, while low agreement or limited evidence resulted in the lowest confidence in the evidence. Agreement and evidence scores were combined to get a confidence score (Figure 1). In cases where there was no evidence from applicable ecoregions, no confidence level was assigned.

5 Impacts of beaver on abiotic habitat characteristics

5.1 Hydrology and geomorphology

Across beaver ranges, a variety of hydro-geomorphic changes are precipitated by beaver damming's primary impact: decreased stream velocity and discharge (Ecke et al., 2017; Green & Westbrook, 2009; Larsen et al., 2021; Meentemeyer & Butler, 1999). Decreased stream flow due to damming leads to ponded and pooled areas forming within the stream channel, fundamentally shifting the ecosystem from a lotic state to a lentic state. This shift and the habitat heterogeneity it creates allows for both high and low flow impacts to be attenuated by beaver dams. During storm events, streams without beaver dams allow water to flow quickly and suddenly after peak rainfall, resulting in difficult-to-control flooding. In beaver-impacted sites, high flow storm events are slowed by beaver dams, and there is an increased lag between peak rain and peak flows due to slower water movement through the system (Puttock et al., 2021). As high flows hit beaver dams, they are slowed down and spread out across the floodplain, resulting in less discharge through the stream channel immediately following a storm event (Puttock et al., 2021).

Slow-flowing water and ponded stream morphology also attenuate drought conditions because water storage capacity increases. Both groundwater and surfacewater storage increases in beaver-dammed streams; slower-flowing water forms ponds that stretch laterally to increase wetted area, and water tables rise due to increased hyporheic exchange and increased water residence time (Dittbrenner et al., 2022; Westbrook et al., 2006). The increased surface- and groundwater storage makes beaver-occupied streams relatively unlikely to dry during periods with little rainfall compared to unoccupied streams (Hood & Bayley, 2008; Westbrook et al., 2006). Small streams with beaver dams have higher water tables and more surface water, resulting in greater water storage capacity throughout the dry season (Larsen et al., 2021; Hood & Bayley, 2008). However, increased surface- and groundwater storage also leads to increased evaporation and evapotranspiration rates, and there is some contention around whether the increase in evaporation may counteract the increase in water storage (Correll et al., 2000; Fairfax & Small, 2018; Larsen et al., 2021; Nash et al., 2021). Greater wetted soil leads to increased plant productivity (Fairfax & Small 2018), and therefore evapotranspiration, and increased surfacewater also evaporates faster than consolidated water in a stream channel. Both of these sources of evaporation can negatively impact water storage, and air temperatures and moisture levels could alter the net water storage capacity of stream systems. Given how dependent evaporation is on other climatic variables, net water storage may be highly context dependent and may vary across Washington State's ecoregions. Despite this concern, beaver-impacted streams are generally less subject to fluctuations in water level due to both flooding and drought, making them resilient to multiple types of disturbance.

Thermal fluctuations can also be buffered and altered by beaver damming. Thermal minima and maxima of beaver-engineered streams were both buffered relative to unoccupied streams in northeastern Oregon (Weber et al., 2017). Overall stream temperatures were initially thought to increase due to beaver activity, since beavers create pools of slow-moving water, which are more vulnerable to heating (Majevora et al., 2015). Majevora et al. (2015) found that beaver ponds in northern Utah increased temperature heterogeneity across a stream reach, with some pockets of warm, slow-moving water, and other pockets of cold, fast-flowing water. Furthermore, some evidence shows that overall stream temperature downstream of beaver dams decreases due to increased hyporheic exchange (Dittbrenner et al., 2022; Pollock et al., 2007). Hyporheic, sub-surface flows are more likely to mix with surface water if, as in beaver-modified landscapes, the water table is higher and water moves slower, allowing the water to sink into the ground and promote down-stream up-welling (Dittbrenner et al., 2022). This mixing and exchange between cool, sub-surface water and warm, surface water results in overall stream cooling, even if some pockets of beaver ponds remain relatively warm (Dittbrenner et al., 2022). Also, the extent to which streams cool may depend on the type of beaver complex; older beaver complexes with large, ponded areas are more likely to result in cooling effects compared to smaller complexes (Dittbrenner et al., 2022; Fuller & Peckarsky 2011). Smaller complexes create lower hydraulic pressure, resulting in lower groundwater upwelling downstream and less vertical connectivity (Dittbrenner et al. 2022).

Another range-wide result of decreased stream flow is increased sediment aggradation (Larsen et al., 2021). Slower flowing water carries smaller particulate matter, so smaller sediments are deposited at the dam impoundment compared to free-flowing reaches. Over time, these small sediments aggrade to create soft sand or silt substrates (Larsen et al., 2021). These sediments build up at the dam site, and beavers also pack sediments into their dams to strengthen them. Over time, these sediments contribute a to a significant portion of landscape sedimentation (Kramer et al., 2012; Persico & Meyer, 2009). Older, larger dams lead to even slower flowing water, resulting in smaller sediment deposition (Meentemeyer & Butler, 1999). The positive-feedback cycle continues until large, lentic ponds with soft substrates form. Across a watershed scale, a patchwork of beaver activity leads to areas of sediment aggradation where beavers are present as well as areas of erosion where dams have breached and beavers no longer maintain them (Burchsted et al., 2010). When beavers are not present, fast-moving water leads to incision and erosion, which results in faster-flowing water (Pollock et al., 2014). This feedback results in highly scoured, deep channels with little stream complexity, and these systems become vulnerable to both floods and drought (Jordan & Fairfax, 2022).

Few peer-reviewed studies consider beaver impacts to hydrology or geomorphology in Washington state, and only one study is likely to be applicable to montane regions of western Washington. In the Skykomish River Watershed of northwestern Washington, Dittbrenner et al. (2022) evaluated beaver impacts to stream temperature and water storage. Beavers were relocated to 5 sites within the watershed, allowing for a before-after-control-impact (BACI) design for relocation and control sites. Besides the 5 successful relocation sites, Dittbrenner et al. (2022) also surveyed 20 other sites consisting of unimpacted control sites, established beaver colonies, and relict dams. The authors found that beaver activity increased surface water storage and groundwater elevation while decreasing downstream temperature; the impact on temperature depended on pond size, with larger ponds causing a greater decrease in downstream temperature.

Other relevant studies conducted in western North America are from arid ecoregions applicable to eastern Washington and the east slopes of the Cascades. Most notably, several studies have been conducted in the Bridge Creek Intensively Monitored Watershed in northeastern Oregon (Demmer & Beschta, 2008; Pollock et al., 2007; Weber et al., 2017). This area has similar precipitation and temperature regimes to much of eastern Washington and the Columbia River Basin, making these studies highly applicable to some Washington systems. Weber et al. (2017) used a BACI design to evaluate temperature regimes at four monitoring stations. The authors found that diel stream temperatures were buffered by beaver dams, resulting in fewer days with maximum temperatures exceeding salmonid limits during hot summer months. Pollock et al. (2007) considered sediment accumulation upstream of 13 beaver dams of varying ages and found that sediments aggraded rapidly following dam construction, but that rates of aggradation declined by year six. Similarly, Demmer and Beschta (2008) found that beaver dams on Bridge Creek increased sediment storage. Other studies throughout the American West are likely also applicable to Washington systems to some extent, although differences in rates of evaporation and evapotranspiration, precipitation, and snow- or rain-driven hydrology should be taken into consideration.

5.2 Water Chemistry

As a result of altered water exchange and sediment entrapment, water quality and chemistry are impacted by beaver activity across their range; biologically and climatically relevant variables such as dissolved oxygen, phosphorus and nitrogen retention, and carbon and methane fluxes are all impacted by dams. Dams decrease longitudinal connectivity and downstream water velocity, and velocity is linked to dissolved oxygen because flowing water allows for greater diffusion of oxygen. Decreased flow in beaver impoundments therefore leads to decreased dissolved oxygen relative to upstream reaches with higher flow velocity (Brazier et al., 2020; Ecke et al., 2017; Larsen et al., 2021).

Low dissolved oxygen conditions lead to anaerobic bacterial metabolism, therefore slowing the rate of nutrient cycling and altering net fluxes of nitrogen (Larsen et al., 2021). Nitrogen may be removed from the water, increasing water quality, via several mechanisms. First, nitrogen accumulated in beaver ponds as ammonium

(NH_4^+) or nitrate (NO_3^-) can be taken up by plants within the beaver wetland or converted to atmospheric nitrogen (N_2) through denitrification (Larsen et al., 2021; Maret et al., 1987; Naiman et al., 1994). Alternatively, nitrogen compounds may be retained within beaver impoundments under sediments rather than being incorporated into plant biomass or released to the atmosphere (Devito & Dillon, 1993). Beaver ponds are considered nitrogen sinks with relatively high amounts of accumulated nitrogen (Coleman & Dahm, 1990; Lazar et al., 2015), but some evidence suggests that beaver ponds act as nitrogen sinks only when discharge is relatively high and transform into nitrogen sources when discharge is low (Wegener et al., 2017). Given this discrepancy, nitrogen fluxes in beaver ponds may be context dependent, and, while Devito & Dillon (1993) suggest using beaver ponds to improve water quality in eutrophic systems, managers should take location-specific context into consideration.

Another way that nutrient cycles are impacted by beaver impoundments is increased sediment entrapment. Fine sediments often carry nutrients such as phosphorus, which deposit and can be retained within beaver dam impoundments (Brazier et al., 2020; Ecke et al., 2017; Muskopf, 2007). However, phosphorus retention in impoundments is context-dependent; older, larger dams generally have a greater capacity to store nutrients because these nutrients are transported on suspended sediment, and more sediments are stored behind larger dams (Brazier et al., 2020; Meentemeyer & Butler, 1999). For example, phosphorus is often transported on sediments, so phosphorus retention is often greater in larger impoundments (Ecke et al., 2017; Maret et al., 1987). Phosphorus and other chemical retention also depend on discharge (Correll et al., 2000), with higher spring discharge leading to reduced phosphorus content compared to lower summer discharge (Maret et al., 1987). This pattern is explained by greater channelization and erosion during summer flows (Maret et al., 1987). However, other studies present contrasting evidence indicating that phosphorus is retained during low summer flows and released during high spring flows, and this pattern is explained by phosphorus accumulation during low flows and flushing during high flows (Devito & Dillan, 1993; Devito et al., 1989). Also, phosphorus content downstream of ponds may increase during low flow periods (Fuller & Peckarsky, 2011). Multiple interacting mechanisms are likely at play, and the results may vary depending on location (Fuller & Peckarsky, 2011), so more research is needed to understand phosphorus source-sink dynamics in beaver systems (Brazier et al., 2020).

Sediment entrapment also results in deposits of organic carbon in beaver impoundments and surrounding wet meadows (Ecke et al., 2017; Laurel & Wohl, 2018; Wegener et al., 2017; Wohl et al., 2012; Wohl, 2013). Beaver-influenced habitat on wide, unconstrained portions of rivers contribute disproportionately to carbon storage, with 75% of carbon stored within only 25% of one study's river reaches (Wohl et al., 2012), and another study estimated that relict beaver meadows contributed 8% of total landscape-scale carbon storage (Wohl, 2013). Furthermore, relict beaver meadows do not store as much carbon as active beaver meadows (Laurel & Wohl, 2018; Wohl, 2013), so Wohl (2013) hypothesizes that the historical decline of beaver populations may have led to a reduction in carbon storage capacity at the landscape scale. However, from a greenhouse gas perspective, beaver activity is not necessarily beneficial despite sequestering large amounts of carbon, because carbon flux to the atmosphere via CO_2 and CH_4 both increase in beaver impoundments (Ecke et al., 2017; Weyhenmeyer, 1999).

Research on nutrient cycling and water chemistry is limited to areas outside of Washington, and it appears to be highly context dependent. While general trends presented in Ecke et al. (2017) and above may be transferrable to Washington, more research is needed to understand regional differences in these trends.

5.3 Habitat heterogeneity and connectivity

Across their range, beavers increase habitat heterogeneity by creating multiple habitat types within a river reach, and these habitat patches are distributed across the landscape at a larger scale. Over time, landscapes shift from streams to beaver ponds to wet meadows, creating an ever-shifting mosaic of habitat types that support diverse organisms (Pollock et al., 2014). In this way, beaver engineering impacts individual habitat patch availability at the site scale as well as heterogeneity at the landscape scale, and both site and landscape scale impacts depend on time since beaver activity or abandonment.

At the site scale, beavers can increase longitudinal and lateral connectivity. Beaver dams create ponds or pools that break up stretches of faster-flowing water; the resulting increased lateral connectivity creates patches of varying habitat types that would otherwise be absent (Wegener et al., 2017). These pools also sometimes spill out over the stream banks and onto the floodplain, forming side-pools. Side pools are particularly common when beavers dig canals to move between foraging habitat and their lodge or den (Grudzinski et al., 2020 and references therein). Side pools, channels, or small ponds alongside the main stem of the stream are often very slow moving or even still water, which creates unique lentic habitat adjacent to the main lotic system (Grudzinski et al., 2020). These shallow pools and canals adjacent to rivers also serve as a connection between terrestrial and aquatic habitats, supporting organisms with biphasic aquatic-terrestrial life cycles as well as nutrient cycling across aquatic-terrestrial boundaries (Grudzinksi et al., 2020; Larsen et al., 2021). Also, lateral connectivity leads to long-term longitudinal connectivity because of the water storage effect and increased hyporheic exchange, which leads to lengthened hydroperiods. In this way, beavers can transform intermittent streams to perennial or perennial streams to permanent, depending on the permeability of the dam (Nash et al., 2021).

Many variables within each site depend on both dam size and age. Older, larger dams create greater increases in capacity for nutrient cycling, decreases in flow velocity, increases in sediment aggradation, and decreases in temperature, as discussed above (Dittbrenner et al., 2022; Laurel & Wohl, 2018; Meentemeyer & Butler, 1999). A beaver complex with multiple dams may have varying impacts on abiotic variables depending on the age of the dams, creating another layer of heterogeneity within the site. For example, some dams may be abandoned, while others may be actively maintained. All of these patch-scale differences can be present within a given beaver-occupied stream reach, watershed, and landscape, resulting in high heterogeneity both within a site and at larger scales.

At the landscape scale, beaver-engineered habitats are distributed throughout watersheds, and they come and go as beavers move when resources are depleted or predation is high. This patchy distribution of habitat types creates complex habitat mosaics within the watershed due to beaver pond legacy effects and the differing successional stages of engineered sites (Kramer et al., 2012; Larsen et al., 2021; Levine & Meyer, 2014). Abandoned beaver dams can exist for decades, but when they breach, some sediment is released downstream (Levine & Meyer, 2014). However, not all accumulated sediments erode after breaching, and sediments may remain in deposits for centuries (Kramer et al., 2012; Persico & Meyer, 2009). After a dam breaches, the stream may begin to rechannelize, and the previously wetted area may dry, allowing vegetation to grow and form wet meadows (Polvi & Wohl, 2012). Meanwhile, beavers will recolonize other parts of the stream where food is plentiful or predators are limited, and the cycle will repeat. The result is a continuum of stream, pond, and meadow habitat across each watershed at any given time.

5.4 Wildfire resistance

A landscape with all stages of beaver ponds (from new, relatively lotic habitat to abandoned lentic pond to filled wet meadow) will have greater overall moisture content compared to a landscape lacking the beaver mosaic, and this increased moisture has a direct impact on wildfire resistance and resilience. Beaver ponds provide resistance because large wildfires depend on continuous fuel availability, but wet meadows and beaver complex wetlands can act as a fire block where no dry fuel is available (Fairfax & Small, 2018). Because beaver dams increase water storage during dry periods of the year (Hood & Bayley, 2008), riparian vegetation in beaver-modified wetlands is more likely to remain green and fire-resistant compared to vegetation in areas without beavers (Fairfax & Whittle, 2020). Also, vegetation in floodplains with more heterogeneity grows back faster and more completely following wildfires, indicating fire resiliency as well as resistance (Wohl et al., 2022). One reason ecosystems are often slow to recover post-fire is loss of soil and remaining vegetation due to erosion. Erosion is limited by beaver dams, which lessen peak flows after storm events as described above. Lower peak flows lead to less erosion, allowing remaining vegetation to recover faster (Wohl et al., 2022) Therefore, beaver activity promotes both ecosystem resistance and resilience to wildfires.

No peer-reviewed studies on the beaver cycle and legacy effects have been done in Washington systems, but the broadscale impacts across time and space are likely applicable across ecosystems. The cycle of stream to pond to meadow to stream described above has been studied in both Europe (Rudemann & Schoonmaker, 1938) and across North America (Pollock et al., 2014; Polvi & Wohl, 2012; Westbrook et al., 2011) with minimal differences in the overarching patterns that emerge (Rosell et al., 2005). More specific impacts regarding wildfire resistance and resilience may vary depending on vegetation type and fire regime, but studies from Colorado (Wohl et al., 2022) and throughout the American west (Fairfax & Whittle, 2020; Fairfax & Small, 2018) are likely applicable to much of the montane and Columbia River Basin Regions of Washington, which shares ecoregions with these areas (US EPA, 2022). Additionally, one thesis focused on the east slope north Cascades region compared beaver impounded stream reaches and unimpounded stream reaches in burned and unburned regions (Weirich, 2021). Weirich (2021) found that beaver impoundments interacted with slope and solar radiation to affect burn severity, and all beaver impounded riparian sites in the study burned with relatively low severity. However, no studies have considered beaver impact to fire resistance in regions with infrequent fire regimes and high precipitation, as in western Washington, so applicability west of the Cascades is limited.

6 Impacts of beaver on biotic communities

6.1 Vegetation

Impacts of beaver herbivory

Beavers are herbivores that impact riparian and aquatic plant communities through both direct and indirect mechanisms. Beavers are choosy generalist herbivores that primarily eat deciduous, flood-tolerant woody plants such as aspen (*Populus tremuloides*), poplars (*Populus spp.*), birch (*Betula spp.*), and willows (*Salix spp.*), though preferred species can vary by region (Baker & Hill, 2003; Naiman et al., 1988; Westbrook, 2021). Beavers are unique in that they can harvest and fall mature trees but also heavily use emergent and submerged aquatic vegetation, particularly during summer months. Patterns of herbivory and food selection vary throughout the year and can vary with the distance from water, primarily occurring within 50m of the water's edge (Stoffyn-Egli & Wilson, 2011). Because of these behaviors, the territorial nature of beavers, and the high quantity of vegetation consumed and altered, beavers are agents of disturbance and can have large impacts on plant communities in riparian areas of their home ranges (Westbrook, 2021).

No peer-reviewed studies have been conducted in Washington freshwater systems investigating direct beaver impacts to riparian plant communities. However, a wide variety of peer-reviewed studies and reviews, primarily focusing on beaver impacts to riparian communities in boreal forests, the Upper Midwest of the United States, and Europe indicate specific temporal impacts related to the beaver-cycle that likely apply well to areas of western Washington despite being in different EPA level 1 ecoregions (US EPA, 2022). During initial colonization of a site, beaver herbivory can decrease canopy cover and basal area (average amount of area occupied by stems). Over time, this has a positive effect on sub-canopy woody species and wetland plant species, and herbivory favors early successional shrubs and water tolerant species. As browsed plants recover and respond to opened canopies, beaver herbivory increases basal area and productivity through re-sprouting and coppicing of chewed woody plants, and alterations of age, size, and structure of riparian communities from mature trees to immature shrub-like smaller trees (Baker & Hill, 2003; Brazier et al., 2020; Donkor & Fryxell, 1999; Johnston & Naiman, 1990; Larsen et al., 2021; Law et al., 2017; Naiman et al., 1988; Rosell et al., 2005; Westbrook, 2021). Beaver herbivory can decrease canopy cover at the local scale, have a positive effect on sub-canopy woody species and wetland plant species, and favor early successional shrub and water tolerant species. Initial increased wetted area from dams may also shift community composition towards more water tolerant species, which beavers tend to prefer. Alternatively, beaver preferences can lead to shifts in community composition towards less preferred species, like conifers, when sites are occupied for long periods of time (Larsen et al., 2021; Naiman et al., 1988). Long-term, preferred foods, such as aspen, may decline due to beaver herbivory (Barnes & Mallik, 2001). The changes in community composition are context dependent, temporally dependent, and no single study adequately captures the potential dynamic impacts of beaver engineering coupled with herbivory on plant communities. However, these well documented trends correspond with the “beaver-cycle,” and beaver herbivory in western parts of Washington state and heavily forested areas likely results in strong shifts in riparian community composition and structure to favor increased basal area, fewer mature trees, and increased canopy openings at least during initial colonization and active occupancy of beaver sites.

Dryland studies, generally in semi-arid regions with limited precipitation, may be more applicable to the east Cascades and Columbia River Basin ecoregions of Washington state. A 2014 review of beaver impacts in dryland systems, including areas of central Washington east of the Cascade crest through the Great Basin and into the southwestern United States, notes close associations and limited population effects to willows (Salix spp.) from beaver herbivory. Studies in Arizona and Nevada note beaver herbivory did not result in declines of rare willow species and even promoted willow density and growth (Gibson & Olden, 2014). In southeast Oregon, a 1985 study of beaver herbivory impacts to red willow (Salix lasiandra) corroborates these findings, with no population impacts from heavy sustained browsing of willow and increases in growth in Jordan Valley, OR (Kindschy, 1985). Furthermore, a southwest Montana study in a snowmelt-driven, low precipitation headwater system found increased rates of willow recruitment associated with beaver herbivory because of the increased number of dispersed cuttings (Levine & Meyer, 2019). However, Gibson & Olden (2014) also note potentially significant reductions in populations of cottonwood (*Populus* spp.) due to beaver herbivory where other woody riparian vegetation is limited. No studies summarized in Gibson & Olden (2014) focus on Washington, but these dominant patterns in the literature likely hold true for some of the drier areas of Washington State. In dryer areas of Washington, beaver herbivory likely leads to increased spread and recruitment of willow but may negatively impact populations of mature riparian trees or other food plants that are less regenerative than willow.

While most studies on the impacts of beaver herbivory focus on woody species, beaver diets often shift seasonally to include a high proportion of emergent and submerged aquatic vegetation during summer months. However, no studies have been conducted on impacts of beaver herbivory on these groups of plants in the western US or Washington State. A single study conducted in Georgia’s wetlands investigated the impacts of beaver herbivory on biomass and community composition of aquatic vegetation over two years, finding that beaver herbivory significantly reduced biomass and suppressed total plant abundance. Shifts in dominant plant species were also noted (Parker et al., 2007). This is primarily a high precipitation, rain driven system, and parallels between this habitat and those found in Washington state are not clear.

Impacts of beaver engineering and hydrologic shifts

Hydrologic and geomorphologic changes associated with beaver engineering can impact riparian and aquatic plant communities. Beaver damming results in flooding and raised water tables in areas that were previously dry by comparison. This can cause many plant species that existed prior to damming to die; resulting in an initial decline in plant species richness and biodiversity (Brazier et al., 2020; Franczak & Czarnecka, 2015; Rosell et al., 2005; Westbrook, 2021). Flooding alters riparian plant communities and structure because inundation of riparian communities for lengthy periods results in anaerobic conditions that can kill plants; however, if inundation periods are shorter, seed banks may remain viable and beaver abandonment may promote re-establishment of the original community (Rosell et al., 2005; Westbrook, 2021). Abandoned sites and dam breaches can create primary succession habitat for sedges and grasses and induce patterns of terrestrial succession (Rosell et al., 2005). The beaver meadow formation theory is a general conceptual model for beaver engineering (Polvi & Wohl, 2012). According to the model, flooding leads to an initial reverse succession, and subsequent abandonment and draining leads to a delayed forward succession of meadows (Larsen et al., 2021; Westbrook, 2021). This ultimately has been shown to lead to increases in vegetation species richness at the landscape scale because of the creation of habitat mosaics and increases in habitat heterogeneity with patches of differing age and succession trajectories (Larsen et al., 2021; Naiman et al., 1988; Wright et al., 2002). This pattern likely applies across ecoregions as this successional pattern has been documented across a large geographic expanse of both North America and Europe.

Studies in dryland systems may apply more directly to east Cascades and Columbia River Basin ecoregions of Washington state. Gibson & Olden's review of beaver impacts in dryland streams indicates positive associations of beaver dam density and riparian vegetation and cover density (Cooke & Zack, 2008; Gibson & Olden, 2014). Further, this review hypothesizes that patterns of colonization and abandonment increase habitat heterogeneity that promotes species diversity at the landscape scale, consistent with the beaver meadow formation theory discussed above, though studies in regions applicable to Washington have not been conducted. Levine and Meyer (2019) demonstrated that beaver engineering alters geomorphology and hydrology that favors willow establishment and dispersal in semi-arid snow melt driven systems of Southwest Montana. Additionally, in areas of Nevada with low precipitation and seasonal drought dynamics, beaver presence and damming intensity was shown to increase riparian plant productivity, likely through increased groundwater availability for riparian plant communities (Fairfax & Small, 2018). Finally, a master's thesis investigated riparian plant diversity in burned and non-burned watersheds of the Methow River valley with and without beavers (Whipple, 2019). Whipple (2019) found that in unburned sites, beavers increased overall riparian plant diversity, but, in burned watersheds, beavers reduced species richness but increased woody species density (Whipple, 2019). This literature suggests that in dryer parts of Washington state, such as the East Cascades and Columbia River Basin ecoregions, beaver engineering and patterns of site colonization and abandonment likely increase species richness in plant communities at the landscape scale and may increase productivity and recovery of riparian vegetation in degraded or disturbed systems.

6.2 Invertebrates

Ecosystem engineering by beavers can have strong influences on both aquatic, benthic, and terrestrial invertebrate communities. Alterations to flow regimes and water velocity, changes in substrate composition and organic matter deposition, increased input of woody debris, and alteration of trophic interactions can all impact the density, biomass, and community composition of invertebrate communities (Bush & Wissinger 2016;

Washko et al., 2022). Impacts to invertebrate communities are highly context dependent, though recent reviews and meta-analyses have summarized general trends.

Aquatic Invertebrates

Aquatic invertebrates are often characterized based on their associations with lentic or lotic habitats. Thus, beaver engineering that impounds water alters the community composition and biodiversity of aquatic invertebrate communities within impacted habitats. Beaver complexes are more likely to contain lentic taxa, such as *Odonata* (dragon/damsel flies), *Chironomidae* (non-biting midges), *Dytiscidae* (diving beetles), and *Mollusca* (mollusks), compared to stream reaches unmodified by beavers, which are more likely to contain lotic taxa such as *Ephemeroptera* (mayflies), *Plecoptera* (stoneflies), and *Trichoptera* (caddisflies) (Brazier et al., 2020; Bush & Wissinger, 2016; Rosell et al., 2005; Washko et al., 2022). Washko et al. (2022) conducted a meta-analysis using studies that compared species richness between paired lotic streams and lentic beaver engineered sites and found that, in general, species richness is reduced within engineered habitat patches. However, because stream reaches with beaver populations tend to contain habitat heterogeneity with lotic and lentic patches at varying successional stages, these systems can generally support multiple different invertebrate communities within a relatively small space. This ultimately results in patterns of higher beta and gamma diversity compared to stream systems without beavers and can support a metacommunity effect within a stream reach that promotes community resilience at the landscape scale (Bush & Wissinger, 2016; Washko et al. 2022).

Hydrologic and geomorphologic changes caused by beaver engineering also alter substrate composition and organic matter deposition that can impact the biomass and density of aquatic invertebrates. McCaffery & Eby (2016) and McDowell & Naiman (1986) demonstrated increases in density and biomass of aquatic invertebrates related to beaver engineering, and this result is reiterated in reviews (Brazier et al., 2020 and references within; Rosell et al., 2005 and references within; Washko et al., 2022). Changes in abundance are often accompanied by changes in the relative abundance of functional-feeding groups; predator and gatherer functional groups increase, while scrapers decrease. Despite many studies finding increased biomass and density in beaver-engineered patches compared to lotic patches, Washko et al. (2022) found these increases to be highly context-dependent because site specific geology, topography, ecology, and setting can heavily influence geomorphic and biological outcomes of beaver dam building, making generalization across ecoregions difficult.

While these general trends exist across the literature, many of the studies included in these reviews and meta-analyses are not easily comparable to freshwater systems in Washington state, such as studies conducted in boreal forests and areas of the south-eastern United Sates. However, three peer-reviewed studies particularly apply to Washington systems. First, Roper (2022) implemented a before-after-control-impact study design utilizing PacFish InFish Biological Opinion (PIBO) Effectiveness Monitoring Program surveys to investigate how beaver colonization impacted aquatic invertebrate community composition**.** Roper (2022) conducted surveys across ten years in low gradient streams within the greater intermountain region. Surveys included samples collected upstream and downstream of beaver impoundments but excluded sampling the ponded area specifically. This study included sites in NE Washington (Okanagan and Canadian Rocky Mountain ecoregions) and found few changes in the macroinvertebrate communities within the fast-water habitats between or below the beaver dams, indicating no stream level impacts on aquatic invertebrate community composition or biomass/density, but the author notes the limitations of the sampling design for determining patch level impacts of beaver engineering within the impounded habitat (Roper, 2022). The second applicable study was conducted in semi-arid snowmelt driven stream systems in northeastern Utah (Washko et al., 2020). Washko et al. (2020) found that beaver impoundments lowered species richness, biomass, and density of aquatic macroinvertebrates compared to paired lotic reaches, although this conflicts with other evidence that macroinvertebrate biomass increases at beaver engineered sites. Beaver engineering shifted community composition and dominant functional feeding groups in this study as well, but the restructuring of communities did not have a clear trajectory and differed by stream reach. The authors do conclude that overall stream diversity may have been increased by beaver engineering because of the addition of taxa not found in lotic reaches. Lastly, McCaffery & Eby (2016) conducted a study in semi-arid snowmelt driven stream systems in southwestern Montana. In this study area, beaver impoundments increased total abundance of macroinvertebrates, including both aquatic larval life stages and emerging adult life stages, when compared to paired lotic stream reaches (McCaffery & Eby, 2016). While community composition did shift in beaver impounded areas, taxa that had lower relative larval stage abundance were generally found to have higher abundance in emerging adult life stages. In some cases, invertebrates emerged at more than two times higher rates in beaver sites than lotic streams for all taxa. These studies were conducted in snow melt driven, semi-arid systems that are likely comparable to snowmelt systems in montane ecoregions and areas in the Columbia River Basin of Washington.

Terrestrial Invertebrates

Beaver engineering often creates heterogeneous habitats with complex combinations of semiaquatic, emergent, and submergent vegetation, as well as an abundance of woody debris that can impact terrestrial invertebrate communities. Beavers may alter the structure of plant communities, increase dead woody debris, and alter canopy closure, which can impact invertebrate abundance and community composition (Bush & Wissinger, 2016; Rosell et al., 2005). However, few studies have investigated beaver engineering impacts to terrestrial invertebrate communities. Bush & Wissinger (2016) reviewed beaver engineering impacts to invertebrate communities and concluded that wetted edges, shallow regions, and abandoned beaver wetlands created refuges for terrestrial and semi-terrestrial taxa. From studies conducted in Georgia, they found that the relative abundance and composition of the invertebrate communities increasingly shifted towards terrestrial invertebrates with increasing site successional stage, corresponding with a decrease in water surface area (Bush & Wissinger, 2016 and references therein). *Coleoptera*, a representative group of saproxylic beetles, were found to prefer beaver sites; emergence holes (evidence of the completion of a single beetle's life cycle) occurred in higher abundance at beaver sites when compared to control sites in New Brunswick, Canada (Mourant et al., 2018). While these beetles will not colonize snags below the water line or wood within beaver dams, the authors attribute increased abundance of beetle emergence holes to the increase in dead and decaying terrestrial wood and snags caused by beaver engineering. To date, no peer-reviewed studies have been conducted investigating beaver impacts to terrestrial invertebrate communities in Washington state. However, these patterns discussed in the studies above are likely ubiquitous for heavily engineered sites where extensive overbank flooding and tree harvest can create significant accumulations of dead woody debris and snags. These finding likely apply to areas in the western part of Washington state and montane regions, but it is not clear that these studies will apply directly to stream habitats without significant numbers of larger woody riparian species, such as semi-arid regions of eastern Washington.

A single peer-reviewed study (McCaffery & Eby, 2016) of beaver impacts to terrestrial invertebrate species conducted in a semi-arid montane snow-melt driven system of southwest Montana likely provides some context to impacts in drier areas of Washington, specifically the East Cascades montane ecoregion. In this study, spider abundance and percent of aquatic-based carbon diet were compared between beaver impounded streams and control streams to investigate aquatic-terrestrial food web linkages (McCaffery & Eby, 2016). Spider abundance was found to be 60% higher at beaver impounded sites, and a higher percentage of their diet was aquatic-based. The authors attribute this increase in terrestrial predatory spiders to increases in the abundances of emerging aquatic invertebrates and overall higher stream-to-land aquatic subsidies. However, the study was limited by lumping of spider species and a lack of control for other beaver-caused structural impacts. Overall, there is limited research indicating how beaver engineering will impact terrestrial invertebrate communities in freshwater systems of semi-arid regions of Washington state.

6.3 Amphibians and reptiles

Amphibians

Beaver engineering impacts to amphibians have been relatively well studied across areas of North America and Europe and are summarized in multiple recent reviews. Beavers create complex, heterogenous lentic systems with associated increases in hydroperiod, connectivity, wetted area, emergent vegetation, woody debris, soft organic substrates, and opening of canopy closers. These factors increase amphibian species richness and occupancy; provide habitat for breeding and development; and increase abundances of some amphibian species (Brazier et al., 2020 and references within; Dalbeck et al., 2020; Larsen et al., 2021 and references within; Rosell et al., 2005). These impacts are often greater in headwater systems than in low elevation sites (Brazier et al., 2020). In arid and semi-arid systems, the importance of beaver impacts for amphibians is likely greater, as beavers create perennial lentic sites that may hold water in areas that previously dried completely, providing habitat that facilitates the use, reproduction, and persistence of dryland amphibian species (Gibson & Olden, 2014; Smith & Goldberg, 2022). However, beaver engineering may shift community composition and favor lentic species over lotic species; specifically, lotic obligate species may be negatively impacted (Brazier et al., 2020; Rosell et al., 2005). This has been observed in studies where terrestrial salamanders were included in the amphibian assemblages, although only site scale impacts were considered (Metts et al., 2001). Additionally, beaver engineered sites may also contain more amphibian predators (fish) that could negatively impact amphibian populations because of lengthened hydroperiods, shifting these wetlands into sink habitats. However, in most cases, the increase in habitat heterogeneity within the site is hypothesized to allow fish and amphibians to coexist (Dalbeck et al., 2007; Dalbeck & Weinberg, 2009; Karraker & Gibbs, 2009; Petranka et al., 2004; Stringer & Gaywood, 2016), though few studies have investigated this extensively. In general, the greater body of literature spanning North America and Europe indicates that beaver engineering is beneficial to species richness, occupancy, and production in amphibian communities.

Beaver and amphibian associations have been directly studied in Washington systems and other freshwater systems in the Great Basin and Rocky Mountain regions that may apply to specific habitats in Washington. In the southern Washington Cascade montane region of Washington state, beaver impounded sites had 2.7 times higher species richness when compared to similar un-impounded sites (Romansic et al., 2021). This was primarily due to the addition of slow-developing species such as red-legged frogs (*Rana aurora*) and northwestern salamanders *(Ambystoma gracile*). Occupancy of both slow and variable-developing (rough-skinned newt *Taricha granulosa* & long-toed salamanders *Ambystoma macrodactylum)* species was also higher in beaver impounded sites, as was breeding density for three of the four species considered. In these high precipitation, snowmelt driven systems, beaver sites had deeper water, lengthened hydroperiods, and increased quality of reproductive and nursery habitats that ultimately benefited amphibian communities and slower-developing species. In areas of the Great Basin, associations between beaver engineered sites and Columbia spotted frogs (*Rana luteiventris*; candidate for state listing) have been well studied. Studies found that frog occupancy at beaver ponds was higher than non-beaver engineered sites, and frogs were significantly more likely to occupy beaver engineered sites than stream reaches without signs of beaver (Arkle & Pilliod, 2015; Smith & Goldberg, 2022). However, this pattern reversed as average precipitation increased. In areas with higher precipitation, spotted frog occupancy declined with beaver presence, suggesting that where water and suitable habitat is less limited, frogs may have been avoiding beaver sites (Smith & Goldberg 2022). The presence of predatory fish in some beaver sites was one hypothesized explanation (Smith & Goldberg, 2022). In both cases, beaver ponds provided most of the suitable habitat for Columbia spotted frogs in terms of water quantity, hydroperiod, and flow regime across the study areas. These study sites in the Great Basin may reflect conditions found in the Columbia River Basin and East cascades ecoregions where water can be limited. In the East Cascades ecoregion in Oregon, Oregon spotted frog (*Rana pretiosa*; federally listed as Threatened) metapopulation dynamics and patch occupancy were studied with beaver engineered and non-engineered sites as distinct habitat patches. The odds of a habitat patch remaining occupied across the multi-year study were 9.37 times greater when a beaver dam was present. The authors found that Oregon spotted frog meta-demographic rates were strongly tied to water availability, and beaver dams had the greatest positive effect on local persistence out of all explanatory variables considered (Duarte et al., 2020). Additional work in this system has shown that Oregon spotted frogs commonly used beaver structures and engineered environments for overwintering sites, positing that these altered habitats provide refuge from predators and thermal buffering (Pearl et al., 2018). Finally, in areas of the Rocky Mountains, generally semi-arid snowmelt driven systems, beaver engineering increased colonization rates, occupancy, and breeding occupancy for anurans, some salamanders, and western toads (*Anaxyrus boreas*) across multiple states, primarily due to beaver engineering creating larger, deeper, and longer lasting areas of surface water and increased connectivity of sites (Barille et al., 2021; Hossak et al., 2015; Zero & Murphy, 2016). While these studies from the greater western United States may not have direct links to habitats in Washington state, the montane, semi-arid sites can provide some insight into how beavers might impact amphibian communities in the Cascades and eastern portions of the state.

Reptiles

Very few studies have been conducted on reptile and beaver associations. Increased heterogeneity of habitats on the landscape coupled with larger deeper pools, increases in dead and downed woody material, decreases in canopy closure, and varying ages of beaver engineered sites at different successional stages may be expected to benefit different reptile species and diversity at the landscape scale. For example, increases in basking structures and ponded areas may benefit different turtle species, which have been recorded at beaver sites in Canada (Reddoch & Reddoch, 2005). While this ecoregion does not have direct links to ecoregions of Washington state, increases in basking structures, such as downed trees, combined with increased pond depth and wetted area may be expected to benefit turtle species of conservation concern in Washington, like the western pond turtle (*Actinemys marmorata*). Additionally, lizard and snake species may benefit from increases in basking and foraging opportunities, as well as increases in the abundance of prey, such as invertebrates and pond-breeding amphibians. Only two studies directly measured reptile species richness and diversity related to beaver engineering in a comparative study design. These studies, conducted in South Carolina, found increases in reptile species richness at beaver sites that increased, and shifted composition, with pond age (Metts et al., 2001; Russell et al., 1999). Newer beaver ponds had higher diversity of turtle species compared to un-impounded and old ponds, but older ponds had higher diversity of lizards and snakes consistent with these taxa's need for early successional habitat. In general, impacts of beavers on reptile communities are likely to increase species richness, but data is lacking for Washington habitats.

6.4 Fish

Beaver engineering impacts to, and interactions with, fish is a well-researched and somewhat contentious topic across beaver ranges. Through their ecosystem engineering, beavers have strong impacts on fish communities because they alter habitat structure, habitat quality, and hydrologic connectivity (Brazier et al., 2020; Kemp et al., 2012; Larsen et al., 2021). These abiotic changes can influence migration patterns, survival, production, diversity, and composition of fish communities. Attributes of beaver engineered sites can favor fish production and survival including increased production of prey, increased vegetation structure, slowing of water velocities, larger edge-to-surface water ratios, and increased hydroperiod (Collen & Gibson, 2001; Kemp et al., 2012; Pollock et al., 2003, 2004). Studies have demonstrated that beaver engineering increases both spatial and temporal habitat heterogeneity through patterns of colonization and abandonment that can benefit overall fish diversity (Schlosser & Kallemeyn, 2000; Smith & Mather, 2013). However, negative impacts may include localized increases of stream temperatures outside of thermal maximum, impacts to spawning habitats via increased fine sediment and inundation of gravel substrates, and potential barriers to fish movement and passage during low flow periods (Brazier et al., 2020; Kemp et al., 2012; Larsen et al., 2021). Kemp et al. (2012) conducted the most thorough review and meta-analysis of beaver impacts on fish to date. This review focused on studies in low-order stream systems and found that positive effects of beavers were more common than negative effects across the literature. Additionally, a survey of expert opinion included more favorable views of beaver impacts than negative views. The greater body of literature primarily emphasizes North American salmonid species and focuses primarily on temperate systems; outcomes are often highly context- and species-dependent. The general trend across the literature from both North America and Europe is that beavers are beneficial for creating complex fish habitat, can increase fish diversity by increasing habitat heterogeneity at the patch and landscape scale, and can increase fish abundance and production but may limit fish passage in certain hydrologic scenarios.

Beaver impacts on salmonids in Washington

In Washington state, much of the interest in beavers and their ecosystem-engineering is derived from their impacts on anadromous fish. There have been a number of studies conducted in western Washington and Oregon investigating the importance and impacts of beavers on salmonids in small coast range streams, larger coastal river basins, and streams in semi-arid regions of the Columbia River Basin. Within the Pacific coastal ecoregion, fishes identified as making substantial use of beaver ponds include coastal cutthroat trout (*Oncorhynchus clarki)*, sockeye salmon (*O. nerka)*, steelhead (*O. mykiss)*, Dolly Varden (*Salvelinus malma)*, and Chinook salmon (*O. tshawytscha)* (Pollock et al., 2004). Beaver created habitats in coastal river basins of Washington, Oregon, and California were shown to benefit juvenile Coho (Leibholt-Bruner et al., 1992; Parish & Garwood, 2015; Pollock et al., 2004). Pollock et al. (2004) analyzed historic trends of beaver created habitats in the Stillaguamish river basin and concluded that Coho production could be drastically increased if beaver engineered sites were returned to historic prevalence within the watershed. Another study in the Skagit river delta of western Washington found that intertidal beaver populations tripled pool habitats. These pools benefited juvenile Chinook, resulting in low-tide Chinook densities multiplying by 12.2 times in beaver engineered sites compared to sites without beavers in shallow tidal marshes (Hood, 2012). Similarly, a study in small streams in the Oregon Coast Range found that beavers created the largest pools and ponds within these drainages, and the abundance of Coho fry was 3-times higher in these beaver sites compared to control sites (Leibholt-Bruner et al., 1992).

A series of studies from the Bridge Creek Intensively Monitored Watershed in the Columbia River Basin of Oregon provide the best evidence for beaver impacts to salmonids (including studies on mechanisms for impacts) that likely apply to areas of Washington east of the Cascade crest and in the Columbia River Basin. These studies primarily focus on steelhead. Bouwes et al. (2016) found large increases in the quantity of juvenile salmonid habitat that increased juvenile abundance, survival and production by 168%, 52%, and 175% respectively. This occurred over the multiple years of monitoring, a period where 171 new natural beaver dams were built within the monitored area. Further studies into the mechanisms of these positive impacts on steelhead populations demonstrate that beaver engineering increased the quality and quantity of salmonid habitat¸ including buffering thermal regimes that benefit cold water fish (Weber et al., 2017) and increased habitat heterogeneity that allows microhabitat partitioning, which is hypothesized to correlate with the increases in survival and abundance of steelhead (Wathen et al., 2018). It's important to note that the results from studies in the Bridge Creek watershed are complicated by active restoration and implementation of BDAs. While much of the 8-fold increase in natural beaver damming activity occurred in non-BDA treated sections of the watershed, BDAs and natural beaver dams both increased over the monitoring period and contributed to the impacts on steelhead described above.

Beaver impacts on other fish in Washington

Impacts of beaver engineering on other non-salmonid fish species have not been well studied in Washington state. To our knowledge, a single study in Washington investigated beaver impacts to a non-salmonid fish in the Skagit river delta. Like the findings for Chinook, intertidal beaver engineering was found to increase low-tide habitat by 2.3-fold for three-spined stickleback (*Gasterosteus aculeatus),* resulting in 6.5-fold higher stickleback density in beaver engineered sites compared to controls (Hood, 2012). Data for both prickly sculpin (*Cottus asper*), and juvenile river lamprey (*Lampetra ayresi)* showed similar patterns in this study, suggesting that intertidal beaver dams provide valuable fish habitat for a diversity of species. In small snowmelt reliant tributaries of the Upper Snake River, the northern leather-side chub (*Lepidomeda copei*) was found to occur primarily in beaver sites because of increased habitat complexity, heterogeneity, and flow complexity associated with beaver engineering (Dauwalter et al., 2014; Dauwalter & Walrath, 2018). In this semi-arid region of the great basin, higher flow complexity associated with beaver engineering increased the co-occurrence of flowing and standing water, creating habitat necessary for this drift-feeding fish species. Similarly, an Oregon Department of Fish and Wildlife monitoring project for the endemic Oregon chub (*Oregonichthys crameri)* found that the chub was positively associated with beaver engineered sites because of the habitat characteristics created by beaver engineering, such as increased sedimentation, alterations of vegetation structure, and slower flow regimes in the Santiam and mid-Willamette river drainages (Scheerer et al., 2004).

No studies on beaver impacts to fish diversity and community composition have been conducted in regions applicable to Washington state. While the general conclusion is that habitat complexity increases fish diversity across the landscape it is not clear that this pattern applies to the systems of Washington. In snow-melt driven tributaries of rivers in semi-arid regions of Arizona, beaver engineering significantly shifted fish community composition to include a variety of non-native invasive fish species (Gibson et al., 2014). These engineered sites also had higher abundances of non-natives compared to control sites. While this system does not relate well to freshwater systems of Washington, it is important to note that the overall effect of dams on native fishes may depend on the presence of non-native species that may also benefit from the habitats created by beaver engineering.

Beaver impacts on fish passage

Among potential negative impacts of beavers on fish, restriction of movement and barriers to migration routes for anadromous fish are the most common. In Kemp et al. (2012), 43% of the 108 papers included in the review discussed beaver dams as barriers to fish movement. However, ~78% of these were speculative instances of disruptions to fish movement and were not supported with data. Furthermore, anadromous fish and beaver have coexisted across the United States for millennia, providing further support that beaver dams likely impose limited impediments to fish movement. Within the western United States, multiple studies have addressed fish passage of beaver dams in a variety of systems. The Bridge Creek study system in the Columbia River basin of Oregon is perhaps the most applicable to regions of Washington state. PIT-tagged spawning steelhead migration success was not impacted by the 200+ BDAs and beaver dams built over three years within Bridge Creek; similar proportions of fish passed specific passive instream antennae (PIAs) before and after the dramatic increase in dams (Bouwes et al., 2016). Additionally, more than 1000 PIT-tagged juveniles migrated downstream each year of the study, consistent with expected survival and production for the system. These results likely apply to Columbia River basin ecoregions of Washington, specifically east of the Cascade crest. In Utah, native Bonneville cutthroat (*Oncorhynchus clarkii utah)* and nonnative brook and brown trout were all able to pass beaver dams in semi-arid snowmelt driven intermontane streams (Lotkeff et al., 2013). Both cutthroat and brook trout passed large beaver dams while brown trout were restricted to passing smaller beaver dams. The native cutthroat passed dams from base to peak flows. In this system, it's hypothesized that beaver dams helped native trout find habitats free of invasive competitors. In southwest Montana tributaries of the upper Missouri river, average Artic grayling (*Thymallus arcticus)* passage over unbreached dams was 88% when other factors were controlled (Cutting et al., 2018). However, passage fell to less than 50% over specific dams, and breached dams had less successful fish passage, likely due to increased water velocity through breaches. In this study, the probability of fish passage was highest for single sided linkages (i.e. water moving around a single side of the dam) rather than no linkages or two-sided linkages, likely due to the increased depth of downstream scour pools associated with single-linkage dams. Both of these studies were conducted in semi-arid, snow melt driven headwater stream systems that likely apply to montane snow-melt driven steams in the Cascades areas of Washington. While outcomes for fish passage may vary by species of interest and hydrologic status of the systems (i.e. drought flow conditions; Kemp et al., 2012), studies that may be applicable to Washington systems indicate that most beaver dams likely do not pose significant fish passage barriers for anadromous fish species.

6.5 Other Taxa

Mammals

Beaver engineering impacts to other mammal species have been historically noted across North America, and contemporary studies are increasing in Europe as Eurasian beaver populations recover from widespread extirpation. Numerous mammalian species use beaver created habitats, including dams, lodges, and canals; different species benefit during different phases of beaver succession (reviewed in Rosell et al., 2005; Rosell & Campbell-Palmer, 2022). Small mammals may benefit from altered insect abundance and vegetation structure, and increased habitat complexity provides shelter. Meso-mammals may benefit from increased prey abundance and habitat complexity, and larger herbivores, including a variety of *Cervid* species, can benefit from increased foraging opportunities (Nummi et al., 2019; Rosell & Campbell-Palmer, 2022).

While information on mammalian community associations with beaver habitat is limited, several species' associations with beaver habitat have been studied individually. For example, semi-aquatic mammals, such as river otter (*Lontra canadensis*) and muskrat (*Ondantra zibethicus),* benefit from beaver created habitats and may use beaver structures for shelter (Depue and Ben-David, 2010; Mott et al., 2013). Aquatic and riparian associated mammals, such as the short-tailed weasel (*Mustela richardsonii*) and the New Mexico meadow jumping mouse (*Zapus hudsonius luteus*), benefit from beaver-created habtitat in dryland systems of the western United States (Frey & Malaney, 2009; Frey & Calkins, 2014; Gibson & Olden, 2014; Rosell & Campbell-Palmer, 2022). A variety of bat species benefit from beaver engineered landscapes, likely due to increased prey availability and roost structures, although evidence from applicable ecoregions is lacking (Nummi et al., 2011; Ciechanowski et al., 2011; Wright et al., 2023). Across ecoregions, beaver engineering creates temporally and spatially heterogenous habitats that benefit a variety of mammalian species including increasing abundance and diversity of mammals. However, these conclusions are drawn in large part from studies conducted in boreal forests and areas of central Europe.

There have been no studies on beaver impacts on mammal communities specific to Washington state. However, a study conducted in the Oregon Coast Range found increased abundance and capture rates of deer mice (*Peromyscus*), voles in the genus *Microtus*, Pacific jumping mice (*Zapus trinotatus*), and certain species of shrews (*Sorex sp.*) in beaver occupied stream reaches compared to non-occupied stream reaches (Suzuki & McComb, 2004). This was likely related to beaver created changes in the vegetation structure and increases in cover provided by dense grasses and sedges in the riparian zone. These findings likely apply to areas of western Washington with coastal streams dominated by red alder and Douglas fir. Similarly, in semi-arid snowmelt montane stream systems of southern Idaho, the riparian areas of a beaver engineered complex had significantly higher densities and 2.7 times more biomass of small mammals, primarily shrews and voles, than control sites without beaver influence (Medin & Clary, 1991). Again, these changes were attributed to foraging opportunities and cover provided by dense and structurally complex vegetation created by beavers. In snowmelt montane stream systems in southwest Montana, deer mouse (*Peromyscus*) abundance was 75% higher at beaver engineered sites when compared to control sites. This difference was attributed to aquatic-derived nutrient subsidies to the mice in beaver habitats (McCaffery & Eby, 2016). These systems of Idaho and Montana likely apply to semi-arid montane and shrub-steppe regions of Washington state such as the East Cascades and Columbia River Basin ecoregions.

Birds

Beaver engineering impacts to avian species have been well documented, with beaver engineering positively impacting the richness, diversity, density, and abundance of a variety of bird species. Waterfowl and other aquatic and riparian birds have been shown to benefit through the creation of new wetland habitats and altered riparian structure, which can increase foraging, nesting, and breeding habitat (Hood & Bayley, 2008; Johnson & Van Riper, 2014; McKinstry et al., 2001; Nummi & Hahtola, 2008; Nummi & Holopainen, 2014; and reviewed in Rosell et al., 2005; Rosell & Campbell-Palmer, 2022). These alterations can increase waterfowl production through increases in invertebrate prey, increases in nesting structures, and protection from predators (Nummi & Hahtola, 2008; Nummi & Holopainen, 2014). Songbirds also benefit from expansions and alterations of riparian structure and increases in open water, which increase songbird abundance, biomass, and breeding (Cooke & Zack, 2008; Johnson & Van Riper, 2014; Medin & Clary, 1991; Rosell et al., 2005; Rosell & Campbell-Palmer, 2022). Cavity-nesting birds, perch-hunting avian predators, and woodpeckers may benefit from beaver-created snags and dead wood (Fern, 2001; Rosell et al., 2005; Rosell & Campbell-Palmer, 2022). Additionally, the legacy effects of beaver engineering and the creation of early successional habitats increase avian diversity after sites have been abandoned (Aznar & Desrochers, 2008; Rosell & Campbell-Palmer, 2022). A recent review summarized beaver impacts to avian species across 47 studies and indicated that the vast majority (88%) found beaver engineering had positive impacts on avian communities (Stringer & Gaywood, 2016). The general trend in the literature is that beaver engineering creates complex heterogenous habitats that benefit avian abundance, diversity, density, and production across a variety of species and habitats.

There have been no studies on beaver impacts on avian communities specific to Washington state. However, a variety of studies from semi-arid regions of the intermountain west may provide some information on potential impacts to avian communities in semi-arid regions of Washington state including the East Cascades and Columbia River Basin ecoregions. A study in semi-arid snowmelt driven montane stream systems of Idaho found that beaver engineering altered avian community composition and increased songbird species richness, density, and biomass. Community composition shifted to include more foraging and bush nesting birds, and species richness was found to be 3.25 times higher at beaver impounded sites when compared to control sites (Medin &

Clary, 1990). Additionally, bird density was 10.22 birds/hectare as compared to 3.38 birds/hectare with a corresponding increase in bird biomass at beaver engineered sites. These differences were connected to increases in surface water, shrub biomass, vegetation height, and canopy cover at beaver engineered sites. Similarly, in semi-arid shrub-steppe habitats of central Wyoming, total songbird species richness and abundance was correlated with the number of beaver dams at a site (Cooke & Zack, 2008). These increases were hypothesized to stem from expansions in open water area and width of the riparian zone. Mckinstry et al. (2001) found significantly higher waterfowl diversity and breeding at beaver impounded stream reaches compared to control sites across semi-arid regions of Wyoming. Additionally, waterfowl were found to occupy and breed in ponds formed within two-years by recent beaver reintroduction efforts. A master's thesis from Portland State University investigated snag use by woodpecker and cavity nesting species in beaver impounded habitats compared to riparian control habitats in the Western Oregon Cascades, finding that snag habitat use was higher in controls but that older beaver ponds provided snags similar to control reaches (Fern, 2001). Decay rates, decay class, and size of snags were significantly different in newer beaver sites and were hypothesized to influence snag use, but results indicate that beaver succession does create high quality cavity nesting and excavator habitat. While there is generally a lack of studies investigating beaver impacts to waterfowl, songbird, and other avian groups in areas comparable to ecoregions of Washington state, these four studies suggest that beaver engineering likely promotes avian abundance, production, diversity, and density in riparian communities east of the Cascade crest. Studies on most avian groups in ecoregions west of the Cascade crest are lacking, with the exception of snag using species.

7 Impacts of beaver dam analogues on abiotic habitat characteristics

7.1 Hydrology and geomorphology

Hydrologic changes to freshwater systems refer to alterations of the depth and width of aquatic habitat, the velocity of water, and the timing and magnitude of water movement which drive both hydrologic and geomorphic responses to restoration activities. Desired hydrologic changes from BDA construction are intended to mimic those of natural beaver dams and typically include the pooling and slowing of water, creating deeper and longer lasting pools, modulation of flow and water temperature, increased sinuosity and area of wetted habitat, and the creation of hydrologic irregularities that lead to desired changes in geomorphology (Pollock et al., 2014; Shahverdian et al., 2019).

Surface Water

A number of peer-reviewed studies, theses, and monitoring reports have investigated hydrologic changes in surface water related to BDA installation, typically by measuring wetted area, pooling depth, and stream elevation or stage. Within restored reaches, BDAs have been shown to increase stream height (Norman, 2022; Pearce et al. 2021a) and create pools deeper than untreated streams (Bouwes et al., 2016; Scamardo & Wohl, 2022). However, in the Great Salt Lake basin, BDA pools were found to be 0.43m shallower than beaver created pools, though elevation of stream reaches was not controlled for (Wolf & Hamill, 2023). Studies have also demonstrated increases in the quantity of surface water and wetted area within restored reaches (Bouwes, et al., 2016; Scamardo & Wohl, 2020; Vanderhoof & Burt, 2018; Weber et al., 2017; Anderson & Khechfe, 2021; Yokel et al., 2018). However, the magnitude and longevity of these changes is not well understood, and factors such as BDA integrity, design, and water-use within the vicinity can impact these results (Munir & Westbrook, 2020; Munding-Becker, 2022). For example, heavy groundwater withdrawal for agricultural use adjacent to a BDA installation in the Scott River Valley of CA reduced the volume and size of BDA ponds, and these ponds did not recover during the water year, ultimately drying completely (Munding-Becker, 2022). Further, Munir &

Westbrook (2020) demonstrated that BDA design can impact the quantity of surface water, where three BDAs installed adjacent to each other created an additive effect and created larger, deeper pools than a single BDA. However, few studies have monitored these changes at spatial scales more than 1-4 treatment reaches of 1-2 km and temporal scales of more than 3 years after installation at the treatment reach, and BDAs that are not maintained drain surface water that was previously stored (Munding-Becker, 2022). These studies on BDA impacts to surface water primarily come from semi-arid regions of southwest Montana, montane regions of Colorado, and semi-arid montane regions of northern California. These results likely apply to semi-arid regions of Washington state where precipitation is generally low, and streams are primarily snow-melt reliant.

Perhaps the best monitored BDA installation comes from the Bridge Creek Intensively Monitored Watershed in Bridge Creek, OR where >100 BDA structures were installed, and the area was rapidly colonized by beavers, resulting in an additional >100 natural beaver dams from 2005-2013 (Bouwes et al., 2016; Pollock et al., 2012). In this 32km stretch of degraded high desert stream, intermixed natural and BDA dams increased quantity of pools, the depth of pools, and area of inundation. Area of inundation increased 228% in treatment reaches when compared to 120% in controls and 34% in reference sites during the monitoring period (Bouwes et al., 2016). Additionally, BDAs impacted stream complexity: the number of side channels increased 1216% in treatment reaches and 479% in controls, with no corresponding increases in reference reach side channels. Bridge Creek is a tributary of the John Day River and ultimately the Columbia River, and these findings apply best to semi-arid regions in the Columbia River Basin ecoregion of Washington state.

BDA installation has also been shown to impact stream discharge and stage, though this has been studied considerably less in the peer-reviewed literature. In a study investigating the impacts of different BDA configurations on stream stage and discharge, it was found that single BDAs lowered stream stage and flow peaks, double BDAs modulated peaks but had little impact on base flows, and triple BDAs increased stream stage and flow in a spring-fed treated reach in the Canadian Rockies (Munir & Westbrook, 2020). However, this study lacked clear control reaches, and results may be confounded with an unexpected groundwater spring found during the monitoring period. A master's thesis in a snowmelt driven headwater system in southwest Montana showed that BDAs had smaller increases in flow rate when compared to reference reaches, indicating an attenuation of flow (Norman, 2020). Norman (2020) also indicated that flow loss (seasonal reductions in flow) was higher in the BDA reaches compared to untreated reaches, likely due to increased connectivity to the aquifer and flow diversion into groundwater recharge rather than surface flow. Other theses projects in snowmelt systems in northern California have shown that, without maintenance, discharge from BDA sites can either decrease in dry periods as the BDA is no longer holding water or increase as the BDA is no longer obstructing water at high flows (Anderson & Khechfe, 2021; Munding-Becker, 2022). Additional information about the impacts of BDAs on stream stage and discharge can be gained from theoretical hydrologic modelling. Single BDA structures are expected to increase stream stage above the structure as water level is elevated and spread laterally across the stream course. This is expected to increase dry season discharge from increased groundwater storage (Bobst et al., 2022). Given interest in the ability of BDAs to maintain water on the landscape through dry periods, it is surprising that no studies to our knowledge have investigated patterns and changes in net stream discharge through time. These studies on discharge and stream stage have primarily been conducted in semi-arid snowmelt reliant systems that apply to areas east of the Cascade crest in Washington.

Ground Water

An additional hydrologic goal of BDA restoration is often to raise the water table. A higher water table results in increased rates of hyporheic exchange, ground water storage, and summer baseflows (Lautz, 2019; Pollock et al., 2012; Shahverdian et al., 2019). Groundwater level response to BDAs has been extensively studied in peer-reviewed literature, theses, and monitoring reports. In montane snowmelt driven streams in semi-arid regions of Oregon, Montana, and Wyoming, BDA installation has been shown to increase the ground water elevation and maintain ground water throughout the water year, in some cases > 100m upstream of the BDA structure (Askam et al., 2022; Bouwes et al., 2016; Munir & Westbrook 2020; Orr et al., 2020; Pearce et al., 2021a; Munding-Becker, 2022; Norman, 2020; Yokel et al., 2018). However, in montane regions of Colorado, no ground water changes were observed in BDA reaches (Scamardo & Wohl, 2020), and in the foothills of the Canadian Rockies, ground water elevation increases were laterally limited to within 6m of the stream (Munir & Westbrook, 2020). Hyporheic exchange has also been fairly well studied with findings concluding that BDAs can result in flow reversals where water is flowing from the BDA pool into the groundwater aquifer, transitioning from a gaining to a losing reach (Askam et al., 2022; Munir & Westbrook, 2020; Pearce et a., 2021; Scamardo & Wohl, 2020; Wade et al., 2020; Norman, 2020). However, these transitions can be controlled by seasonal flows (i.e., high versus low flow conditions) (Norman, 2020), and the height and position of the BDA (Wade et al., 2020). Again, these results primarily come from semi-arid ecoregions with low precipitation and high reliance on snowmelt, and they likely apply best to montane areas east of the Cascade crest and the Columbia River Basin in Washington state. In wetter western areas of Washington, BDAs may not result in the same flow reversals seen in more arid regions.

Water Temperature

Impacts to water temperatures that result from impoundment are highly relevant for biological value of restoration. More water surface area and shallow water may be expected to increase water temperatures; however, this may be offset by deeper pools and increased groundwater- surface water exchange (Lautz, 2019; Pollock et al., 2012; Shahverdian et al., 2019). Water temperature changes related to BDA installation have been well studied in the peer-reviewed literature, including in the Bridge Creek Intensively Monitored Watershed. Within the Bridge Creek treatment watershed, water temperature was shown to drop or remain constant (Bouwes et al., 2016; Weber et al., 2017). BDA sites buffered water temperature extremes and increased channel and watershed scale thermal heterogeneity (Bouwes et al., 2016; Weber et al., 2017). These authors conclude that BDAs increased the amount of cool water refugia within the watershed. Other studies in semi-arid regions have shown trends of decreasing water temperature and maintenance of the cool water throughout summer peaks within smaller treatment reaches (Corline et al., 2022; Orr et al., 2020; Yokel et al., 2018). Pearce et al., (2021a) found that surface water temperature was more related to air temperature rather than restoration treatment, but BDA treatment did decrease the groundwater temperature within a BDA treatment reach in semi-arid systems of southwest Wyoming. Munir & Westbrook (2021) found that stream temperature increased farther downstream such that water temperature increased with increasing number of BDAs upstream, though no control reaches were included. However, increases in pond depth decreased water temperature in pools once a certain depth was reached within the BDA impoundment (Munir & Westbrook, 2021). These studies likely apply best to areas of the Columbia River basin and semi-arid montane regions of Washington state.

Geomorphology

One of the key functions the BDA plays in beaver-related restoration is reversing stream incision and reconnecting degraded streams to floodplains. BDAs are particularly useful in this sense because they can be installed in streams that are degraded beyond the likelihood or capacity of natural beaver recolonization (Pollock et al., 2014; Lautz, 2019; Shahverdian et al., 2019). By altering the hydrology of stream courses, BDAs are designed increase rates of aggradation and reverse incision (Pollock et al., 2014; see **Figure 2** of conceptual diagram of process). Patterns of erosion and aggradation at BDA treatment sites have been well studied in peer-reviewed literature and theses, and observations from project monitoring reports also note these patterns. Aggradation of sediments above BDAs has occurred rapidly at many treatment sites, in some cases filling in BDA pools and burying structures within 1-3 years of installation, primarily in montane and semi-arid regions of the western US (Bouwes et al., 2016; Munding-Becker, 2022; Niezgoda, 2019; Orr et al., 2020; Scamardo & Wohl, 2020; Yokel et al., 2018). This has led to the creation of new channels and braided streams, especially in the Bridge Creek sites. In eastern Washington, slight aggradation was observed one year after BDA installations, with fill only occurring around BDA structures within the treatment reach on a tributary of the Spokane River (Niezgoda, 2019). This monitoring also noted an increase in fine particle sediment consistent with slowing of water velocity. Patterns of erosion and aggradation were extensively studied in the BDA treatment reach in Red Canyon Creek of southwest Wyoming, where rates of aggradation and erosion were twice as high in the BDA treatment reach than control reaches, patterns were more heterogenous across the reach, and BDA treatment resulted in no net erosion during the study period, when net erosion was observed in control stream reaches (Davis et al., 2021; Pearce et al., 2021b.). This heterogeneity was driven by BDA design, placement, and relation to other BDAs, and short-term events such as floods or BDA breaching. Three studies indicated that, in many cases, rates of aggradation were highest at the most upstream BDA within a series and decreased and sometimes transitioned to erosion at BDAs lower within a series (Davis et al., 2021; Orr et al., 2020; Pearce et al., 2021b). No long-term (>3 years post-installation) monitoring or studies of detailed geomorphologic changes related to BDA restoration have been published, which may reflect the longevity and/or maintenance periods associated with BDA installation or the complexity of tracking these changes. In the short term, aggradation does appear to increase upstream of BDAs, and BDA treatment increases rates of geomorphologic changes that may be difficult to predict, though studies have been primarily conducted in degraded stream systems in semi-arid regions.

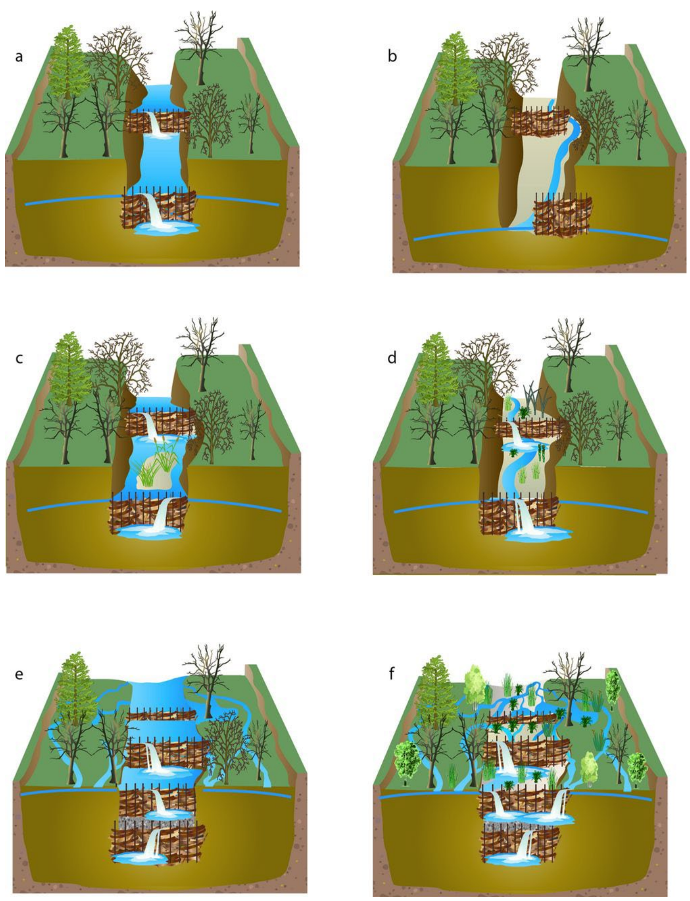

Figure 2. Sequence of observed stream ecosystem changes when beaver dam analogues (BDAs) are used to aggrade a stream. BDAs mimic many functions of beaver dams but can be placed where they will most benefit streambed aggradation and at higher densities than those typical of natural beaver dams. Their key advantage over beaver dams is that they are structurally sound enough to be used in narrow incision trenches and have less potential for failure once ponds are formed. This can substantially lower the time required for floodplain reconnection, because the volume of fill needed is lower in narrower trenches. Where sediment supplies are abundant, high BDA densities can rapidly reconnect streams to their former floodplains. (Pollock et al., 2014)

8 Impacts of beaver dam analogues on biotic communities

There has been limited research on the biological outcomes associated with BDA restoration. Studies have primarily focused on fish, invertebrates, amphibians, and vegetation. There are no studies on BDA impacts to other taxonomic groups at this time. To the best of our knowledge BDA impacts on mammals and birds have not been rigorously studied.

8.1 Vegetation

Restoration of riparian vegetation is a common goal of BRR, including BDA projects (Pilliod et al., 2018; Pollock et al., 2014). Hydrologic and geomorphologic changes associated with BDAs (i.e., increased lateral water movement, increased surface water, increased hydroperiod, increased overbank flooding) are expected to improve the quantity of riparian vegetation and lengthen seasonal availability. Two peer-reviewed studies investigated riparian vegetation response to BDA installation using aerial imagery and vegetation indices, such as Normalized Difference Vegetation Index (NVDI) and Enhanced Vegetation Index (EVI), with mixed results. In the Bridge Creek restoration sites, productivity of riparian zones increased by 20% across the treatment reaches when compared to controls (Silverman et al., 2019). This response was almost immediate, was maintained at this higher level over multiple years, and this productivity extended longer in the growing season. An additional study in eastern Oregon measured growth of willow plantings adjacent to BDAs and plantings in control reaches of the streams, finding willow growth was 1.32 times higher adjacent to BDAs when compared to control sites (Orr et al., 2020). However, in a BDA treatment reach in Montana headwater systems, no apparent increase in riparian productivity or evapotranspiration was seen post BDA installation (Askam et al., 2022). The authors of this study hypothesize that groundwater was not a limiting factor for riparian growth in this system (as opposed to semi-arid regions such as eastern Oregon), such that the increased water attributed to BDA installation did not translate into riparian vegetation response. Together, these studies suggest that robust riparian vegetation response is likely in areas where water is a limiting resource and streams are incised but may be less pronounced where groundwater levels are already elevated.

8.2 Invertebrates

Another common goal for BDA or BRR projects is to improve fish and wildlife habitat through increases in habitat heterogeneity and the associated increases in food web biodiversity (Pilliod et al., 2018). Invertebrates, which are a crucial food source for many fish, are likely to be impacted by BDA installation and the associated hydrologic and geomorphologic changes. Only one peer-reviewed study and one master's thesis have investigated the impacts of BDA installation on aquatic invertebrate communities. The peer-reviewed study investigated invertebrate community response to BDA restoration in the Scott River drainage in northwest California, finding increased invertebrate beta and gamma diversity because BDA installation created unique productive lentic habitats (Corline et al., 2022). While there was lower alpha diversity in the BDA treated reach, 50% of species in BDA pools were unique to these habitats when compared to three control reaches. BDAs also increased the densities of benthic macroinvertebrates and zooplankton when compared to untreated controls. The master's thesis, (Broderius, 2021), investigated changes in the aquatic invertebrate communities related to the installation of 25 BDAs in a tributary of the upper Columbia River flowing from Moses Lake in eastern Washington. Broderius (2021) found lower species richness but higher abundance and biomass in the treatment reach when compared to controls. Additionally, there were shifts in the community composition, with increases in the relative abundance of collector gatherers and burrower functional groups within the treatment reach. While research is limited, BDA installation appears to increase the density and abundance of aquatic invertebrates, create novel conditions that may increase gamma diversity, and may lead to shifts in community composition, specifically in regions of Washington state with prolonged dry periods in the summer months.

8.3 Amphibians

The physical changes associated with BDA installation are also likely to impact amphibian communities, as shifts from lentic to lotic conditions and increases in riparian habitat and aquatic habitat fundamentally alters amphibian habitats. While there are multiple studies on the impacts of natural beaver dam complexes on amphibian communities, only a single study and single conference proceeding have investigated patterns of amphibian habitat, diversity, and occupancy of BDA sites. In the peer-reviewed article, amphibian occupancy of nine BDA sites was compared to 24 natural beaver complexes in four drainages in the Great Salt Lake area of Utah. Of the nine BDA sites, only one site was occupied by a single species of amphibian, tiger salamander *(Ambystoma tigrinum*)*,* as compared to 14 of the 24 beaver complexes occupied by tiger salamanders, though no unmodified controls were included in the study (Wolf & Hamill, 2023). While physical conditions did not significantly differ between the BDA and beaver sites, additional species were found at beaver complexes, and the authors hypothesized that the significant difference in ages of the sites -- BDA sites (<6 years old) were 32 years younger than beaver complexes (29-40 years old) on average -- likely played an important role in these differences. Lastly, Habitat use of Sierra Nevada yellow-legged frogs (*Rana sierrae)* and Cascades frogs (*R. cascadae*) were assessed at three control meadows and compared to habitats at a BDA restoration site in the southern Cascades/northern Sierra Nevada mountains. These conference proceedings report that with regular maintenance, the BDA site contained suitable habitat structure and juvenile Cascade frog occupancy was observed, but no abundance or density comparisons were made between BDA sites, control sites, or other restored sites (Pope et al., 2019). These studies likely apply best to semi-arid and montane regions of Washington state.

8.4 Fish

A primary goal of many BDA restoration projects is increasing the quality and quantity of habitat for threatened and endangered salmonid species, including steelhead trout (*Oncorhynchus mykiss)* and Coho salmon (*Oncorhynchus kisutch)* (Pilliod et al., 2018; Pollock et al., 2014; Yokel et al., 2018). Rebuilding the steelhead population that historically occupied the John Day River Basin was one of the primary goals of the Bridge Creek Intensively Monitored Watershed BDA project (Bouwes et al., 2016; Pollock et al., 2012), and Coho survival and reproduction was the main goal of BDA projects undertaken in northern California (Yokel et al., 2018). In general, BDAs have been shown to increase the abundance of fish at the local and watershed scale, increase survival of salmonids, and increase the production of juvenile fish (Bouwes et al., 2016; Pollock et al., 2022; Broderius, 2022; Yokel et al., 2018). Bouwes et al. (2016) studied juvenile steelhead survival, production, and abundance from 10 years of monitoring data spanning before and after major BDA implementation in the Bridge Creek site. They found that restoration led to a 168% increase in abundance, 52% increase in juvenile survival, and 172% increase in smolt production, comparing post restoration years to pre-restoration in treatment reaches. In the Scott River BDA sites in northwest California, BDAs increased Coho survival and created summer rearing habitat (Pollock et al., 2022; Yokel et al., 2018). When comparing natural beaver dams to BDA sites in Utah, Wolf & Hamill (2023) found BDA sites increased abundance of fish, with BDA sites containing three times as many fish as natural beaver complexes. Additionally, a master's project conducted in eastern Washington found BDAs did not impact species diversity but did increase the density of red sided shiners (*Richardsonius balteatus*) within the treatment reach when compared to controls (Broderius, 2022). These studies primarily apply to the Columbia River Basin and semi-arid regions of Washington state with prolonged dry periods in the summer months.

Fish passage and BDAs

One of the main concerns that may limit BDA installation and impact structure design is fish passage. Two works (one peer-reviewed paper and one master's thesis) have explicitly investigated BDA passage by Coho and steelhead in the Scott River BDA sites in northwestern California. Monitoring of fish movement, combined with relocation experiments, indicated that both Coho and steelhead had little difficulty crossing BDAs during high flow conditions (O'Keefe, 2021; Pollock et al., 2022). Less fish moved during low flows, but it is not clear whether this was because they couldn't or chose not to as low flows primarily occurred during periods when fish do not typically migrate (O'Keefe, 2021). Additionally, experiments indicated that fish primarily moved across BDAs using side channels and jumping, rather than submerged passages. In hatchery passage experimental trials, juvenile steelhead trout were able to consistently pass 24 cm jump heights with passage success of around 75%, while higher jump heights were more achievable as fish increased in size (O'Keefe, 2021). Only about 5% of the fish were able to pass the subsurface structures (O'Keefe, 2021). These studies apply to regions of Washington with prolonged dry periods in summer months where base flows are low and can sometimes become subsurface.

9 Synthesis and Conclusions

9.1 Modulating habitat change

Beaver-related restoration has the potential to ameliorate climate-change related increases in stream water temperatures. Both beavers and BDAs can enhance exchange between streams and associated groundwater (i.e., hyporheic exchange), which can buffer thermal maxima and decrease mean stream temperature (Table 1; sections 5.1, 7.1). However, these effects are associated with older, established beaver/BDA complexes with larger ponded areas and may not occur in newer, smaller beaver complexes. Furthermore, both beaver dams and BDAs also increase thermal heterogeneity within a site, with some areas warming up and others cooling down. The buffering effects of BRR on stream temperature may be most impactful at lower elevations in eastern Washington (e.g., Columbia River Basin and surrounding foothills), where stream temperatures are projected to rise the most (section 2.1). However, these effects may also be important in areas where stream temperatures are not buffered by other factors (e.g., riparian shading, coastal fog, extensive existing groundwater inputs) and areas where buffering from snowmelt is being lost (e.g., montane transitional basins).

Beaver-related restoration is likely to modulate climate change-related reductions in summer streamflow, including the complete loss of surface water from streams and wetlands. Both beavers and BDAs increase water storage in streams, floodplains, and associated groundwater reservoirs (i.e., vertical and lateral connectivity), which can enhance dry-season water availability (Table 1; sections 5.1, 7.1). Increased dry-season water availability in floodplains and beaver-associated wetlands supports riparian productivity, which can increase carbon fixation (sections 5.2, 6.1). It can also slow the spread of fire across landscapes and enhance post-fire regrowth, and beaver engineering can reduce post-fire runoff and erosion; it is unclear whether BDAs provide the same benefits (Table 1; section 5.4). However, increased surface and groundwater storage may be offset by increased evapotranspiration, especially in semi-arid areas where evapotranspiration is limited by water availability (e.g., east of the Cascade crest; section 2.1), and may also be compromised by groundwater withdrawals for human use. Enhanced summer streamflows may be particularly important in western Washington (especially montane areas), where the most dramatic reductions in summer flow are projected (section 2.1). However, most of the research on BRR and water storage comes from arid and semi-arid parts of interior western North America; it is not clear whether these findings translate to wetter ecoregions.

Beaver-related restoration is likely to reduce the magnitude of climate-related increases in the frequency and magnitude of high-flow events by interrupting in-channel flows (reduced longitudinal connectivity) and facilitating the spread of water into floodplains (increased lateral connectivity) (Table 1; sections 5.1, 7.1). This reduction in high flow events may be particularly important in smaller, higher-elevation catchments (e.g., montane areas throughout Washington), which are projected to have the biggest increases in high flow events (section 2.1). The slowing and spreading of water associated with beavers and BDAs can also prevent channel incision, increase sediment aggradation (and in some cases erosion), increase nutrient retention, and increase carbon sequestration (though greenhouse gas emissions can be higher in beaver impoundments) (sections 5.1, 5.2, 7.1). The flow-buffering capacity for both natural dams and BDAs likely depend on the size and density of the impoundments, where higher densities of BDAs or more complex natural beaver structures more effectively slow and laterally move large volumes of water without failing.

Beaver-related restoration is likely to increase habitat heterogeneity at multiple spatial and temporal scales (Table 1; sections 5.1, 5.3, 7.1). At smaller spatial scales, increased heterogeneity may result in the persistence of key microclimates (e.g., patches of cool water). At larger spatial and temporal scales, beavers enhance heterogeneity by creating an ever-shifting mosaic of different habitat types in watersheds where they are common (section 5.3). The construction of BDAs may contribute to this process if they facilitate beaver colonization and recovery. However, when BDAs do not lead to substantial increases in beaver occupancy and abundance, it is not clear what level of ongoing management is required to realize and sustain benefits, given that BDAs degrade over time without maintenance. There is still a paucity of long-term (>3 years) and large-scale studies of BDA-based restoration (section 7.1). Additionally, while there are certainly examples of beavers colonizing BDAs, there has been little systematic study of this process, and it is not clear what proportion of ongoing BDA-based restoration projects are likely to enhance beaver colonization and persistence.

9.2 Biodiversity conservation

Beaver-related restoration is often motivated by a desire to enhance salmonid populations, which are vulnerable to both habitat destruction and climate change. Cold-water refugia are critical for salmonid rearing and spawning, and natural beaver dams and BDAs both have the potential to decrease stream temperatures (Table 1; sections 5.1, 7.1). Furthermore, beaver activity and BDAs increase the quantity of pooled habitats, which are commonly used by juvenile salmonids. Juvenile salmonids experience increased survival, production, and densities in beaver-affected sites relative to sites without beaver engineering. Overall, beaver engineering impacts on salmonids across ecoregions and species are consistently positive (Table 1; sections 6.4, 8.4). Studies directly applicable to Washington systems have demonstrated that coastal beaver activity positively impacted Coho and Chinook salmon through the creation and maintenance of favorable habitats. In addition, beaver activity on Bridge Creek in the Columbia River Basin supported steelhead populations through similar mechanisms. While steelhead, Coho, and Chinook are relatively well-studied, other salmonid species have not been well researched and further studies are needed to understand impacts to species with varying life history traits including resident non-anadromous species. Additionally, across salmonid species, studies have primarily focused on juvenile life stages with little emphasis on adult stages or growth rates at different life stages. Much of the evidence for steelhead use of both beaver and BDA habitats comes from Bridge Creek, which has mixed natural beaver dams and BDAs. While this is a large-scale and well-implemented study, it is difficult to attribute specific outcomes to natural beaver dams or BDAs alone, and more studies of BDA impacts in isolation are needed to confirm impacts of this type of restoration for Washington ecoregions.

While fish passage across beaver dams and BDAs is a persistent concern, especially for salmonids, evidence shows that steelhead and Bonneville cutthroat trout, among other native species, can pass beaver dams without obstacle (section 6.4). Coho and steelhead can also pass BDAs without obstacle at high flows (section 8.4). Most often, fish move up beaver dams via water spilling over one side of the dam. It is possible that passage rates could decline at low flows, when water spillover is minimal and dam height is relatively large, but BRR is also likely to increase base flow rates, which may counteract this issue especially when combined with increased lateral water movement and channel complexity associated with beaver engineering. Smaller juvenile fish may also have more trouble passing high jumps than larger fish, but relationships between passage rates and fish age remain largely unexplored (section 8.4). In general, passage rates likely depend on stream stage, fish species, and fish age, but all current and historic evidence suggests that the positive benefits of BRR outweigh any slight decreases in passage rates that may exist in certain circumstances.

Beaver-related restoration is likely to have beneficial impacts on a variety of amphibian species by creating suitable habitat and maintaining surface water in streams and wetlands. Pond-breeding amphibians that inhabit stream-associated wetlands are most likely to benefit both from increased hydroperiods and from the creation of still-water habitats associated with BRR (sections 6.3, 8.3). Beaver ponds are associated with increased occupancy of Oregon spotted frog [Federally threatened], Columbia spotted frog [Candidate for state listing], and other pond-breeding species when water is scarce; however, there is limited evidence as to whether BDAs provide the same benefits (Table 1; sections 6.3, 8.3). Reduced water temperatures and increased summer streamflow associated with BRR may benefit stream-associated species (e.g., Cascade torrent salamander [Candidate for state listing], Rocky Mountain tailed frog [Candidate for state listing]), though these species may also be negatively impacted by reduced availability of free-flowing stream habitat. In addition, increased occupancy and abundance of fish (which frequently prey on amphibians) and other natural enemies may limit the beneficial effects of BRR on amphibians. These hypotheses are largely unexplored.

Terrestrial and semi-aquatic vertebrate species may also benefit from BRR (Table 1; section 6.5). Terrestrial vertebrates including small mammals like mice, shrews, and bats are likely to increase in abundance at beaver-occupied sites due to changes in vegetation structure and food resources. Food resources utilized by these terrestrial organisms may be subsidized by aquatic sources that likely increase in habitats engineered by beavers, strengthening connectivity between aquatic and terrestrial food webs. Other terrestrial organisms, like songbirds and woodpeckers, rely on wetlands for habitat structure including snags and mosaics of high and low canopy cover, and may also benefit from aquatic-derived prey. Semi-aquatic mammals like otters and muskrats benefit from beaver engineering via increased prey and dense vegetation. While there is some evidence that many mammal and bird species are associated with beaver engineering, little data comes from Washington or applicable ecoregions. Furthermore, no studies to our knowledge explore the context dependence of mammal or bird associations with beavers (i.e., dam age or size, climate, species, life stages). Lastly, there are no studies considering BDA impacts to terrestrial or semi-aquatic vertebrates, despite the likely impact restoration could have.

Changes in invertebrate and vegetation abundance and composition are often a mechanism invoked to explain responses of organisms in higher trophic levels. Many of the organisms discussed above, including fish, amphibians, and mammals, depend on invertebrates as a primary food source and vegetation to create habitat structure. BRR is likely associated with increased aquatic invertebrate abundances at the site scale, and increased diversity at the watershed scale; the result is greater food sources for insectivorous predators as well as high biodiversity across the watershed (Table 1; sections 6.2, 8.2). The vegetation changes in beaver ponds driven by the beaver cycle create a landscape mosaic of early- to late-successional habitat structures, and each of these habitats can benefit different taxonomic groups (sections 5.3, 6.1, 8.1). We expect that increases in habitat heterogeneity associated with beaver populations are beneficial to overall biodiversity at the watershed scale, but existing studies are generally applicable only to the montane and semi-arid regions of the state. More multi-taxa studies are needed to quantify how BRR, and especially BDAs, impact overall biodiversity of Washington’s freshwater systems.

9.3 Conclusions

There is substantial evidence that beaver-related restoration (BRR), via beaver translocation and beaver mimicry, has the potential to increase the climate resiliency of Washington’s stream and riparian ecosystems. By reducing summer water temperatures, increasing summer flows, and enhancing floodplain habitat, BRR can benefit species of conservation concern, including trout, salmon, and amphibians. In addition, BRR can ameliorate the negative impacts of high-flow events, create fire-resistant habitat patches in fire-prone landscapes, and foster heterogeneous mosaics of habitat that enhance the watershed-level biodiversity of aquatic and riparian ecosystems. While the impacts of beavers and BDAs on hydrology, geomorphology, salmonid fish, and pond-breeding amphibians are relatively well studied, impacts on other species (e.g., non-salmonid fish, stream-associated amphibians, birds, invertebrates) are relatively understudied. In addition, there is a relative paucity of studies from western Washington (or comparable ecosystems) despite the fact that some relevant impacts of climate change are likely to be quite pronounced in this region, especially at higher elevations. Finally, there are relatively few investigations of the ecosystem impacts of BRR specifically (i.e., beaver translocations and beaver mimicry), as opposed to naturally occurring beavers and beaver complexes. Thus, there remains a relatively large gap between our understanding of the aspirational potential of BRR (what it ***can*** accomplish) and the realized benefits of restoration actions (what it ***does*** accomplish).

While the scientific literature on BRR is developing rapidly, there are important limitations in our understanding of BRR and its impacts. For example, most studies of BRR are still relatively limited in spatial and temporal scope, raising fundamental questions: What spatial scale of BRR project is needed to achieve restoration goals at both local and watershed scales? How long does BRR take to yield different outcomes? How long do the impacts of BRR last? In addition, key aspects of BRR practice are not well understood. Translocated beavers must persist and create dams and other structures to realize the benefits of BRR, but for a variety of reasons many do not. Systematic studies of translocation success and the drivers of wild beaver distributions may help us understand why. Similarly, beaver dam analogs must be colonized by beavers or maintained by humans to persist, but the likelihood of BDA colonization by beavers is not clear, and most restoration projects focus on implementation, rather than maintenance. Finally, key drivers of variation in the effects of beavers and BRR are poorly understood, including regional gradients in climate and land use.

As a final note, we want to acknowledge that the effects of BRR on climate resilience may extend beyond beavers and beaver mimicry. The increasing enthusiasm for BRR programs across the western United States demonstrates that working with beavers, and the installation of beaver-mimicking structures, can contribute to strengthening social-ecological linkages. On both public and private lands, and in both rural and urban communities, recognition of the potential benefits of these structures for water resources, wildlife habitat, and livestock is increasing. This ultimately promotes stewardship and monitoring of aquatic resources, increasing the climate resiliency of these systems as they are recognized and protected from other threats that might further degrade freshwater resources.

Table 1. Summarized evidence for effects of beaver engineering and BDAs in Washington State. **Confidence** level (high, medium, or low) is indicated by the degree of shading of the relevant box, with darker shades indicating greater confidence. Confidence is based on validity and agreement. validity is assigned to three categories (robust, medium, limited) based on the quantity of published literature, agreement (high, medium, or low) is assigned based on the percent of published literature agreeing on specific effects. **Region (Reg.)** indicates the parts of Washington for which there is applicable evidence supporting the described effect. Importantly, this does not mean the effect will not occur in regions that are not mentioned, only that there is not evidence available from comparable ecoregions. The regions are: Montane (M), locations 500-2000 meters in elevation, including parts of the Olympic Mountains, Cascades Range, Okanogan Highlands, Blue Mountain, and Rocky Mountain; Western Washington (WW), areas of the Puget Lowlands, Willapa Hills, and Portland Basin, generally less than 500 m in elevation; Columbia River Basin (CRB), semi-arid shrub-steppe areas east of the Cascades but south of the North Cascades and Rocky Mountain regions, extending south to the Oregon border.

		Beavers			Beaver Dam Analogues		
Topic	**Variable**	**Confidence**	**Reg.**	**Effect Summary**	**Confidence**	**Reg.**	**Effect Summary**
Hydrology Section 5.1 Section 7.1	Overall stream temperature	ROBUST evidence MEDIUM agreement	M, CRB	Larger, older beaver complexes reduce mean temperature; smaller, younger complexes may not.	ROBUST evidence HIGH agreement	M, CRB	Decrease in stream temperature.
	Thermal maxima	ROBUST evidence MEDIUM agreement	CRB	Buffering of thermal maxima; lower maximum water temperature value in summer.	ROBUST evidence HIGH agreement	M, CRB	Buffering of thermal maxima.
	Thermal Heterogeneity	MEDIUM evidence HIGH agreement	M	Increase patchiness of temperatures with pockets of both warm and cold water present.	MEDIUM evidence HIGH agreement	CRB	Increase patchiness of temperatures with pockets of both warm and cold water present.
	Surfacewater	MEDIUM evidence HIGH agreement	M	Increase surface water storage and wetted area.	ROBUST evidence HIGH agreement	M, CRB	Increases in quantity of surface water, wetted area, and depth of pools.
	Groundwater	MEDIUM evidence HIGH agreement	M	Increase in groundwater storage, which is greater than surfacewater storage. Elevated water tables.	ROBUST evidence HIGH agreement	M, CRB	Water table levels increase, groundwater storage increases, and hyporheic exchange increases. Reaches can transition from gaining to losing.
	Discharge	ROBUST evidence HIGH agreement	CRB	Decrease in water velocity; high flows attenuated.	MEDIUM evidence LOW agreement	M	Stream stage and discharge may increase, decrease, or be attenuated.

	Evaporation	MEDIUM evidence MEDIUM agreement	M	Evaporation & evapotranspiration rates increase because water is more accessible to plants and spread more over the surface, resulting in some water loss.	MEDIUM evidence LOW agreement	CRB	Evapotranspiration is expected to reduce the water storage gains from BDAs in arid regions, but may not be applicable in wetter regions.
	Hydroperiod	MEDIUM evidence HIGH agreement	M	Beaver-dammed streams are more likely to retain water year round.	LIMITED evidence	CRB	BDAs are expected to increase hydroperiod.
Geo-morphology Section 5.1 Section7.1	Aggradation	ROBUST evidence HIGH agreement	CRB	Increase sediment aggradation, raising channel elevation; rates decline with age of structure.	ROBUST evidence HIGH agreement	M, CRB	Increase in sediment aggradation.
	Erosion	LIMITED evidence	CRB	Erosion occurs in abandoned beaver colonies and beaver meadows.	MEDIUM evidence MEDIUM agreement	M, CRB	Context-dependent erosion occurs at lower BDAs in a series and sometimes in conjunction with aggradation. No long-term studies have considered erosion over time.
Water Chemistry Section 5.2	Nitrogen	MEDIUM evidence MEDIUM agreement	CRB	Nitrogen is retained in impoundments to some extent, but may depend on discharge.	Data deficient		
	Phosphorus	MEDIUM evidence LOW agreement	M, CRB	Phosphorus retention may be increased in some contexts.			
	Carbon	ROBUST evidence HIGH agreement	M, CRB	Carbon is stored in sediments and within downed woody debris.			
Connectivity Section 5.3 Section 7.1	Vertical connectivity	ROBUST evidence HIGH agreement	M, CRB	Increase in hyporheic exchange.	ROBUST evidence HIGH agreement	M, CRB	Increase in hyporheic exchange.
	Lateral connectivity	MEDIUM evidence HIGH agreement	M	Increase in lateral connectivity.	Data deficient		
	Longitudinal connectivity	MEDIUM evidence HIGH agreement	CRB	Increase in longitudinal connectivity long-term by increasing hydroperiod, but decrease in			

				longitudinal connectivity short-term by limiting downstream flow.			
Wildfire Section 5.4	Resistance	MEDIUM evidence HIGH agreement	M, CRB	Increase in wetted area creates fireblocks and slows fire spread.	Data deficient		
	Resilience		M, CRB	Increase in vegetation productivity & regrowth post fire.	LIMITED evidence	M, CRB	Increase in riparian density post fire.
Riparian Vegetation Section 6.1 Section 8.1	Productivity	ROBUST evidence HIGH agreement	WW, M, CRB	Initial decrease in canopy cover and basal area followed by increase in basal area and productivity.	MEDIUM evidence MEDIUIM agreement	M, CRB	Increase in productivity and longevity.
	Richness	LIMITED evidence	NA	Initial decrease in species richness, followed by an increase in species richness.	Data deficient		
	Community compostion	LIMITED evidence	NA	Initial shift to water-tolerant plants (preferred beaver food) followed by long-term shift to vegetation not preferred by beaves (e.g., conifers) and declines in preferred foods (e.g., aspen).			
Aquatic Invertebrates Section 6.2 Section 8.2	Community compostion	ROBUST evidence HIGH agreement	M, CRB	Shift community composition to include more lentic species.	LIMITED evidence	CRB	Increase in the relative abundance of collector gatherers and burrower functional groups
	Diversity		M, CRB	Increase beta/gamma diveristy, but decrease alpha diversity.		M	Increase beta/gamma diveristy, but decrease alpha diversity.
	Abundance	ROBUST evidence MEDIUM agreement	M, CRB	Increase density and biomass.	MEDIUM evidence MEDIUM agreement	M, CRB	Increase in abundance, biomass, and density
Terrestrial Invertebrates Section 6.2 Section 8.2	Abundance	LIMITED evidence	M, CRB	Increase in abundance.	Data deficient		
Amphibians Section 6.3 Section 8.3	Occupancy	ROBUST evidence HIGH agreement	M, CRB	Increase in pond-breeding amphibian occupancy and breeding density.	LIMITED evidence	M, CRB	BDAs do not provide comparable habitat to beaver ponds, although BDA impoundments may be used for
	Richness	LIMITED evidence	M	Increase in species richness.			

							amphibian breeding.
Salmonid fish Section 6.4 Section 8.4	Abundance	MEDIUM evidence HIGH agreement	WW, CRB	Increase in salmonid density, abundance, and production.	ROBUST evidence HIGH agreement	M, CRB	Increase in density, abundance, and production.
	Habitat availability	ROBUST evidence HIGH agreement	WW, CRB	Increase in habitat quantity and quality.	MEDIUM evidence HIGH agreement	CRB	Increase in habitat quantity, especially summer rearing habitat.
	Passage	ROBUST evidence HIGH agreement	M, CRB	Dams do not pose significant passage barriers, although passage rates may depend on species, flow level, and dam maintenance.	MEDIUM evidence HIGH agreement	M, CRB	BDAs do not pose significant passage barriers, although movement may be limited at low flows.
	Survival	LIMITED evidence	CRB	Increase in salmonid survival.	ROBUST evidence HIGH agreement	M, CRB	Increase in salmonid survival.
Non-salmonid Fish Section 6.4 Section 8.4	Abundance	ROBUST evidence HIGH agreement	M, WW	Increase in abundance and density of other fish such as stickleback and chub.	LIMITED evidence	CRB	Increase in abundance of other fish such as red sided shiner.
Mammals Section 6.5	Abundance	ROBUST evidence HIGH agreement	WW, M, CRB	Increase in small mammal abundance.	Data deficient		
Birds Section 6.5	Abundance	MEDIUM evidence HIGH agreement	M, CRB	Increase in songbird abundance and density, waterfowl production.	Data deficient		
	Diversity	LIMITED evidence	CRB	Increase in avian diveristy after sites are abandoned.			
	Habitat availability	LIMITED evidence	M	Increase in habitat for cavity nesters/foragers.			

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