PROJECT

USING BEAVER DAM ANALOGS TO RESTORE RIPARIAN ECOSYSTEMS INFLUENCED BY LARGE UNGULATES: A REVIEW FOR THE SOUTHERN ROCKY MOUNTAINS

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In partial fulfillment of the requirements

For the Degree of Fish, Wildlife, and Conservation Biology Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2021

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ABSTRACT

USING BEAVER DAM ANALOGS TO RESTORE RIPARIAN ECOSYSTEMS INFLUENCED BY LARGE UNGULATES: A REVIEW FOR THE SOUTHERN ROCKY MOUNTAINS

Beaver (*Castor canadensis*) are recognized as ecosystem engineers and a keystone species due to their ability to modify landscapes to suit their needs. Beaver engineering activities are focused around constructing dams that alter both abiotic and biotic environmental components. Over millennia, the altering of system hydrology, geomorphology, and species compositions by beavers and dams change the shape and structure of landscapes by lowering stream gradients and increasing habitat heterogeneity. Although beaver, and the effects they create, were once ubiquitous across most of North America, centuries of over-harvesting and habitat loss led to steep beaver population declines. Concurrently, the removal of top-level predators, such as the gray wolf (*Canis lupus*), released large ungulates, including elk (*Cervus elaphus*) and moose (*Alces americanus*), from top-down control, allowing these ungulates to flourish and reach unprecedented densities throughout their ranges. As elk and moose increased in abundance, they competed with beaver for forage by consuming the smaller size classes of woody riparian vegetation (e.g., willow, *Salix* spp.; aspen, *Populus tremuloides*; birch, *Betula* spp.; and alder, *Alnus* spp.). In many places, elk and moose ultimately drove beaver from the landscape by preventing willow and aspen from regenerating.

With beavers functionally extirpated, many ecosystems lost the ecological conditions associated with beaver meadow habitats including high water tables and complex, braided streams. In areas

dominated by elk, beaver meadows transitioned to elk grasslands, wherein streams became incised and water tables receded across the floodplain, allowing upland grasses and shrubs to invade the former riparian zone. In moose dominated systems, beaver meadows transitioned to spruce-moose savannas, wherein woody riparian species favored by moose and beaver (e.g., willow, birch, and aspen) declined in abundance leaving grasses and unpalatable woody species (e.g., spruces, *Picea* spp.). As these new habitats are relatively simple compared to beaver meadows, biodiversity declined across all taxonomic levels. In recent decades, land managers and researchers have been mimicking beaver impoundments via structures called Beaver Dam Analogs (BDAs) to reverse these effects and restore beaver meadow habitats.

In this review, I evaluated over 300 publications that examined the effects of natural and artificial beaver impoundments and of elk and moose browsing on abiotic and biotic ecosystem components as well as how these herbivores compete. I also reviewed detriments of beaver and their activities, including flooding, property damage, and disease. I concluded with a case study on Rocky Mountain National Park (RMNP) which is home to beaver, elk, and moose and has seen beaver-less ecosystem transitions play out since the 1910s.

With regards to abiotic components, beaver dams tended to increase stream temperature, nutrient retention, water quality, and sedimentation above the dam as well as overbank flows, groundwater, and hyporheic exchange on the floodplain. Beaver dams tended to decrease stream flow rate as well as dissolved oxygen in the pond. Some of the literature indicates that beaver dams also decrease stream pH.

With respect to biotic components, willows, aquatic macrophytes and invertebrates, fish, amphibians, birds, and small mammals all had larger total biomass in stream reaches with beavers than in non-impounded stream reaches. Beaver dams also tended to increase species diversity of aquatic invertebrates, fishes, and birds. Additionally, beaver dams, and associated flooding, tended to decrease terrestrial herbaceous standing crop, the prevalence of invasive vegetation species and overall plant species richness. At larger scales, beaver dams increased the extent and quality of river otter (*Lontra canadensis*) and moose habitat. Of the publications that examined the effects of beaver dams and ungulate browsing, 48% did not provide quantitative data and 39% of those reported inconvertible results thereby prohibiting the calculation of averages.

Based on the literature, I suggest that managers and researchers install multiple BDAs in a stair-step profile with one BDA for every foot of elevation drop in the stream and structures no more than 100 m apart. When these recommendations are followed, BDAs have the potential to reconnect streams with their former floodplains within a few years. Prior to installing BDAs, I suggest managers research the temperature and acidity tolerances of aquatic species in their ecosystems as altering temperature and pH regimes can negatively affect aquatic organisms.

Many of the beaver-less ecological effects described above are present in RMNP where wolves were extirpated in the early 1900s and elk populations subsequently reached unprecedented levels. This high-density elk population facilitated the loss of beaver in RMNP via overbrowsing and still averts beaver recolonization by preventing willow and aspen regeneration. The loss of beaver allowed the RMNP ecosystem to transition from a series of beaver meadows to elk grasslands, with a consequent loss of biodiversity. Active elk management in RMNP has succeeded in reducing the elk herd, however, much of the landscape was so damaged that managers began installing BDAs to restore the historic abiotic and biotic cycles of this system. To compound the complexity in RMNP, moose have been expanding in abundance since 2015. Moose must be accounted for as RMNP managers seek to continue restoration projects.

Although the elk population has fallen, RMNP managers will likely need to alter their current restoration plan, or devise a new plan, by instituting new, moose-specific management strategies (e.g., taller browse exclosures) to account for the expanding moose population. With the results of this review, managers in RMNP and throughout the Southern Rocky Mountains will be able to account for elk and moose browsing in their restoration goals and, consequently, use their limited resources more effectively to restore habitat heterogeneity and biodiversity.

ACKNOWLEDGMENTS

An endeavor of this magnitude is never merely the work of one person and, while there are many to thank, I will restrict myself to the largest contributors. I would like to thank the Lord God for making my paths straight throughout this process. Truly, the many necessary pieces fell together far too easily to be the result of only my work and I am grateful. I am also grateful to my graduate committee, Dr. Paul Doherty, Jr., Dr. Dana Winkelman, and Dr. Ellen Wohl, for their support, guidance, and constructive criticism throughout this process. I am especially thankful for my advisor, Dr. Paul Doherty, Jr., for his undying patience and for giving me a chance when few others would have. I would like to thank the staff of Rocky Mountain National Park, particularly Hanem Abouelezz, Landscape Ecologist, and Allison Konkowski, Lead Wildlife Technician, for their unfailing support and friendship and for unfettered access to their documents and projects. I am grateful to my parents, Paul and Cindy, for recognizing my passion for wildlife at such a young age and for continually going out of their way to foster that passion. I would like to thank my uncle, Allen Chapman, for his remarkable generosity and support from beginning to end. I would like to give special thanks to my friend, Laci Ulrich, for invaluable edits to this manuscript and for love and support through every moment of these past couple years. Finally, I am thankful for my friend and colleague, Alliyah Gifford, for always making me smile and for making every day brighter.

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1. INTRODUCTION

Prior to European arrival, an estimated 60 – 400 million beaver (*Castor canadensis*) inhabited North America (Naiman et al. 1988). After centuries of over-harvesting and habitat loss, the North American beaver population dwindled to 6 – 12 million by 1988 (Naiman et al. 1988). As the beavers disappeared, their dams deteriorated and failed, sending water, sediment, and nutrients downstream. Over time, without dams impounding the water, water tables in the surrounding floodplains receded, drying out riparian vegetation and creating space for upland plant colonization (Munther 1984; Gurnell 1998). Without riparian shrubs and trees, stream channels began to erode and incise, disconnecting streams from their floodplains (Polvi Pilgrim 2011). Changing public values, increased management protections and successful reintroduction programs have allowed beaver populations to recover in many areas. However, many degraded areas still lack sufficient food, construction material, and environmental conditions to meet basic beaver needs and are unlikely to be recolonized (Naiman et al. 1988; Baker and Hill 2003).

Concomitant with the loss of beaver, large predators, such as the gray wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*), were removed from the same landscapes thereby releasing wild ungulates, such as elk (*Cervus elaphus*) and moose (*Alces americanus*), from top-down regulation (Wolf et al. 2007; Beschta and Ripple 2009; Ripple et al. 2015). This induced a trophic cascade whereby ungulate populations reached unprecedented high levels which led to equally unprecedented declines in the stature and diversity of woody riparian species (e.g., willows, *Salix* spp.; aspen and cottonwoods, *Populus* spp.; and birch, *Betula* spp.; Beschta and Ripple 2009; Ripple et al. 2010; Beschta and Ripple 2019). This loss of woody riparian species contributed to the stream degradation described above and further damaged beaver populations as they no longer had a supply of food and construction material.

These conditions, along with changing land management practices during the 1800 – 1900s, created a positive feedback loop that resulted in many western North American landscapes transitioning from their historic stable states to alternate stable states (Howard and Larson 1985; Wolf et al. 2007). These historic states, referred to as beaver meadows, contained lush riparian corridors with complex river channels that regularly overtopped their banks carrying water, sediment, and nutrients onto the floodplain (Westbrook et al. 2011). The new alternative states, referred to as elk grasslands or spruce-moose savannas, are characterized by incised stream channels and a consequent loss of habitat heterogeneity and biodiversity (Johnston et al. 1993; Wolf et al. 2007).

Landscapes across western North America that once housed beaver fall along a spectrum between these extreme alternative states. Some areas are just transitioning into the new alternative stable state, meaning their vegetation communities are degraded due to overbrowsing but underlying hydrologic processes remain intact. These areas may be restored by simple measures, such as ungulate browse exclosures, which alleviate the main cause of habitat degradation. Other landscapes have transitioned to the alternate stable state, where the underlying abiotic processes have changed to the point that simple restoration measures alone are not effective. In these areas, a large disturbance is required to force the system out of its elk grassland or spruce-moose savanna state and back to a beaver meadow (Beisner et al. 2003; Suding et al. 2004). Restoration efforts in such areas should focus on reestablishing historic abiotic processes to achieve restoration goals (Polvi and Wohl 2013).

Over the past 30+ years, studies have shown that manmade beaver structures, often referred to as Beaver Dam Analogs (BDAs), can achieve this end (Apple 1985; Albert and Trimble 2000; Pollock et al. 2014; Pollock et al. 2015; Pilliod et al. 2018). BDAs are designed to mimic the effects of natural beaver dams (e.g., slowed stream flows, increased sedimentation and increased overbank flows) to reduce stream incision and reestablish the ecosystem's historic abiotic processes (Pollock et al. 2014; Pollock et al. 2015). With planning and luck, BDAs may be adopted by dispersing, or reintroduced, beavers. These beavers then maintain and reinforce the BDAs, assuming the work from resource managers.

In this review, I focus on BDAs as tools to restore Southern Rocky Mountain (i.e., Colorado, New Mexico, Utah, and Wyoming) riparian ecosystems and on how browsing by elk and moose may influence restoration efforts. While hundreds of studies have examined beaver ecology and dozens more have investigated BDA efficacy and the coactions of beavers and large ungulates, no review has summarized all these facets. To help managers select BDA restoration sites, I first provide a general background on BDAs and an overview of studies showing where beavers place their dams. I then summarize the effects of beaver dam construction and of ungulate browsing on abiotic and biotic ecosystem components. Next, I examine the coactions of, and competition between, beavers and wild ungulates as well as the detriments of beaver activities such as flooding, dam failure, and disease. I then provide recommendations and future directions for practitioners and researchers to consider when conducting BDA work. Finally, I weave these sections together in a case study of Rocky Mountain National Park, Colorado, U.S.A. where these effects and ecosystem transitions have played out since the 1910s. By following my recommendations, BDAs can be used to restore self-sustaining riparian ecosystems throughout the beaver's historic range.

2. METHODS

I began by examining beaver-related publications in the Rocky Mountain National Park library and, to supplement these papers, I searched 14 scientific literature databases using search terms for variants of BDA singly and variants of moose and elk (Table 1). I selected journal articles, reports, theses, dissertations, and books that contained any variant of BDA in the title, dealt with moose and/or elk effects on riparian ecosystems, and those that contained effects of beaver dams on 18 abiotic and biotic environmental components (Table 2). I selected publications that dealt with North American beaver (*C. canadensis*) or publications that examined North American beaver and European beaver (*C. fiber*) in unison. I did not consider papers that focused on *C. fiber* alone as this species does not have as strong an affinity for dam construction as *C. canadensis* (John and Klein 2004). I also included publications that examined the effects of both natural and artificial beaver dams as studies have shown that both structures render similar environmental effects (Gard 1961a; Pollock et al. 2015). I identified additional sources from the Literature Cited sections of papers I found in the databases.

I modified Kemp et al.'s (2010) vote counting method to calculate averages for both quantitative and qualitative studies. I tallied the number of papers that examined a given effect and then calculated the percentage of these papers that reported their results quantitatively and anecdotally, respectively. For publications that offered quantitative support, I evaluated their results for comparability, meaning they measured the same effect, and convertibility, meaning they measured the same effect in convertible units (e.g., cm of sedimentation vs meters of sedimentation) with similar studies. For those papers reporting results using the same, or convertible, units I calculated a weighted average (weighted by sample size) and standard error for the effect size. I report any inconvertible results, meaning those who units could not be mathematically converted to match (e.g., measured percent change in species richness versus number of species), separately.

For example, seven publications examined beaver dam effects on bird species richness. Of these, five reported quantitative results and four of these reported comparable results; number of species. I calculated a weighted average and standard error for these four results. The remaining study with quantitative support reported their results in inconvertible units (e.g., percent change in species richness) and are reported separately.

To account for the results of both quantitative and qualitative publications, I used indicator variables to code for whether a given effect in each study had a positive (1), neutral (0) or negative (-1) direction. I then averaged these values (reported as indicator variable averages, IVA) over the publications examining a given effect. This method is simple to implement and can incorporate quantitative and qualitative results but may be biased due to a lack of weighting.

For example, four studies examined the effects of beaver dams on nitrogen (i.e., nitrate and ammonium) retention. Three of these studies found that nitrogen retention increased when beaver dams were present and the fourth found that nitrogen retention decreased. The first three studies received a "1" while the fourth received a "-1" for an average of 0.50. Thus, I concluded that the literature shows that beaver dams increase nitrogen retention.

3. RESULTS

I reviewed 331 peer-reviewed journal articles, government reports, books, symposium abstracts, master's theses, and doctoral dissertations to synthesize the environmental effects of beaver dams, both natural and artificial, and of large ungulate browsing. These publications, from 1932 to 2020, come from five countries in North America, Europe, and Asia, and cover the ranges of both *Castor* species. First, I give an overview of beaver dam analogs and beaver dam site preferences. I then detail the effects of beaver dams and large ungulates before discussing some of the detriments of beavers and their activities.

3.1 Beaver Dam Analogs as Restoration Tools

Beaver engineering activities (e.g., dam construction) affect multiple taxonomic levels on temporal scales ranging from decades to millennia (Jones et al. 1994; Jones et al. 1997; Wright et al. 2002; Wright et al. 2004). The impounding and subsequent passive sedimentation work of beavers over millennia is responsible for many of the wide, low-gradient valleys across western North America (Ruedemann and Schoonmaker 1938; Ives 1942; Polvi and Wohl 2012). These valleys historically housed large beaver complexes with dozens to hundreds of dams and lodges as well as miles of beaver-dug canals (Ives 1942; Gurnell 1998; Polvi and Wohl 2012). These beaver-created features carried water, sediment, and nutrients from the stream channel onto the floodplain via overbank flows and groundwater exchange which created heterogeneous habitats and facilitated the infilling of valley bottoms (Ives 1942; Lautz et al. 2006; Westbrook et al. 2006; Polvi and Wohl 2012; Wegener et al. 2017). These heterogeneous habitats are ecological stable states known as beaver meadows (Ruedemann and Schoonmaker 1938; Ives 1942; Polvi and Wohl 2012). This concept of beaver meadow valley formation led researchers and managers to attempt to use BDAs to restore riparian ecosystems.

3.1.1 BDA Construction

BDAs have various forms, but all have two fundamental characteristics. First, BDAs are constructed mainly of materials that beavers use. These materials include aspen (*Populus tremuloides*), willow, birch, and alder (*Alnus* spp.) stakes as well as mud, stream rocks, and gravel. This practice has the advantages of not introducing alien material and making BDAs appear natural which is particularly advantageous in areas, such as national parks, where preservation and natural aesthetics are key considerations. Secondly, BDAs are semi-porous, temporary structures (Pollock et al. 2014; Pilliod et al. 2018). This aspect makes BDAs relatively cheap to install. However, BDAs also require regular upkeep, at least until beavers take over.

Four common BDA designs include Starter Dams, Post-Line-Wicker-Weaves, Post-Lines, and reinforcing existing beaver dams, however, designs vary to accommodate site terrain and available resources (e.g., vegetation, funding, and personnel; Pollock et al. 2012; Pollock et al. 2015). Starter Dams begin with wooden stakes driven into the streambed about 0.3 – 0.5 m apart with the tops approximately level with the streambank (Bouwes et al. 2016). Next, branches from nearby woody plants, such as willow, are woven between the stakes, perpendicular to the water flow, to create the dam structure. Finally, mud and gravel from the streambed are packed onto the upstream side of the dam to make the structure waterproof (Pollock et al. 2015). Starter Dams are designed to immediately begin impounding water and may be covered with new growth a couple years after installation (Davee et al. 2017).

Post-Line-Wicker-Weaves (PLWWs) are a non-waterproofed version of the Starter Dam (Pollock et al. 2015). The two designs are built in the same manner, but PLWWs lack a mud and gravel layer. As such, PLWWs are more permeable and will not immediately impound water to a great degree. The primary advantage of PLWWs compared to Starter Dams is lower cost, in terms of time, effort, and money. Additionally, PLWWs result in less streambed disturbance. Over time, PLWWs accrue sediment and organic material and, consequently, impound more water. The amount of time until a PLWW becomes waterproof depends on a variety of factors including stream discharge and sediment load (Pollock et al. 2003; Pollock et al. 2007).

The third design, known as a Post-Line (PL), involves driving wooden stakes vertically into the streambed spanning the channel. PLs are not intended to impound water but, rather, to be used by dispersing beavers as new dam foundations. PLs are best placed in sites suitable for a future dam and in close proximity, i.e., a few hundred stream meters, to active beaver colonies (Pollock et al. 2012). PLs require the least material but rely on beavers to make the PL functional.

The fourth design reinforces natural beaver dams with wooden posts to prolong the dams' lifespans (Pollock et al. 2015). These posts are placed 0.5 – 1 m apart and are driven a meter into the streambed. This is the least expensive design and is best implemented when project objectives or possible damage to infrastructure make a beaver dam breaching undesirable.

Variations on these four designs exist and use materials not often found in beaver dams (e.g., manmade posts, wire netting, and rubber matting; see Section 5; DeBano and Heede 1987; Harmon et al. 2004; Abbe and Brooks 2011; DeVries et al. 2012), but such strategies introduce alien material to the environment and may have additional material and transportion costs.

All these BDA designs, aside from PLs, require upkeep to continuously impound water (Pollock et al. 2012; Pollock et al. 2014). A dam's lifespan, sans regular maintenance, depends largely on stream discharge and local topography (DeBano and Heede 1987; Pollock et al. 2012; Davee et al. 2017). Dams built in incised channels in steep, narrow valleys will fail more often due to concentrated stream flows as compared to dams built in shallow channels in wide, low-gradient valleys where stream energy is more dissipated (Munther 1984; Beechie et al. 2010). In addition to high flow events, BDAs may fail due to the stream cutting around or overtopping the dam (Butler and Malanson 2005; Pollock et al. 2015). To mitigate end cutting, BDAs can be extended onto the streambank. To overcome the latter failure, managers install BDAs in a stair-step profile with five to eight structures placed no more than 100 m apart (Pollock et al. 2015; Pilliod et al. 2018). Davee et al. (2017) suggest building one dam for every foot of elevation drop in the stream. This slows stream flows and creates a cushioning effect as water overtops each dam and falls into the downstream pond. This stair-step system also provides a series of checks should one dam fail (Naiman et al. 1988; Baker and Hill 2003). Water circumventing dams is part of the process for reconnecting the stream with its former floodplain. The combination of sedimentation behind the dam and controlled erosion around the dam raises the streambed and flattens the incised banks. Managers can control these processes by designing BDAs to direct water flows as needed (Pollock et al. 2014).

BDAs have also been installed in areas with nearby beaver colonies, i.e., within a few hundred stream meters, with the hope that dispersing beavers will find and adopt the BDAs (Pollock et al. 2012; Davee et al. 2017; Weber et al. 2017). When this strategy succeeds, little additional work is required as the beavers assume the dam maintenance work. Weber et al. (2017) found that beavers enhanced BDA effectiveness by making BDAs less permeable and taller, which leads to increased overbank flows, groundwater, and hyporheic exchange (Lautz et al. 2006; Westbrook et al. 2006). Beavers may be reintroduced after BDA installation, however, the BDA adoption and beaver reintroduction strategies both require adequate food and building material nearby to sustain beavers (Leege 1968; Jackson 1990; Van Deelen 1991).

Beavers typically disperse at the age of two, although they may disperse earlier if high-quality, empty sites exist or later (3 years old) in high-density populations (Townsend 1953; Leege 1968; Sun et al. 2000). Time of year and distance for dispersal vary widely, but subadults typically leave their natal colonies in April – June (range: late January – mid-November) and travel 4 – 10 km (range: 0 – 110 km; Leege 1968; Jenkins and Busher 1979; Jackson 1990; Van Deelen 1991; Van Deelen and Pletscher 1996; DeStefano et al. 2006; Mcnew and Woolf 2018). Dispersing individuals tend to move downstream, but may explore both directions to find the best site (Leege 1968; Sun et al. 2000). Dispersing beavers colonize high-quality sites (e.g., those with vegetation and soil characteristics described below and moderate to high stream braiding) first, filling in lower-quality sites as beaver density increases (see Section 3.1.2; Harris 1991).

3.1.2 Beaver Dam Site Preferences

In eastern Oregon, beavers prefer dirt substrates, likely because they struggle to push dam starter stakes into rocky substrates, although this finding may be a byproduct of the studied population preferring bank dens to lodges (McComb et al. 1990). Beavers in Oregon and Washington selected sites with flatter bank slopes, lower stream gradients (1.5 – 4%) and higher amounts of hardwood cover (McComb et al. 1990; MacCracken and Lebovitz 2005). These habitat preferences are seen throughout the species range (Howard and Larson 1985; Gurnell 1998; Pollock et al. 2015; Macfarlane et al. 2017). Furthermore, beavers are not deterred by humans and often build dams and lodges near roads and homes provided that all other habitat requisites are present (McComb et al. 1990; Curtis and Jensen 2004).

For beavers to adopt a BDA, a readily available supply of food and construction material is required (Allen 1983). Beavers select sites with high-density vegetation less than 10 cm in diameter, although some research suggests beavers prefer stems less than 4 cm in diameter (Hall 1960; Basey et al. 1988; Barnes and Mallik 1997). Beavers prefer aspen over any other food source and rarely consume conifers (Jenkins 1979; Muller-Schwarze and Sun 2003; Gallant et al. 2004). Despite their preference for aspen, beavers avoid juvenile-form aspen, likely due to the higher concentrations of unpalatable secondary compounds (Basey et al. 1988; Basey et al. 1990; Baker and Hill 2003). Beavers also prefer willow and birch for food, but alder is typically reserved for construction (MacDonald 1956; Slough 1978; Doucet et al. 1994; Barnes and Mallik 1996; Rolauffs et al. 2001). Although beavers prefer the above species, they are generalist herbivores and use all manner of deciduous, riparian trees and shrubs as well as terrestrial and aquatic forbs (Jenkins 1975; Belovsky 1984; Doucet and Fryxell 1993; Parker et al. 2007).

3.1.3 Financing and Permits

BDAs are less expensive than riparian restoration strategies that use mechanized equipment to regrade incised streams. In Oregon, Bouwes et al. (2016) found that each BDA required one to four hours of work for three people. They also estimated that 30 Starter Dams spread over one stream kilometer cost under $11,000. Davee et al. (2017) estimated that BDA restoration cost under $20,000 per stream mile on a private Oregon ranch. Costs vary depending on wages, materials purchased (e.g., hydraulic post pounders versus sledgehammers for the stakes) and site access difficulty.

As with most impoundments in the United States, BDAs require permits (Pollock et al. 2015; Davee et al. 2017). Specifically, Pollock et al. (2015) highlight the need for a nationwide permit, known as an NWP 27, which allows impoundments that adhere to the Clean Water Act.

Permitting structures vary by state, county, and land management agency, and some agencies, particularly in the Pacific Northwest, have beaver restoration memorandums of understanding (MOUs) that ease permitting restrictions (Pollock et al. 2015). Pollock et al. (2015) note that requisite permits may be included in ongoing projects. I encourage managers and researchers interested in BDAs to check their unit’s permits and local regulations to ensure all mandates are followed. As one last side note, managers may consider using an alternative name for BDAs, such as Simulated Beaver Structures or SBSs, while obtaining permits and project approval to avoid the stigma that often accompanies the word “dam”.

3.2 Beaver Dam Effects

Hundreds of studies have examined the effects of beaver herbivory and construction on ecosystem abiotic and biotic components (Naiman et al. 1988; Pollock et al. 1995). Of the 331 publications I reviewed, 172 (51.96%) addressed beaver dams and their environmental effects. I review these 172 publications in the current section beginning with effects on abiotic factors and then work vertically through the trophic levels.

3.2.1 Abiotic Effects

Of the 172 publications that considered beaver dam environmental impacts, 80 addressed abiotic effects. 48.75% of these publications reported quantitative results (Table 3). Of the 39 quantitative publications, 16 provided comparable results. The remainder were either the only paper to examine a given effect or presented their results in inconvertible units. The comparable effects include flow rate, sedimentation, water temperature, pH, total phosphorus discharge, nitrate and ammonium retention, and methane evasion.

3.2.1.1 Flow Rate

One study each in Ontario and Montana yielded numeric results when examining the effect of beaver dams on flow rates (Sprules 1941; Meentemeyer and Butler 1999). They determined that beaver dams slowed stream flows by a weighted average of 44.1% (SE = 17.3). Older beaver dams (>6 years) slowed stream flows more than younger dams, 72.2% versus 14.6% (Meentemeyer and Butler 1999). Slower flows also led to sediment and nutrient deposition, thus keeping these components from discharging downstream (Hanson and Campbell 1963; DeBano and Heede 1987; Maret et al. 1987; Naiman and Décamps 1997; Gurnell 1998). Indeed, Correll et al. (2000) calculated that beaver ponds in Maryland retained 27% more suspended solids than free-flowing stream reaches. Slower flows also favor the production and survival of lentic invertebrate species over the lotic species more typical of free-flowing streams. Shifts in invertebrate species assemblages affects vegetation, fish, and bird species assemblages in and around the pond (see Section 3.2.2; Sprules 1941; McDowell and Naiman 1986; Snodgrass and Meffe 1998). In sum, both publications that examined stream flow rate found that streams slowed due to passing through beaver dams.

3.2.1.2 Sedimentation

One well established effect of beaver dam installation is sedimentation upstream of the dam. Six of the reviewed studies provided comparable, quantitative results on sedimentation. These studies took place in California, Oregon, Montana, and Germany, and had a range of sedimentation rates between 3.89 – 555.05 cm/yr with a weighted average of 75.57 cm/yr (SE = 78.25; Gard 1961b; Butler and Malanson 1995; Meentemeyer and Butler 1999; John and Klein 2004; Butler and Malanson 2005; Pollock et al. 2007). Pollock et al.'s (2007) reported average sedimentation rate of 555.05 cm/yr far surpassed the next highest result of 15.05 cm/yr from Butler and Malanson (1995). The reasons behind such a large value are unclear, but may include sediments being more erodible and more easily transported, more vegetation present to trap sediments, or more beaver dams in the study area which slowed stream flows more compared to other study sites. One additional study quantitatively examined sedimentation in beaver ponds, but reported inconvertible results. This publication, from Rocky Mountain National Park, Colorado, calculated a sedimentation rate of 0.75 cm/monitoring period (Westbrook et al. 2011). An additional eight studies, covering beaver impoundments in four additional states as well as Ontario, anecdotally stated that sediment also accumulated behind their studied dams (Ruedemann and Schoonmaker 1938; Sprules 1941; Ives 1942; Rupp 1955; Albert and Trimble 2000; Pollock et al. 2003; Pollock et al. 2015; Bouwes et al. 2016). I calculated an IVA of 1.0 across all fifteen sedimentation studies, indicating unanimous support for increased sedimentation following beaver dam construction (Table 3).

Sedimentation, possibly more than any other impoundment effect, leads to changing species assemblages. Sedimentation also disperses water, sediment, and nutrients across the floodplain by forcing them out of the stream channel (Naiman et al. 1988; Westbrook et al. 2006; Wolf et al. 2007; Westbrook et al. 2011; Wegener et al. 2017). Moreover, a Wyoming study found that sediment immediately upstream of beaver dams is finer than that in non-impounded reaches (Jin et al. 2009). This change in substrate can shift invertebrate and fish assemblages from gravel adapted species to silt adapted species (see Sections 3.2.2.2 and 3.2.2.3; Rupp 1955; Gard 1961a; Snodgrass and Meffe 1998). Scamardo and Wohl (2020) found three significant predictors of sediment volume behind BDAs: BDA height, pool volume, and pool surface area. However, Scamardo and Wohl (2020) also determined that there is a small change in sediment volume as pool volume increases, but there was a large change in sediment volume as BDA height increases. As such, these authors concluded that the dimensions of a BDA have more impact than BDA design.

3.2.1.3 Overbank Flows

All four publications that examined beaver impoundment effects on overbank flows determined that beaver dams increase overbank flows, but none provided quantitative support. Rather, the authors relied on the observation of increased flows across their studied floodplains following beaver dam installation (John and Klein 2004; Westbrook et al. 2006; Westbrook et al. 2011; Majerova et al. 2015). The extent to which beaver dams cause overbank flooding depends on the pond depth relative to streambank height and local topography (Westbrook et al. 2006). Slow overbank flows increase the water table height and allow the water to more efficiently infiltrate floodplain soils (Wohl et al. 2012). Only one study measured the changes in water table depth due to BDA installation and they found that BDAs increased the water table height by 0.37 m, on average, which facilitated willow growth (Bilyeu et al. 2008). Additionally, a Wyoming study found that overbank flows from beaver dams increased the riparian area width by 23.4 m on average, creating bird, amphibian, and mammal habitat (see Section 3.2.2; Brown et al. 1996; McKinstry et al. 2001; Cunningham et al. 2007; Dalbeck et al. 2014; Anderson et al. 2015).

3.2.1.4 Groundwater and Hyporheic Mixing

One study each in Germany and Colorado determined that beaver dams facilitate groundwater mixing. These publications relied on a suite of quantitative and qualitative metrics to inform this conclusion (John and Klein 2004; Westbrook et al. 2006). A third study, from Wyoming, examined beaver dam effects on hyporheic mixing, i.e., when water moves from the stream through floodplain sediment and back to the stream some distance downriver (Findlay 1995). Findlay (1995) determined that beaver dams increase the rate of hyporheic mixing which, according to Lautz et al. (2006), further slows the flow of water and nutrients through the system. Via slowed flows and increased mixing, beaver dams at large scales can recharge aquifers, mitigating aquifer depletion resulting from climate change (Hood and Bayley 2008;

Pollock et al. 2015). Moreover, permeable soils are particularly conducive to mixing and, consequently, may decrease the water temperature, benefiting fish and aquatic invertebrate species near their upper thermal tolerance limits (Pollock et al. 2015).

3.2.1.5 Water Temperature

Four of the reviewed publications provided numeric results from water temperature analyses. Effect sizes ranged from -18.56 – 21.11°C with a weighted average increase of 6.92°C (SE = 7.48) (Rupp 1955; Gard 1961b; Błędzki et al. 2011; Malison et al. 2015). Seven additional studies anecdotally considered the effects of beaver dams on water temperature. Six of these claimed there was no significant difference in water temperature between impounded and unimpounded reaches (Sprules 1941; Nummi 1989; McRae and Edwards 1994; Sigourney et al. 2006; Bouwes et al. 2016; Weber et al. 2017). The seventh reported increased water temperatures in impounded areas (Majerova et al. 2015). Over all 11 studies reviewed, which covered the breadth of North America and included one study from Finland, I calculated an IVA of 0.3 indicating that water temperatures tended to be higher in impounded versus free-flowing habitats, however, there is significant disagreement in the literature (Table 3).

Many fish species, most notably salmonids, are sensitive to changes in water temperature and high temperatures can kill individuals in short time spans (Rupp 1955; Gard 1961b; Kemp et al. 2012). Whether or not this occurs is largely dependent upon the initial site conditions (Pollock et al. 2015). For instance, if a given site is near the upper temperature tolerance of a given fish species and BDAs are installed, this may increase temperature above a species maximum threshold and lead to die-off or emigration (Gard 1961b; Kemp et al. 2010). However, if a given site is near the lower temperature tolerance of a given species, BDA installation may ease any temperature stress that species is experiencing. I encourage managers to consider the tolerance limits of aquatic species in their systems before installing BDAs to minimize the possibility of adverse effects. Groundwater mixing may mitigate temperature increases as covered in Section 3.2.1.4, however more research is needed to parse out these effects.

3.2.1.6 pH

Changing pH levels in a stream can affect the production and survival of many aquatic species (Rupp 1955). Additionally, acidic soils may slow nutrient uptake by vegetation after the beaver pond drains, negating the influx of new plant growth shown in the literature (see Section 3.3.4; McMaster and McMaster 2001).

Two studies examined pH differences in beaver-influenced habitats versus control sites. One, from New England, showed that beaver ponds had 0.45 lower pH on average, resulting in acidic streams at 6.72 pH (Błędzki et al. 2011). The other, from Finland, revealed that beaver dam installation had a negligible effect on pH, maintaining 6.1 – 6.2 pH (Nummi 1989). Overall, these studies yield a weighted average pH decrease of 0.19 (SE = 0.23). A third study found that beaver dam construction increased pH but did not provide further data (Smith et al. 1991). I calculated an IVA across these three studies of 0.0 which suggests that beaver dams have a neutral effect on pH (Table 3). However, I encourage managers to research the pH tolerance levels of local aquatic species to determine if lowered pH levels are likely to harm these taxa.

3.2.1.7 Phosphorus

Phosphorus is an important, often limiting, element in natural processes (Bilby 1981; Klotz 1998). As such, increased phosphorus retention due to beaver impoundment increases primary productivity once the pond drains and aerobic conditions return (Naiman et al. 1994; Klotz 1998).

One study each in Minnesota and Maryland examined beaver dam effects on phosphorus discharge and both found that beaver dams decreased total phosphorus discharge (Naiman et al. 1994; Correll et al. 2000). The two studies revealed very different effect sizes, likely due to the different environments in which the studies were conducted. On the Maryland coastal plain, beaver ponds decreased total phosphorus discharge by 58 µg/l while in Minnesota phosphorus discharge decreased by 3,095 µg/l. Together, these studies yield a weighted average decrease in total phosphorus discharge of 1,359.57 µg/l (SE = 1,518.50). A third study found that total phosphorus discharge decreased by 89% in terms of total suspended solids due to passing through beaver ponds (Maret et al. 1987).

3.2.1.8 Nitrogen

Various studies have reported a 9- to 1000-fold decrease in nitrogen discharge from beaver ponds compared to non-impounded habitats which suggests nitrogen is stored in the sediment (Naiman and Melillo 1984; Francis et al. 1985; Maret et al. 1987; Naiman et al. 1994; Correll et al. 2000). As with phosphorus, nitrogen is often limiting for plants and, when properly fixed, can increase primary productivity (Naiman et al. 1994; Pollock et al. 1995). However, the reviewed publications are split as to whether beaver impoundments facilitate nitrogen fixation (Francis et al. 1985). If nitrogen remains unfixed, it is unavailable for plant uptake. The level to which nitrogen fixation occurs is dependent on whether anaerobic conditions prevail in the pond, which is a function of stream flow. Slower flows, as are found in beaver impoundments, contribute to anaerobic conditions and decrease nitrogen fixation (Pollock et al. 1995; Correll et al. 2000).

The ability of beaver dams to retain nitrate (NO_3-N) and ammonium nitrogen (NH_4-N) was quantitatively examined in one study each in Minnesota and New England (Naiman et al. 1994; Błędzki et al. 2011). These studies found that beaver ponds retained a weighted average of 0.21

mg/l (SE = 0.18) more nitrate and 0.71 mg/l (SE = 0.47) more ammonium nitrogen than non-impounded habitats. The Minnesota beaver ponds retained 10 times the nitrate and five times the ammonium nitrogen as those in New England. Again, this difference is likely due to the different environments in which these studies were conducted. A third study reported that beaver ponds retained three times as much nitrogen as non-impounded habitats, but did not separate nitrate from ammonium nitrogen (Johnston and Naiman 1990). A fourth study, from Wyoming, reported that beaver ponds had less nitrate and ammonium nitrogen than non-impounded habitats but did not provide any data (Maret et al. 1987).

In all, the reviewed publications reveal that beaver ponds discharge less total nitrogen (IVA = -1.0) and store more nitrate and ammonium nitrogen (IVA = 0.7 for both metrics) than free-flowing reaches (Table 3).

3.2.1.9 Oxygen

Altered dissolved oxygen (DO) levels in a beaver pond can alter aquatic species assemblages, which can affect assemblages outside the pond (Rupp 1955; Schlosser and Kallemeyn 2000; Kemp et al. 2012). Additionally, lower pond DO concentrations lead to anaerobic conditions in the sediment which can alter biogeochemical cycles. For instance, anaerobic conditions can hamper nitrogen uptake by plants and be ideal for methanogenesis, as covered above and below, respectively (see Sections 3.2.1.8 and 3.2.1.11; Ford and Naiman 1988; Pollock et al. 1995; Correll et al. 2000). However, anaerobic conditions can be negated by mixing water from direct beaver activity and from water reflecting off the dam (Naiman et al. 1984).

Three studies examined DO levels in beaver ponds and all three concluded that DO was lower than in non-impounded reaches. However, none of the three provided quantitative evidence (Sprules 1941; Smith et al. 1991; Snodgrass and Meffe 1998). Smith et al. (1991) speculated that increased organic matter retention and decomposition in the pond caused the low DO. If this speculation is correct, lower DO will likely occur, but at a lower magnitude, in BDA-created ponds without beavers versus active colonies where beavers regularly bring in organic material. Another study, by Błędzki et al. (2011), determined that increased nitrogen and dissolved organic carbon (DOC), as shown above and below, respectively, lead to poorer water quality and decreased DO due to increased bacterial production (see Sections 3.2.1.8, 3.2.1.10, and 3.2.1.12).

3.2.1.10 Carbon

Three studies examined beaver impoundment effects on carbon discharge. Two of these examined beaver dam effects on DOC retention. Both determined that beaver ponds store more DOC than undammed habitats (Smith et al. 1991; Błędzki et al. 2011). Błędzki et al. (2011) found that ponds stored 8.37 mg/l (SE = 0.20) more DOC than non-impounded reaches. The one remaining study examined beaver dam effects on total organic carbon (TOC) discharge and found that beaver dams decrease TOC discharge by 28% over free-flowing reaches, suggesting that beaver ponds store all carbon, not just DOC (Correll et al. 2000). In a pair of related studies, Wohl et al. (2012) found that most carbon associated with former and active beaver meadows resides in the sediment rather than large woody debris and Wohl (2013) found that carbon stored in these areas made up 8-23% of the TOC stored on the study floodplains in RMNP.

Although many allochthonous and autochthonous carbon sources may remain the same between natural beaver dams and BDAs, I note that a large allochthonous carbon source, i.e., beaver herbivory, is absent when beavers are absent. As such, the effects discussed here, which were established in systems containing beaver, may not hold true in systems that lack beaver even though they contain BDAs and ponds. Regardless, the reviewed studies all agreed that beaver dams retain more carbon than non-impounded stream reaches.

3.2.1.11 Methane

Two studies in Canada found that beaver ponds generated more methane than non-impounded reaches (Naiman et al. 1986; Ford and Naiman 1988). Together, they yield a weighted average increase in methane evasion of 24-fold (SE = 9). As methane is a well-known greenhouse gas, anaerobic conditions in beaver ponds may contribute to climate change, however, these effects may be dampened in BDA ponds that lack regular carbon introduction via beaver herbivory. Conversely, beaver ponds store large amounts of carbon and have long turnover rates (Naiman et al. 1986). This aspect may cause ponds to act as carbon sinks, slowing climate change rather than facilitating it. More research is needed to parse out these effects.

3.2.1.12 Water Quality

Three studies, using many of the above effects as metrics, determined that beaver complexes improved water quality, primarily due to increased sedimentation and contaminants adhering to that sediment (Skinner et al. 1984; Maret et al. 1987; Błędzki et al. 2011). In a Wyoming system with cattle (*Bos taurus*), Skinner et al. (1984) found that beaver ponds trapped three times as many fecal streptococci as non-impounded reaches. Maret et al. (1987) state that these filtration effects are pronounced in high flow events, however, they note that this filtration only transfers a short distance downstream. Therefore, to take full advantage of this filtration, Maret et al. (1987) suggest encouraging natural beaver impoundments, and by extension, placing BDAs, close to reservoirs. Błędzki et al. (2011) note that beaver dam filtration may be reversed by a catastrophic dam breach, or multiple breaches within a complex, that drains the pond and washes sediment downstream (see Section 3.4).

3.2.2 Effects on Species Compositions

By changing stream hydrology, geomorphology, and chemistry, beavers alter nearly every level of species composition in their environments (Naiman et al. 1986; Barnes and Dibble 1988;

Naiman et al. 1988; Collen and Gibson 2000). Beavers remove much of the canopy through herbivory and flooding (Wilde et al. 1950; Naiman and Melillo 1984; Green and Westbrook 2009; Westbrook et al. 2011) which bathes the pond in sunlight, creating ideal conditions for riparian and aquatic vegetation growth (McMaster and McMaster 2001; Parker et al. 2007). The increased primary production, sedimentation and presence of slower, deeper water shift aquatic invertebrate assemblages from those typically found in lotic systems to those of lentic systems (McDowell and Naiman 1986; Hood and Larson 2014). These hydrologic and biotic changes lead to shifts in species compositions throughout the trophic levels (Gard 1961b; Chadde and Kay 1991; Albert and Trimble 2000; Karraker and Gibbs 2009). In this section, I review 89 publications that examined how beaver impoundments affect these various taxonomic levels. Of these 89 publications, 50 (56.18%) provided quantitative evidence.

3.2.2.1 Vegetation

3.2.2.1.1 Species Richness

Eight publications examined beaver dam effects on vegetation but only two of these provided numeric evidence (Table 4). One of these publications examined how beaver dams affected plant species richness and the other examined beaver dam impacts on aquatic macrophyte production (Naiman et al. 1994; Bergman and Bump 2015). Naiman et al. (1994) found that beaver dams decreased plant species richness by 6.5 species on average. Naiman et al. (1994) determined that this decrease was largely due to flooding and changes in soil composition, i.e., ponded soils lacked a horizon where organic carbon was stored which dampened growth. Nummi (1989) also examined plant species richness and reported a negligible effect but did not provide data. In Finland, beaver-induced flooding also decreased the terrestrial herbaceous standing crop (Nummi 1992). Conversely, flooding was found to benefit the surrounding ecosystem in New

Mexico as it removed invasive salt cedar (*Tamarix pentandra*), opening more native riparian species habitat (Albert and Trimble 2000).

3.2.2.1.2 Production

The second study to provide quantitative support for beaver dam effects on vegetation examined aquatic macrophyte production in Isle Royale National Park (Bergman and Bump 2015). These authors found that beaver dams increased aquatic macrophyte production by 196 g Dry Weight/m^2. Aquatic macrophytes decrease water temperatures, slow water flows, increase sedimentation and oxygenate water that may otherwise be deoxygenated due to ponding. Aquatic macrophytes are also sources of dissolved phosphorus and organic carbon, both of which are essential for plant growth (Carpenter and Lodge 1986). Additionally, aquatic macrophytes are favorite beaver foods during summer (Brenner 1967; Jenkins 1980; Belovsky 1984; Parker et al. 2007). Therefore, increased aquatic macrophyte production may prolong a beaver colony's lifespan by lessening the beavers' reliance on woody vegetation.

Two of the remaining studies examined beaver dam impacts on willow production in Colorado (Neff 1957; Alstad et al. 1999). Alstad et al. (1999) found that beaver dams had no effect on willow production while Neff (1957) found that dams increased willow production and occurrence. However, Neff (1957) points out that, where beaver ponds are broad and shallow, the loss of willows to flooding may be greater than the gain of willows around the pond. Alstad et al. (1999) speculated that their BDAs had little effect on willow production because the effects were measured in average precipitation years. If the effects were measured in dry years, the BDAs would likely hold water in the system and enhance willow production.

Willows are essential components in many riparian corridors as they provide the majority of primary production while increasing bank stability, shade the water channel, which can decrease and stabilize temperatures, and provide allochthonous inputs that fuel aquatic food chains (Naiman and Décamps 1997; Cooper et al. 2006; Polvi Pilgrim 2011; Pollock et al. 2015). Additionally, willows provide breeding and rearing habitat for birds and mammals (Shaw and Fredine 1956; Gard 1961b; Skovlin 1982; Albert and Trimble 2000; Hornung and Foote 2006). Woody riparian vegetation also functions as a filter by removing sediment, and its adhering nutrients and contaminants, from the stream (Lowrance et al. 1984).

In conclusion, the reviewed publications reveal that beaver dams decrease vegetation species richness (IVA = -1.0), decrease terrestrial herbaceous species standing crop (IVA = -1.0), and remove invasive species (IVA = 1.0) immediately around the pond due to flooding. Conversely, beaver dam construction stimulates aquatic macrophyte (IVA = 1.0) and willow production (IVA = 0.5), although the reviewed publications were split with respect to willow production (Table 4). Whether impounding a stream increases willow production is a function of local topographic and hydrologic conditions as well as the scale considered. If only willows immediately around the pond are considered, the results will likely show decreased production due to flooding. However, if willows across the floodplain are considered, results will likely show increased production due to raised water tables and increased overbank flows.

3.2.2.2 Aquatic Invertebrates

A productive and diverse aquatic invertebrate assemblage is critical for sustainable riparian ecosystems as these species constitute the key connection between primary production and predators such as fish, amphibians, and birds (Hornung and Foote 2006). Moreover, invertebrates can control algae blooms and feed on detritus (Błędzki et al. 2011). Sixteen publications examined beaver dam impacts on aquatic invertebrates and 10 of these provided quantitative support, however, nearly all of these reported incomparable results (Table 4).

3.2.2.2.1 Species Diversity

Ten publications examined beaver dam effects on aquatic invertebrate diversity. Overall, these studies found that beaver dams increase aquatic invertebrate diversity, however, the average effect was slight (IVA = 0.1). Five studies found aquatic invertebrate diversity increased by 2 – 5-fold in beaver ponds compared to unimpounded reaches (Rupp 1955; Gard 1961a; Hanson and Campbell 1963; Rolauffs et al. 2001; Błędzki et al. 2011). Błędzki et al. (2011) reported several Rotifera species that were new to their study state of Massachusetts and one that was new to the United States. Four studies found lower diversity in beaver ponds than in undammed reaches (Sprules 1941; Gard 1961b; McDowell and Naiman 1986; Smith et al. 1991). However, these effect sizes were smaller, with a study in California reporting a loss of 42 species (Gard 1961b). A Quebec study reported that invertebrate diversity decreased by 2.63 using the Shannon-Weaver diversity index but did not report the related species richness (McDowell and Naiman 1986). The final study reported that invertebrate diversity varied depending on feeding guild and time since flooding in dammed and undammed reaches (Nummi 1989). The number of free-swimming species increased in the first year of flooding but decreased thereafter, whereas benthic invertebrates increased in the second year. Nummi (1989) attributed both these changes to increased sedimentation behind the dam. McDowell and Naiman (1986) determined that beaver impoundments shifted invertebrate species compositions from those associated with lotic environments to those associated with lentic environments. In general, McDowell and Naiman (1986) found decreased aquatic invertebrate species diversity at the pond scale, but increased diversity at the landscape scale as beaver ponds of different ages and states of decay support different assemblages not present in purely lotic environments. In an interesting related study, Rolauffs et al. (2001) found that invertebrate diversity within beaver dams was higher than in either the pond or stream. These authors attributed this phenomenon to the dams having a high turnover rate of invertebrate habitats and a large surface area which provided habitat and food from the dams and streams.

3.2.2.2.2 Production

Three studies examined beaver dam effects on aquatic invertebrate production. Overall, they found increased production in beaver-influenced habitats compared to unimpounded reaches. McDowell and Naiman (1986) found beaver dams increased aquatic invertebrate production by 3.5-fold in terms of mg/m^2 on average. The largest differences between ponded and unimpounded sites were observed in the spring and summer while all sites had similar production numbers in the fall. Alternatively, another Quebec study found that beaver dams decreased the production of certain orders (e.g., Plecoptera and Trichoptera) while increasing the production of others (e.g., Diptera and Ephemeroptera) for an average increase of 70 mg Dry Weight/m^2/week (Naiman et al. 1984). This mixed result is likely due to the environment shifting from a free-flowing stream to a pond which favors lentic over lotic species (McDowell and Naiman 1986; Hood and Larson 2014). Rolauffs et al. (2001) found that beaver dams had five times as many emerging insects as ponds and 5.4 times as many as unimpounded sites.

3.2.2.2.3 Density

McDowell and Naiman (1986) were the only researchers to examine beaver dam effects on aquatic invertebrate density. These authors found that impounded segments had 55,600 more individuals/m^2 than control segments during the spring and summer. McDowell and Naiman (1986) speculated that these results were due to lower water discharge which concentrated individuals in smaller areas and changing habitat characteristics due to beaver impoundment.

3.2.2.2.4 Habitat Quality

Two studies evaluated beaver dam impacts on aquatic invertebrate habitat, but neither provided quantitative support. The first determined that beaver dams enhanced aquatic invertebrate habitat by providing cover and food that were not present in the free-flowing stream (Benke and Wallace 2003). Beaver dams are especially valuable as they are present from the benthos to the surface which means all aquatic invertebrates can take advantage of the available food and cover, regardless of their preferred position in the water column. The second study, from New York, examined beaver impoundment effects on mosquito habitat (Butts 1992). Pre-impoundment, Butts (1992) collected 696 *Aedes* spp. specimens in a single summer, but collected only 66 specimens over seven years of surveys roughly 20 years post-impoundment. Specimens collected post-impoundment covered an additional four genera (*Anopheles* spp., *Coquillettidia perturbans*, *Culex* spp., and *Culiseta melanura*). Butts (1992) concluded that this decrease was due to the impoundments flooding former mosquito breeding habitat which drove the population down.

To summarize, beaver dams increase aquatic invertebrate production and density (IVA = 0.7 and 1.0, respectively). Beaver dams may also increase aquatic invertebrate species diversity (IVA = 0.1), especially when viewed at larger spatial scales, but the literature is divided on this issue. Finally, beaver dams may also enhance aquatic invertebrate habitat (IVA = 0.0), but this effect is taxon specific and deserves further research.

3.2.2.3 Fish

A review by Kemp et al. (2010) identified fish-associated benefits and costs engendered by beaver impoundments. These authors found that the most commonly cited benefits included increased fish abundance, productivity, and habitat quality. Among the biggest negatives cited were beaver dams as barriers to fish movements, decreased spawning habitat, and altered temperature regimes. Overall, Kemp et al. (2010) found that beaver dams are not significant barriers to fish movements, however, if beavers dam side channels in addition to the main channel, this may block fish passage.

I reviewed 27 publications that examined beaver dam effects on fish and roughly half (n=14) provided quantitative evidence. Quantitatively measured metrics include fish density, survival, species richness, abundance, and diversity (Table 4).

3.2.2.3.1 Density

Two studies measured beaver dam effects on fish density and both found that density increased in impounded areas compared to unimpounded areas by a weighted average of 502 fish/100 m^2 (SE = 487; Keast and Fox 1990; Bouwes et al. 2016). Bouwes et al. (2016) also determined that steelhead (*Oncorhynchus mykiss*) in impounded reaches had 52% greater survival.

3.2.2.3.2 Production

Five studies examined beaver dam impacts on fish production, however, all reported their results in inconvertible units. Regardless, all five studies reported that beaver dams increased fish production in the upstream ponds. In Oregon, Bouwes et al. (2016) calculated that steelhead production increased 175% while Gard (1961a) found fish production increased up to 5-fold in California, depending on the species examined, following BDA installation. Two studies in Canada found mean increases in fish production up to 778.8 g (Keast and Fox 1990; Sigourney et al. 2006). Additionally, Sigourney et al. (2006) stated that fish within beaver ponds were longer and heavier than conspecifics up and downstream. These authors speculated that the weight difference was due to a greater availability of space and food. Keast and Fox (1990) noted that most of the increase was due to two species, blackchin shiners (*Notropis heterodon*) and redbelly dace (*Chrosomus eos*). The fifth study reported a mean increase in coho salmon (*Oncorhynchus kisutch*) production of 1.24 g/m^2 in Alaska due to beaver impoundment (Malison et al. 2015). Despite these results, Malison et al. (2015) note that beaver impoundments may decrease production on the floodplain scale if beavers block access to rearing habitat.

3.2.2.3.3 Species Richness

Snodgrass and Meffe (1998) examined beaver impoundment effects on fish species richness in low-order (1^{st} – 3^{rd}) South Carolina streams. Snodgrass and Meffe (1998) found that fish species richness per stream meter was four times higher in impounded sections compared to control reaches. These authors highlight that this effect is dependent on the mosaic of habitat effects created by beavers as they move around the landscape (see Section 3.3.4).

3.2.2.3.4 Species Diversity

Two studies from North America and one from Japan examined woody impoundment effects on fish species diversity. Hanson and Campbell (1963) found seven additional species in beaver ponds as compared to non-impounded reaches. In Japan, Nagayama et al. (2012) examined how BDA-like structures affected fish species diversity in an area with no historic beaver influence. These authors calculated that impounded areas had 0.70 – 0.85 more fish diversity, using the Shannon-Weaver species diversity index, than control sections in autumn and winter, respectively. A third study, from Missouri, reported that beaver dams enhanced fish diversity but did not provide quantitative support (Mitchell and Cunjak 2007). These authors determined that Atlantic salmon (*Salmo salar*) were the dominant species below beaver dams, but above the dams, slimy sculpin (*Cottus cognatus*) and brook charr (*Salvelinus fontinalis*) became more frequent. Mitchell and Cunjak (2007) attributed this change to sculpin and charr being able to navigate side channels around dams during high and low flows, whereas salmon struggled during low flows.

3.2.2.3.5 Habitat Quality

Eight studies across the United States examined beaver dam effects on fish habitat and all concluded that beaver dams enhance fish habitat at the landscape scale. Only one study provided numeric support and they concluded that beaver dams created 10.5% more fish habitat, on average, over unimpounded reaches (Leidholt-Bruner et al. 1992). This same study found that beaver ponds in Oregon contained a higher abundance of fish (72.81 fish) than unimpounded reaches. The remaining studies relied on the suite of metrics described in the other Sections of 3.2.2.3 or simply stated that fish habitats improved due to beaver dam construction (Rupp 1955; Gard 1961a; Gard 1961b; Hanson and Campbell 1963; Schlosser 1995; Lokteff et al. 2013; Bouwes et al. 2016). One commonly cited factor contributing to fish habitat enhancement was greater food availability due to greater invertebrate production (see Section 3.2.2.2; Rupp 1955; Gard 1961a; Schlosser 1995). Rupp (1955) noted that whether beaver dams enhance or degrade fish habitat at a given site is largely determined by the abiotic conditions (e.g., temperature, pH, and carbon inputs) present at the site pre-construction (see Section 3.2.1.5). Additionally, Hanson and Campbell (1963) determined that the highest number of species were found in the largest ponds as these areas provided the greatest habitat diversity including refugia during high and low flow events. Large ponds also have deeper areas that function as temperature refugia for fish during hot or cold spells (McRae and Edwards 1994).

3.2.2.3.6 Beaver Dams as Fish Barriers

Five publications examined the effectiveness of beaver dams as fish barriers and all five determined that beaver dams are at least semi-permeable to fish movements (Rupp 1955; Gard 1961b; Schlosser 1995; Taylor et al. 2010; Lokteff et al. 2013). Two of these studies determined that beaver dams were ultimately a hindrance to fish movements in Maine and Nova Scotia (Rupp 1955; Taylor et al. 2010). This result was especially true during low flows in the fall, however, beaver impoundments often become more passable during the high flows of spring and early summer (Mitchell and Cunjak 2007; Taylor et al. 2010). Most fishes, including salmonids, sculpins, dace, and shiners, were able to pass through or around beaver dams during high flows and often at low flows as well (Gard 1961a; Mitchell and Cunjak 2007). However, some species, such as sea lamprey (*Petromyzon marinus*), as well as younger age classes of the above groups of fishes, can find the structures impassable (Mitchell and Cunjak 2007). Gard (1961a) determined that brown trout (*Salmo trutta*) were the most likely of the studied species to pass dams, although rainbow trout (*Oncorhynchus mykiss*) also regularly passed the impoundments. Rupp (1955) found that brook charr in Maine were not hindered by beaver dams. Conversely, Lokteff et al. (2013), found that brook charr and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) crossed beaver dams while brown trout were often stopped by the dams. Lokteff et al. (2013) found that brook charr passed every dam in their study area when moving up and downstream.

In short, the reviewed publications indicate that beaver dams increase fish density, survival, total biomass production, species richness, species diversity, habitat, and abundance (IVA = 1.0 for all metrics; Table 4). Whether fish passage is blocked by beaver dams is debated in the literature (IVA = 0.2), but, overall, studies show that a majority of fish species are capable of navigating beaver dams at all but the lowest stream flows.

3.2.2.4 Amphibians

Amphibians have been declining worldwide during the twenty-first century largely due to habitat loss and disease (Shoo et al. 2011). Beaver impoundments mitigate some of these influences by working as water filters and stabilizing stream conditions (Table 4; Sections 3.2.1.1 and 3.2.1.12; Popescu and Gibbs 2009). Beaver activities also facilitate amphibian movement via canals which spread shallow water across the floodplain (Anderson et al. 2015). For many of the reasons described below, Shoo et al. (2011) recommended recreating beaver dams across their former range to stall amphibian declines via habitat enhancement. Seven of the reviewed studies examined beaver impoundment effects on amphibians and six of these (85.70%) provided quantitative support.

3.2.2.4.1 Production and Habitat Quality

Three studies, two from Alberta and one from New York, considered how beaver dams affect wood frog (*Rana sylvatica*) production (Stevens et al. 2006; Stevens et al. 2007; Karraker and Gibbs 2009). All three studies found that beaver impoundments increased wood frog production by a weighted average of 2.98-fold (SE = 1.42). In their study, Karraker and Gibbs (2009) also found that embryos grown in beaver ponds had a higher probability of surviving to metamorphosis and that the beaver pond metamorphs were 1.3 times larger than those from vernal pools. This created a positive feedback loop wherein beaver ponds had more surviving young which led to higher numbers of metamorphs which led to more eggs produced. This effect seems to increase as the ponds age, as Stevens et al. (2006) found that older ponds (>25 years) recruited nearly 7-times as many metamorphs as new ponds (<10 years) and that young from old ponds developed faster. Furthermore, Stevens et al. (2007) concluded that beaver impoundments in Alberta created habitat for several amphibian species including wood frogs, boreal chorus frogs (*Pseudacris maculata*) and western toads (*Bufo boreas*), as these species were only detected in beaver pond habitats.

3.2.2.4.2 Occurrence

Four studies examined beaver dam effects on amphibian occurrence and three of these provided numeric support. All four studies found that beaver impoundments increased amphibian occurrence although one found that the degree of the increase depended on the species examined (Cunningham et al. 2007). In New York and at sites throughout the American Rocky Mountains, amphibians were detected 22% and 34% more, respectively, in beaver-influenced habitats than in control reaches (Popescu and Gibbs 2009; Hossack et al. 2015). Meanwhile, Stevens et al. (2007)

determined that amphibians occurred more often in beaver-influenced habitats, so much so that they recommended using beaver as a surrogate species for determining viable amphibian habitat. However, Stevens et al. (2007) did not provide numeric support. Cunningham et al. (2007) reported that bullfrogs (*Lithobates catesbeianus*), an invasive species, were only found in active beaver colonies while 81% of captured pickerel frogs (*Lithobates palustris*) were found in beaver-influenced habitats. Hossack et al. (2015) also reported that boreal toads (*Anaxyrus boreas*), a threatened and endangered species, and Columbia spotted frogs (*Rana luteiventris*) colonized beaver-modified habitats at least twice as much as any other examined habitat.

To conclude, the reviewed publications concur that beaver impoundments are beneficial for amphibians as their studied beaver ponds produced and housed more amphibians than non-impounded reaches (IVA = 1.0 for both metrics; Table 4).

3.2.2.5 Birds

Birds constitute the middle and upper trophic levels and often rely on riparian ecosystems for important life history stages; breeding and brood-rearing (Shaw and Fredine 1956). In the western U.S., where riparian areas constitute less than 2% of the land area, beaver-impounded habitats are particularly important for riparian dependent birds at these life cycle stages (McKinstry et al. 2001; Pollock et al. 2015).

Eighteen publications examined beaver dam effects on bird communities and 12 (66.7%) of these provided numeric support. These 12 studies examined bird richness, diversity, abundance, density, and production. Additional studies examined bird occurrence, but these provided only anecdotal evidence (Table 4).

3.2.2.5.1 Species Richness

Seven publications investigated how beaver dams impact bird species richness and all but one found increased richness in beaver-influenced habitats compared to unimpounded sections. The other study found no significant difference (effect size of 0.4 species) between habitat types (Grover and Baldassarre 1995). Four of these seven studies reported comparable results with a weighted average increase of 4.78 species (SE = 1.63) in beaver-influenced wetlands (Hair et al. 1978; Medin and Clary 1990; Grover and Baldassarre 1995; Alza 2014). In New York, Alza (2014) found that bird species richness increased as tree species richness increased. Furthermore, Alza (2014) determined that avian richness increased as wetland size increased and speculated that this may be due to the higher amounts of disturbance present in beaver-influenced areas versus control reaches. If correct, this effect on avian richness may be less pronounced where BDAs are used without beaver as there is only the initial disturbance of BDA installation. However, Alza (2014) also found that beaver influences on canopy cover and understory complexity did not influence richness among high-canopy feeders (e.g., purple finches, *Carpodacus purpureus*, and red-eyed vireos, *Vireo olivaceus*). Furthermore, snags present in beaver ponds provide feeding and rearing habitat for cavity nesting birds such as nuthatches (*Sitta* spp.), woodpeckers and flycatchers (the latter two groups cover multiple genera and species; Naiman and Décamps 1997; Harmon et al. 2004). Alza (2014) further speculated that this richness-area relationship could be due to the high mobility of birds, which allows them to choose the best sites, or to greater habitat heterogeneity, which leads to greater niche availability. Grover and Baldassarre (1995) also found that avian richness increased with increasing wetland size but only to the point that the mix of riparian and upland habitats was 50:50. When wetland habitats occupied more space, they noted a decrease in richness. Working in several study sites across the southeastern U.S., Hair et al. (1978) determined that beaver-influenced habitats housed seven more bird species than surrounding hardwood forests and 5.8 more than surrounding pine forests. Of the remaining three studies, one reported a 20% increase in avian richness following BDA installation (Apple 1985). The final two studies anecdotally stated that bird species richness was higher in beaver-influenced areas compared to control reaches in Wyoming (Brown et al. 1996; Cooke and Zack 2008). These researchers concurred that wetland size and habitat heterogeneity were the most significant factors contributing to increased bird species richness.

3.2.2.5.2 Species Diversity

Two publications examined beaver impoundment effects on bird diversity and both found that this metric was higher in impounded than unimpounded reaches by a weighted average of 0.64 (SE = 0.36) using the Shannon-Weaver species diversity index (Hair et al. 1978; Medin and Clary 1990). In Idaho, Medin and Clary (1990) determined that all bird species found in control areas were also found in beaver-influenced areas in addition to several species, including common yellowthroat (*Geothlypis trichas*), that were only found in beaver-modified habitats. Hair et al. (1978) noted that some species, e.g., high canopy feeders, lost habitat due to tree drowning. This finding contradicts Alza's (2014) findings detailed in Section 3.2.2.5.1. As high canopy feeders occur in both study sites, more work is needed to understand these effects.

3.2.2.5.3 Abundance

In the southeastern U.S., Hair et al. (1978) determined that beaver-influenced areas contained an average of 36 birds whereas surrounding hardwood and pine forests contained an average of 16 and 14 birds, respectively. Cooke and Zack (2008) found similar effects in Wyoming but did not provide numeric support.

3.2.2.5.4 Occurrence

One study each in Colorado and Finland, determined that birds occurred more often in beaver-modified habitats than in control areas (Neff 1957; Nummi 1992). However, a second study in Finland found no significant difference between impounded and control reaches in avian occurrence (Nummi and Pöysä 1997). After installing BDAs, Nummi (1992) noted that the number of teal (*Anas* spp.), goldeneye (*Bucephala* spp.) and mallard (*Anas platyrhynchos*) broods greatly increased in the first two years of flooding but then fell in the third. However, the occurrence of these ducks was still higher than that seen pre-flooding. Nummi and Pöysä (1997) found a similar effect with teal in their study areas but noted no similar increase in use by Eurasian wigeon (*Anas penelope*) or mallard. Nummi and Pöysä (1997) also noted that while mallard was the dominant species pre-impoundment, teals dominated post-impoundment. This shift was due to teal population increases as there was no concomitant drop in mallard populations. Of these species, mallards have proven to be particularly effective at transporting seeds of wetland species over long distances thereby facilitating genetic mixing and possibly extending beaver impoundment effects across landscapes (Mueller and van der Valk 2002). Additionally, birds in northern latitudes may occur more on beaver ponds which often thaw earlier than other water bodies. This gives birds early access to invertebrates and seeds within the ponds which may be especially important for non-migratory species (Bromley and Hood 2013).

3.2.2.5.5 Density

Three studies from across the United States examined beaver dam effects on avian density, however, all three reported incomparable results. Regardless, all three found that bird densities were higher in beaver-impounded areas than in non-impounded reaches (Rutherford 1955; Medin and Clary 1990; McCall et al. 1996). McCall et al. (1996) and Rutherford (1955) examined duck densities and found that impounded habitats supported 7.5 and 12.8 more ducks/stream km and ducks/mi^2, respectively. Indeed, Rutherford (1955) found that ducks used and nested in beaver-influenced habitats exclusively. Medin and Clary (1990) determined there were an average of 6.3 additional birds/ha in beaver-modified areas. In this study, shorebirds, including killdeer (*Charadrius vociferus*), spotted sandpiper (*Actitis macularius*) and common snipe (*Gallinago gallinago*), were found exclusively in beaver-modified habitats.

3.2.2.5.6 Production

Medin and Clary (1990) examined beaver dam effects on avian production and found production increased by 301 g/ha in beaver-influenced reaches compared to other habitats.

To summarize, the reviewed studies indicate that beaver dams increase avian species diversity, abundance, density, and total biomass production (IVA = 1.0 for all metrics; Table 4). The above publications also suggest that beaver dams increase bird species richness (IVA = 0.9) and occurrence (IVA = 0.7) compared to unimpounded reaches, although there is some discrepancy in the literature with regards to these two metrics.

3.2.2.6 Mammals

3.2.2.6.1 Muskrat Occurrence

Four of the reviewed studies considered beaver impoundment effects on mid-sized mammals (Table 4). Two of these stated that muskrat (*Ondatra zibethica*) occurrence increased in beaver-influenced wetlands compared to control areas in Colorado, but they did not provide any data (Rutherford 1955; Neff 1957). In a related study, up to four muskrats shared a beaver lodge with two adult beavers one winter in Quebec (Potvin and Bovet 1975). This suggests that beavers and muskrats share a commensal relationship, as opposed to a competitive one, as one might expect when considering their similar diets at certain times of year.

3.2.2.6.2 River Otter Habitat Quality

The remaining two studies examined how beaver impoundments affect river otter (*Lontra canadensis*) habitat. Although neither study provided quantitative evidence, both concluded that beaver impoundments enhanced otter habitat in Arkansas and Maine, respectively (Tumlison et al. 1982; Dubuc et al. 1990). Both publications posited that this was due to the habitat and species composition alterations that resulted from beaver activities such as: abundant food sources, stable pond levels and increased cover and resting sites. Tumlison et al. (1982) suggested that beaver reintroduction, and reestablishing their activities, creates otter habitat and eases otter stress in marginal habitats by providing more shelter and food.

3.2.2.6.3 Small Mammals

One publication considered beaver dam impacts on small mammals (e.g., voles, *Microtus* spp.; shrews, *Sorex* spp.; and deer mice, *Peromyscus maniculatus*). Medin and Clary (1991) found 30.05 additional small mammals/ha in beaver-influenced habitats versus control areas. Medin and Clary (1991) also determined that small mammal biomass in beaver habitats increased 502.5 g/ha over upland areas. These authors calculated that species richness increased by two species and diversity increased by 0.095 using the reciprocal of Simpson’s diversity index, but these were not considered significant increases. Medin and Clary (1991) reported that montane voles (*M. montanus*), long-tailed voles (*M. longicaudus*), western jumping mice (*Zapus princeps*), and shrews, aside from the water shrew (*S. palustris*), were caught almost exclusively in beaver pond habitats. Conversely, deer mice and water shrews were caught in both wetland and upland areas.

In addition to being vital food chain components, small mammals serve as seed and fungi dispersers (Terwilliger and Pastor 1999). This dispersal is especially relevant considering that extended floods, such as beaver ponds, kill mycorrhizal fungi (Terwilliger and Pastor 1999). Without these fungi, coniferous trees cannot reinvade the meadow when the pond drains. Thus, succession often arrests at a meso-woody riparian community, characterized by willow, alder, and birch with a sedge (*Carex* spp.) understory (Wilde et al. 1950; Cottrell 1995; Westbrook et al. 2011). However, an abundance of small mammals, which eat mycorrhizal fungal spores, increases the chances that spores will be spread across the meadow and subsequently deposited on or very near the roots of seedlings (Terwilliger and Pastor 1999). Terwilliger and Pastor (1999) note that, over time, spreading and deposition of mycorrhizal fungal spores promotes succession to a climax conifer community, at least until beavers reestablish their presence and reset the successional clock.

3.3 Ungulate Effects

Of the 331 publications I reviewed, 46 detailed wild ungulate (i.e., elk and moose) environmental effects and the relationships between beavers and ungulates (Table 5). Thirty (65.2%) of these publications provided quantitative evidence. I examine ungulate effects on abiotic and biotic environmental components that these results may be compared with the previous section before examining the environmental coactions of beaver and wild ungulates and how beaver, elk, and moose ultimately compete.

3.3.1 Ungulate Environmental Effects

3.3.1.1 Vegetation

Eight of the reviewed publications covered elk and moose browsing impacts on willow production. Overall, these researchers determined that browsing decreased willow production, although two of these studies found negligible effects (Case and Kauffman 1997; Alstad et al. 1999; Peinetti et al. 2001; Brookshire et al. 2002; Zeigenfuss et al. 2002; Baker et al. 2003; Bilyeu et al. 2008; Baker et al. 2012). However, these negligible results were not supported by data (Alstad et al. 1999; Peinetti et al. 2001). Five of the remaining six studies provided data to support their conclusions but only two of these rendered comparable results. The first of these two, from Rocky Mountain National Park (RMNP), determined that elk browsing decreased willow production by 90% (Baker et al. 2003). The second found that elk browsing in Oregon decreased willow production by 204% (Case and Kauffman 1997). Together these studies yield a weighted average decrease of 199.5% (SE = 57) in terms of total grams of biomass produced. Another study from RMNP calculated that elk browsing decreased willow production by 73% in terms of kg/ha (Zeigenfuss et al. 2002). Yet another RMNP study found the same effect but did not provide additional data (Baker et al. 2012). In Oregon, elk browsing decreased willow production by 116%/m^2 (Brookshire et al. 2002). Additionally, Bilyeu et al. (2008) determined that willows browsed by elk and moose were 34.07 cm shorter than unbrowsed conspecifics. Baker et al. (2003) stated that decreases in willow production can limit beaver populations where woody riparian vegetation availability is a limiting factor.

While browsing, elk and moose consume the terminal inches of willow shoots, which is where willow flowers (i.e., catkins) are produced (Singer et al. 1998). Thus, elk and moose browsing not only decreases willow stature but also reduces willow reproductive ability. Five of the reviewed studies found that elk and moose browsing decreased the number of catkins produced. Four of these studies determined that browsing reduces catkin production by 5 – 100% for a weighted average decrease of 34.17% (SE = 17.87; Kay and Chadde 1992; Singer et al. 1998; Brookshire et al. 2002; Zeigenfuss et al. 2002). Peinetti et al. (2001) also found no catkins on elk browsed plants in RMNP. Under the high levels of elk and moose browsing observed by Kay and Chadde (1992), Singer et al. (1998) and Peinetti et al. (2001), where >87% of catkins were removed, willow populations will eventually disappear as they are unable to replace themselves.

Moose, unlike elk, browse aquatic vegetation, which can further impact the environment and beaver populations (Aho and Jordan 1976; Edge et al. 1988). Four studies examined moose browsing impacts on aquatic macrophyte production and all four determined that moose decreased these species' overall production (Fraser and Hristienko 1983; Morris 2002; Qvarnemark and Sheldon 2004; Bergman and Bump 2015). Three of these publications reported comparable results and yielded a weighted average decrease in aquatic macrophyte production of 34.84 g Dry Weight/m^2 (SE = 15.81; Morris 2002; Qvarnemark and Sheldon 2004; Bergman and Bump 2015). Additionally, Fraser and Hristienko (1983) reported that moose browsing decreased aquatic macrophyte production by 15-fold. Furthermore, these authors note that browsed plants were small and weak and rarely produced flowers whereas unbrowsed plants regularly developed strong petioles, floating leaves, and flowers. By decreasing aquatic macrophyte production, moose indirectly alter oxygen transport cycles in the pond and increase light penetration, which can increase water temperatures (see Sections 3.2.1.5 and 3.2.1.9; Bergman and Bump 2015). The loss of aquatic macrophytes may increase beavers' reliance on woody vegetation, which may also be declining due to ungulate browsing. Taken together, this loss of aquatic and terrestrial vegetation may decrease beaver colonies' lifespans with impacts reverberating across the floodplain. However, Qvarnemark and Sheldon (2004) note that aquatic macrophytes often have large root structures which allow them to resist moose browsing.

Two studies found different ungulate browsing effects on terrestrial herbaceous production depending on the ungulate species studied. Zeigenfuss et al. (2002) found that elk browsing decreased herbaceous production by 18 – 29% in terms of kg/ha. Conversely, moose browsing enhanced herbaceous production in Isle Royale National Park by 600 kg/ha (McInnes et al. 1992). McInnes et al. (1992) posit that this increase was due to moose decreasing both shrub and canopy tree biomass which allowed more sunlight to penetrate to the forest floor. The different effects of elk and moose browsing on herbaceous production may be due to the different densities at which these species typically congregate. Elk are social animals that form large groups which means they can eat more vegetation from a single area (Baker et al. 2012). Moose, however, tend to be solitary, occasionally forming groups of two to three (Flook 1962).

Six publications considered wild ungulate browsing impacts on vegetation diversity, density, richness, and biomass. In short, these studies found that elk and moose browsing had mixed effects on species diversity, slightly enhanced density and richness, and decreased biomass (Risenhoover and Maass 1987; Chadde and Kay 1988; Despain 1989; Chadde and Kay 1991; McInnes et al. 1992; Hood and Bayley 2009). Two studies examined moose and elk browsing effects on vegetation diversity but neither offered quantitative data (Risenhoover and Maass 1987; Chadde and Kay 1988). Working with elk and moose in Yellowstone National Park, Chadde and Kay (1988) determined that browsing decreased vegetation diversity while Risenhoover and Maass (1987) found that moose browsing increased diversity.

Risenhoover and Maass (1987) determined that moose browsing in Isle Royale National Park increased tree and shrub densities by 4,050 stems/ha. Using the same browse exclosures, McInnes et al. (1992) determined that moose browsing led to 1,700 fewer trees/ha. These findings suggest that moose browsing decreases tree density but increases shrub stem density. This response by shrubs is likely compensatory, however, considering the rest of the findings in this section, these shrubs may not be larger or more productive despite having more stems (Wolff 1978; Belsky 1986; Bergstrom and Danell 1987; Baker et al. 2016). Another study, from Canada, concluded that wild ungulate browsing increased vegetation density but did not provide numeric support (Hood and Bayley 2009). McInnes et al. (1992) were the only authors to examine ungulate browsing effects on vegetation species richness and they found that moose browsed areas contained 3.5 more species than unbrowsed areas.

Four of the reviewed publications examined how wild ungulate browsing affected vegetation biomass. McInnes et al. (1992) calculated that moose browsing decreased tree biomass by 80,000 kg/ha, shrub biomass by 1,200 kg/ha and herbaceous biomass by 600 kg/ha. Additionally, two studies from Yellowstone National Park concluded that moose and elk browsing decreased vegetation biomass (Despain 1989; Chadde and Kay 1991). Chadde and Kay (1991) found that willow heights decreased by 240 cm, on average, and willow cover decreased by 64% due to browsing. Finally, Hood and Bayley (2009) found that wild ungulate browsing decreased vegetation biomass by 8.1%.

In short, wild ungulate browsing decreases catkin (IVA = -1.0), aquatic macrophyte (IVA = -1.0), and overall vegetation production (IVA = -1.0) while increasing vegetation species richness (IVA = 1.0). The reviewed publications show that browsing has negligible effects on herbaceous production as well as vegetation diversity (IVA = 0.0 for both metrics). Most of the literature suggests that browsing decreases willow production (IVA = -0.8) and increases vegetation density (IVA = 0.3; Table 5).

3.3.1.2 Birds and Mammals

The above browsing effects on vegetation can echo across trophic levels that rely on willows and other riparian woody plants for food, shelter, and breeding. A single study in Pennsylvania considered wild ungulate (white-tailed deer, *Odocoileus virginianus*; elk; and Mouflon sheep, *Ovis musimon*) browsing effects on bird abundance, species diversity, and density (Casey and Hein 1983). These authors concluded that wild ungulate browsing had no significant effects on these three metrics; avian abundance increased by 3.33 birds/census, species diversity increased by 0.21 using the Shannon-Weaver species diversity index, and bird density increased by 1.33 pairs/ha in browsed versus unbrowsed areas. Casey and Hein (1983) noted that the browsed area had a browse line reaching up to 2 m and had open clearings with interspersed old, often dead or dying, trees while the unbrowsed area had dense ground cover, although all plots had similar canopy coverage. These authors also noted that the bird species compositions reflected these vegetation differences as the browsed area contained more cavity nesting birds (e.g., nuthatches and woodpeckers) whereas the unbrowsed area contained a wider variety of species, including wild turkey (*Meleagris gallopavo*) and barred owl (*Strix varia*), some rare, including willow flycatcher and hooded warbler (*Wilsonia citrina*). Thus, although the above metrics suggest that these habitats are similar in terms of avian species, differences in avian feeding guilds may exist.

Although no studies detailed wild ungulate browsing effects on small mammals, Medin and Clary (1989) examined cattle grazing impacts on small mammal species diversity, richness and production in Nevada. These authors calculated that grazing decreased small mammal species diversity by 0.73 using a non-standard diversity index. Medin and Clary (1989) also determined that five additional species were caught in ungrazed habitats compared to grazed ones and that small mammal production was 775 g/ac higher in ungrazed habitats. These additional species included two species of voles, the bushy-tailed woodrat (*Neotoma cinerea*), northern pocket gopher (*Thomomys talpoides*) and Townsend’s ground squirrel (*Spermophilus townsendii*) while shrews, deer mice, and the western jumping mouse were caught in both habitats.

In sum, elk and moose browsing creates less structurally diverse habitats characterized by occasional patches of tall, woody vegetation interspersed with herbaceous growth and stunted shrubs and trees (Chadde and Kay 1988; McInnes et al. 1992). These stunted plants produce fewer seeds than their mature counterparts and, what new growth is produced, is often consumed by ungulates (Kay and Chadde 1992; Baker et al. 2003). Ultimately, browsing prevents early successional trees and shrubs from reaching full height which allows less palatable and later successional species more access to sunlight and nutrients (Moen et al. 1990; McInnes et al. 1992). Browsing does not accelerate or slow succession, rather, it transfers the system from one successional path to another (Pastor et al. 1987; Johnston et al. 1993; Wolf et al. 2007). Fortunately, willows are resilient and can tolerate high browsing levels for years before dying. This resilience means that management actions, such as browse exclosures, may ease the browsing burden and allow shrubs to grow past browsing height (~2.5 m for elk and ~3 m for moose; Risenhoover and Maass 1987; Despain 1989; Chadde and Kay 1991).

3.3.2 Coactions of Beavers and Wild Ungulates

Four publications considered how beavers influence moose habitat and all four concluded that moose habitat is improved due to beaver activities, although none provided quantitative support (Flook 1962; Aho and Jordan 1976; Johnston et al. 1993; Collins and Helm 1997). These authors concluded that beavers enhance moose habitat by increasing the density, cover, and production of palatable woody species as well as aquatic macrophytes. Flook (1962) observed that moose in Banff National Park tolerate deeper snows than other ungulates and often spend all winter browsing in one small area, whereas elk are forced to move downslope to montane foothills and plains habitats (Olmstead 1976; Skovlin 1982). Moreover, moose tend to spend winter in high elevation, headwater drainages as these areas provide a concentrated abundance of food in flat valley bottoms, which are easier to navigate in snowy conditions (Peek et al. 1976). Indeed, Flook (1962) noted that moose are drawn to riparian habitats, favoring those influenced by beaver. Not only do beaver dams create the early successional patches preferred by moose, but their networks of side channels and canals create pathways by which moose can access these patches year-round (Collins and Helm 1997). These respective habitat preferences suggest that moose can feed in beaver-influenced habitats all year, but elk may forego these areas in winter.

Six publications examined how concurrent beaver and wild ungulate herbivory affects vegetation standing crop and all six determined that herbivory by these species decreases vegetation standing crop (Pastor et al. 1987; Moen et al. 1990; Baker et al. 2003; Hood and Bayley 2009; Baker et al. 2012; Bergman and Bump 2015). Baker et al. (2003) and Baker et al. (2012) found this effect in RMNP studying elk while Hood and Bayley (2009) found that herbivory from beavers and a suite of wild ungulates decreased vegetation standing crop by 1.7%. The remaining three studies examined a moose dominated system in Isle Royale National Park where Bergman and Bump (2015) found that aquatic macrophyte standing crop biomass decreased by 181 g Dry Weight/m^2 and Moen et al. (1990) found this same metric decreased by 5 m^2/ha. Bergman and Bump (2015) determined that moose consumed more aquatic macrophytes than beaver, although this varied with macrophyte species; beaver consumed mostly pondweed (*Potamogeton* spp.) whereas moose consumed mostly watershield (*Brasenia schreberi*). Pastor et al. (1987) concluded that beaver foraging increased the availability of light and soil carbon and nitrogen for terrestrial plant uptake, however, moose foraging negated these effects. In Canada, Hood and Bayley (2009) found that all shrubs were browsed to some extent but 91% were browsed solely by ungulates, whereas only 3% were browsed by beaver. Despite this, Hood and Bayley (2009) reported no difference in shrub community diversity between high and low ungulate use areas, regardless of beaver presence. In areas where ungulate herbivores and beavers were effectively absent, these authors observed increased vegetation production, particularly by willows; on average, shrubs were four times as tall as their browsed counterparts. Baker et al. (2003) posited that beaver on the landscape are beneficial to willow. They also stated that elk alone are not necessarily damaging to willow as long as high water tables and riparian conditions prevail, for inundated areas tend to prevent elk access into the willow communities. However, Baker et al.

(2003) concluded that beaver and elk, especially at high densities, together can be devastating for willows as they hamper compensatory growth which prohibits regeneration. Baker et al. (2012) concurred, further stating that while willow is not necessary for elk survival, it is for beaver.

Baker et al. (2012) ran a series of models based on RMNP wherein they tested what elk density would allow the coexistence of elk and beaver. They determined that beaver persist in perpetuity at elk densities less than 20 elk/km^2. Higher elk densities, ranging from 30 – 100 elk/km^2, eliminated beaver within 28 – 76 years; values greater than 50 elk/km^2 had no further effect. However, the modeling also revealed that these timelines can be extended if beavers move around the landscape in a cyclical pattern, as is often the case (see Section 3.3.4; Pollock et al. 2007; Westbrook et al. 2011).

3.3.3 Beaver and Wild Ungulate Competition

Five publications considered the competitive relationship between beavers, elk, and moose and all agreed that wild ungulates outcompete beaver and drive them from the landscape at high densities (Moen et al. 1990; Chadde and Kay 1991; Hood and Bayley 2009; Baker et al. 2012; Bergman and Bump 2015). Chadde and Kay (1991) determined that moose and elk overbrowsing in Yellowstone National Park eliminated beaver food, construction material, and, in effect, beaver from the landscape. Chadde and Kay (1991) posit that this competitive exclusion, more than any other process, has led this landscape to transition to the elk grassland state (Wolf et al. 2007).

Once beaver have left an area, the dams fall into disrepair and fail (Remillard et al. 1987). The drained ponds are not suitable as moose feeding areas, but these areas become increasingly suitable for elk as they dry (Flook 1962; Baker et al. 2003). Flook (1962) therefore concludes that, although moose and beaver compete, elk ultimately outcompete both species. In ecosystems with low ungulate densities, woody vegetation can reach larger size-classes (Risenhoover and Maass 1987) and, thus, be suitable for harvest by beavers. In such areas, beavers and large ungulates can coexist in a constant cycle of beaver colonization, site flooding, resource depletion, site abandonment, and rejuvenation that is typical of beaver-modified ecosystems (Westbrook et al. 2011).

Ultimately, with beavers consuming large size classes of woody vegetation (e.g., willows and aspen) around the pond and ungulates consuming small size classes across the landscape, these plants decline in abundance until only unpalatable species (e.g., spruces, *Picea* spp.) remain (Pastor et al. 1987; Miquelle and Ballenberghe 1989; Moen et al. 1990; Johnston et al. 1993; Donkor and Fryxell 1999; Hood and Bayley 2009). Moen et al. (1990) found that moose browsing on Isle Royale decreased aspen to zero regeneration, but white spruce (*P. glauca*) were hardly browsed. Pastor et al. (1987) and McInnes et al. (1992) found the same effect on different points of Isle Royale. Moose browsing in Denali National Park was also found to reduce aspen, willow, and balsam poplar (*Populus balsamifera*) while increasing spruce frequency (Miquelle and Ballenberghe 1989). Interestingly, Hood and Bayley (2009), only found conifers on sites with high ungulate use, regardless of beaver presence. This further suggests that increases in spruce abundance are due to ungulate preference. Taken together, the above effects result in a spruce-moose savanna in moose dominated systems and an elk grassland in elk dominated systems (Johnston et al. 1993; Wolf et al. 2007).

3.3.4 Beaver and Ungulate Landscape Effects

When beavers construct a dam, or a BDA is installed, the successional clock is reset (Nummi 1989). The water surface area in the riparian zone increases and vegetation immediately around the pond drowns (Wilde et al. 1950; Munther 1984; Grover and Baldassarre 1995; Snodgrass and

Meffe 1998; Bilyeu et al. 2008; Westbrook et al. 2011; Majerova et al. 2015; Thompson et al. 2016; Jones et al. 2020). This opens the canopy and allows more sunlight to penetrate to the pond (Naiman and Melillo 1984; Naiman et al. 1986; Naiman et al. 1988; Gregory et al. 1991). Often, this raises the temperature in the shallower pond sections, however, deeper sections may stabilize at cooler temperatures and serve as fish and invertebrate refugia (see Sections 3.2.1.5 and 3.2.2.3.5; Gard 1961a; McRae and Edwards 1994; Pollock et al. 2015).

The increased water surface area raises the water table across the floodplain and expands the riparian area width, creating ideal conditions for riparian vegetation growth (see Section 3.2.1.3; Naiman and Melillo 1984; Apple 1985; Pollock et al. 2003; Pollock et al. 2007). Over time, beavers construct multiple dams along the main channel, creating a beaded string of ponds (Laurel 2019). From these larger complexes, the beaver colony expands onto the floodplain as the beavers exhaust the food and construction material near their ponds (Hall 1960; Basey et al. 1988; Masslich et al. 1988). Indeed, Polvi and Wohl (2013) found that only active beaver colonies and old-growth forests have the potential to create and maintain diverse, self-sustaining, anabranching streams along the Colorado Front Range. Beavers often construct canals and smaller side channel dams that radiate out from the pond to ease food access and provide escape routes from predators. These canals and smaller dams further flood the area compounding the above effects (Gurnell 1998; Baker and Hill 2003; Westbrook et al. 2006; Pollock et al. 2015; Laurel 2019).

Ultimately, beavers' engineering efforts create a patchwork of ponds of various ages. Different aged dams store sediment differently which affects how water flows through the pond. Older ponds accumulate sediment at as little as 1/3 the rate of new ponds, however, older ponds have larger sediment stores that allow them to dampen stream flows more efficiently (Butler and

Malanson 1995; Meentemeyer and Butler 1999; Bigler et al. 2001). This, in turn, affects the biogeochemical processes within the pond and determine which taxa, and age classes of those taxa, use the pond (see Sections 3.2.1, 3.2.2.3, and 3.2.2.4; Skinner et al. 1984; Stevens et al. 2006).

While beaver dams are present, they maintain habitat heterogeneity on a landscape scale by mitigating disturbances at the reach and floodplain scales (Rupp 1955; Correll et al. 2000; Laurel and Wohl 2019). As dams slow stream flows and spread water over the floodplain, they dampen flood events by dissipating high energy flows (John and Klein 2004). Slowed stream flows also allow for greater water storage and mixing across the floodplain (see Section 3.2.1.4) which allows for steadier flows all year round, even during droughts when the stream may have otherwise dried up (Pollock et al. 2003; Westbrook et al. 2006). Additionally, beaver complexes resist wildfires by keeping the floodplain and the vegetation therein more hydrated (Fairfax and Whittle 2020). Thus, beaver complexes can provide refuges for all manner of taxa during disturbances. All this is not to say that disturbance is a negative thing or that managers should be engineering their systems to resist natural disturbances. Rather, it is to say that, when viewed from a landscape scale, beaver-influenced habitats can preserve native species and natural niches and serve as source populations from which disturbed habitats can be filled (Watkinson and Sutherland 1995).

Meanwhile, the beavers’ supply of woody vegetation rejuvenates slowly and eventually runs out, leading the beavers to abandon the site in search of a new home (Remillard et al. 1987). Even with beavers gone, dams often last for decades, building up sediment, keeping water tables elevated and promoting vegetation growth (Naiman et al. 1988; Baker and Hill 2003). However, dams eventually breach, resetting the successional clock (Nummi 1989). When the pond drains, it unveils its stores of nutrient-rich, wet soil that prove to be the ideal germination ground for many riparian species (McMaster and McMaster 2001; Baker and Hill 2003; Gage and Cooper 2004; Butler and Malanson 2005; Gage and Cooper 2005; Cooper et al. 2006). After a few years, the site is often more productive than it was prior to impoundment and is a prime candidate for beaver recolonization (Apple 1985; Howard and Larson 1985; Naiman et al. 1994; Sturtevant 1998; Allen 1999; Albert and Trimble 2000).

Over time, this cycle of colonization, water impoundment, resource depletion, and dam abandonment raises the valley floor due to sedimentation and lowers the incised streambanks via erosion (Martell et al. 2006; Pollock et al. 2007; Westbrook et al. 2011; Gibson and Olden 2014). If undisturbed, this cycle will reconnect incised streams with their former floodplains and lead to a beaver meadow stable state as succession proceeds (Ruedemann and Schoonmaker 1938; Ives 1942; Pollock et al. 2003; Westbrook et al. 2011). On the landscape scale, this patchwork of active, former, and unused sites, all of various ages, leads to a high degree of habitat heterogeneity with correspondingly high biodiversity across numerous taxa (Remillard et al. 1987; Naiman et al. 1988; Johnston et al. 1993; Westbrook et al. 2011).

However, when this cycle is broken by browsing from high-density ungulate populations, the riparian vegetation is lost as are beavers and beaver meadows leading to a non-linear decrease in habitat heterogeneity as the time since beaver abandonment increases (Munther 1984; Naiman et al. 1988; Bilyeu et al. 2008; Beschta and Ripple 2009; Hood and Bayley 2009; Ripple et al. 2010; Beschta and Ripple 2019; Laurel and Wohl 2019). Succession, then, takes a different path characterized by channel incision, stream disconnection from the floodplain, and erosion, forcing the ecosystem into an elk grassland or spruce-moose savanna stable state (Skinner et al. 1984; Johnston et al. 1993; Wright et al. 2003; Wolf et al. 2007; Bilyeu et al. 2008).

The reintroduction of gray wolves to Yellowstone National Park highlighted a possible browsing mitigation tactic known as the ecology of fear (Ripple and Beschta 2004). This concept states that the presence of large predators encourages ungulates to avoid thick vegetation, such as that around beaver ponds, to minimize predation risk. While this concept is still an area of active research, current thinking suggests that self-sustaining riparian ecosystems require large predators to prevent ungulate overbrowsing and avert the consequent effects covered above (Ripple and Beschta 2004). This means that management actions, such as BDAs and browse exclosures, although effective tools and stepping-stones, will likely prove unsustainable as only the reinstitution of predator-induced trophic cascades can fully restore riparian ecosystems.

3.4 Detriments of Beavers

Beavers and their dams are not a panacea for riparian restoration projects. In fact, beavers are now considered an invasive species in Tierra del Fuego, Argentina where they were introduced in a riparian restoration attempt (Fuller and Peckarsky 2011). As beavers were never present in this system, no natural predators or competitors exist to regulate their populations, and beavers have spread rapidly (Gurnell 1998). Whether these rodents, or mimicking their activities, are an effective restoration strategy depends on the initial site conditions, the restoration objectives, and whether the area has a history of beaver influence (Martell et al. 2006; Pollock et al. 2015). Regardless, there are several aspects to consider when examining beavers and BDAs as restoration tools. In this section, I discuss how beavers and BDAs can create risks for human health, life, and property due to flooding, dam failure, and disease.

3.4.1 Flooding

Beaver dam-induced flooding can damage human infrastructure, often at great repair costs. This flooding, along with subsequent herbivory, may destroy trees that are financially, or sentimentally, valuable (Schulte and Müller-Schwarze 1999; Butler and Malanson 2005; Pollock et al. 2015). Additionally, beavers are driven to construct dams and lodges where they hear running water, which makes roadside ditches and culverts prime targets (Jenkins and Busher 1979). Beaver impoundments may flood roads directly or lead to sinkholes as dispersed flows erode the underlying soil (Curtis and Jensen 2004). Additionally, beavers favor wide, low-gradient valleys ostensibly because inundation will be greatest here (Gurnell 1998; MacCracken and Lebovitz 2005). Humans also favor these areas which leads to conflicts with beavers. Such conflicts usually end with relocation or lethal removal of the beaver.

On their own, BDAs circumvent these flooding issues as managers can avoid sensitive areas. However, many BDA-created ecosystem effects can attract beavers and, although this may be a project goal, careful consideration must be given to what happens when beavers colonize the area as well as what happens when beavers begin dispersing across the floodplain.

3.4.2 Dam Failure

In previous sections, I detailed beaver dam installation effects, however, some of these (e.g., sedimentation and nutrient storage) may be undone when the dam breaches, especially during a catastrophic blowout (Błędzki et al. 2011; Wohl and Scott 2017). These events, which occur almost exclusively during severe flooding in high-gradient drainages, send sediment stores downstream with such force that they may blowout additional dams, compounding the problem (John and Klein 2004; Butler and Malanson 2005; MacCracken and Lebovitz 2005). Several such events occurred in the 1900s and early 2000s, the most devastating of which blew out multiple beaver dams and damaged a rail line in Williston, Vermont in 1984 (Butler and Malanson 2005). The train derailed, killing five people and injuring 149. This extreme example highlights the need for managers to consider the hydrology surrounding restoration sites as well as downstream assets that may be damaged if dams fail. Thankfully, most breaches, and subsequent sediment and nutrient losses, are small and temporally acute (Butler and Malanson 2005; Westbrook et al. 2011).

3.4.3 Disease

Beavers are vectors for diseases (e.g., tularemia, *Francisella tularensis*, and giardia, *Giardia intestinalis*) which can be deadly to humans, however, only tularemia harms beavers (Scott 1940; Lawrence and Fay 1956; Muller-Schwarze and Sun 2003). In fact, tularemia eradicated multiple beaver populations in the 1900s (Scott 1940; Lawrence and Fay 1956). A Montana study found that tularemia remains in beaver ponds for at least 16 days and in the soil for at least 31 days (Jellison et al. 1942). These authors also showed that tularemia remains potent in beaver urine for at least 31 days. Managers considering beaver reintroductions should test the water, soil, and beavers for tularemia to ensure that the beavers are not doomed and that tularemia is not introduced to the system. Conversely, giardia, often referred to by the misnomer “beaver fever”, is introduced by human water contamination and merely carried and concentrated by beavers (Mcnew et al. 2003; Muller-Schwarze and Sun 2003). As such, avoiding this infection primarily involves human willingness to follow hygienic backcountry practices (e.g., water filtration).

4. DISCUSSION AND CONCLUSIONS

4.1 Future Directions and Recommendations

In this section, I summarize my findings and provide research recommendations. First, I offer general recommendations for managers and researchers. Next, I offer BDA construction tips as well as recommend specific metrics to measure. Third, I highlight knowledge gaps in the beaver and ungulate literature with respect to beaver restoration. Finally, I suggest future projects concerning ungulate and beaver competition, how beavers and BDAs influence climate change, and how state wildlife agencies can provide more guidance for beaver restoration strategies.

4.1.1 General Recommendations

An overarching recommendation is to quantitatively measure BDA effects to assess the effectiveness of this restoration tool, inform management decisions, and contribute to the literature on this topic. I have shown that a sobering number of publications (48% that examined beaver dams and wild ungulate browsing) did not provide quantitative evidence. Without this quantitative data to inform predictions, justifying and planning projects, and growing the scientific body of knowledge, is difficult. Granted, such measurements may not have been a given study's primary focus and/or financial, temporal, and personnel constraints may have precluded such data collection. While this reliance on anecdotes is understandable, and arguably better than not reporting effects, the lack of data ultimately limits scientific growth.

Too often anecdotes and hearsay have become dogma in the beaver literature. A prime example is the notion that beaver dams effectively remove fish habitat by obstructing fish movements (Kemp et al. 2010; Taylor et al. 2010; Kemp et al. 2012). While beaver dams may be impassable for some fishes, particularly at low flows, a vast majority of species studied successfully navigated beaver dams via side channels or open spaces within the dams (see Section 3.2.2.3.6;

Gard 1961b; Mitchell and Cunjak 2007). The lack of data in the literature allows such ideas to persist and influence thinking for decades when, in actuality, using and mimicking beavers has proven beneficial for fishes and fish habitat across North America (see Section 3.2.2.3; Leidholt-Bruner et al. 1992; Pollock et al. 2003; Pollock et al. 2004; Pollock et al. 2012; Lokteff et al. 2013; Bouwes et al. 2016).

A corollary recommendation is that managers and researchers collect data on the same effects uniformly so that results may be compared and averaged across studies. Of the 120 publications I reviewed that offered quantitative evidence, 47 (39%) reported inconvertible, and therefore incomparable, results. This lack of compatible measurements makes drawing general, quantitative conclusions difficult, if not impossible, and slows knowledge growth.

4.1.2 BDA Construction Recommendations

I suggest managers place BDAs in a stair-step profile with multiple structures no more than 100 m apart using Davee et al.'s (2017) suggestion of one dam for every foot of elevation drop in the stream. To have the most impact, I recommend placing BDAs in incised streams in wide, low-gradient valleys. While BDAs can be used in narrow, high-gradient valleys, managers should bear in mind that dams in these environments are more likely to fail and suffer from uncontrolled erosion (Munther 1984; Beechie et al. 2010). Additionally, I recommend installing BDAs in the early – mid-fall and that managers select installation sites based on the criteria in Section 3.1.2. Installation should be easiest during autumn as streams will often be at low flow levels and efforts are less likely to be hampered by freezing conditions. Moreover, installing BDAs in the fall allows the structures time to integrate into the environment before beavers begin dispersing in late winter and spring (see Section 3.1.1). I also recommend that managers and researchers examine the temperature and pH tolerance levels of aquatic taxa in their ecosystems before installing BDAs to ensure that altering these abiotic regimes does not harm species of concern.

Managers should be cognizant of human infrastructure throughout the watershed, especially downstream, of their proposed BDA sites, particularly if managers are attempting to attract beavers. For instance, managers may want to avoid placing BDAs in reaches immediately upstream of road culverts or rail lines or reaches that border private agricultural fields to avoid future human-wildlife conflicts or property damage.

When selecting BDA sites, especially when attracting beavers is an objective, I recommend managers use the Beaver Restoration Assessment Tool (BRAT) to quantitatively assess habitat suitability with respect to beaver and human requirements (Wheaton and Macfarlane 2014; Macfarlane et al. 2017). Although the BRAT was developed for Utah, it has been successfully used to assess potential beaver reintroductions and restoration in Colorado which suggests the BRAT may be applicable to the Southern Rocky Mountains at large and possibly to similar environments throughout North America (Scamardo and Wohl 2019; Kornse and Wohl 2020).

With regards to the BDA designs covered above (see Section 3.1.1) only Post Lines require beaver to make them functional. Therefore, I suggest placing Post Lines close to Starter Dams, PLWWs or active beaver dams to encourage beaver construction in preferred locations with minimal added effort for the manager. Which BDA designs to use, or whether to use an unorthodox design, as in the case study below, is ultimately a function of cost constraints, site conditions, and management objectives.

4.1.3 Knowledge Gaps

4.1.3.1 Ungulates

No quantitative evidence was reported for ungulate browsing effects on vegetation species diversity. This knowledge gap can be filled by using one of several widely used indices (e.g., Shannon-Weaver species diversity index) to compare vegetation diversity in browsed and unbrowsed areas. Determining how wild ungulate browsing affects vegetation diversity will provide managers with a more complete understanding versus focusing on one vegetation type, genus, or species.

4.1.3.2 Beaver Dams

Of the publications examining beaver impoundment effects, none reported quantitative results for beaver dam effects on overbank flows, dissolved oxygen levels within the pond, groundwater mixing, or alterations to moose, aquatic invertebrate, or river otter habitat. These aspects represent significant knowledge gaps in the beaver impoundment literature. For instance, while a dam forcing the stream over its banks is visually obvious, definitive measurements would be more useful and widely applicable for planning and management. With regards to alterations of the three habitats, I suggest that managers and researchers examine the literature for habitat suitability indices. The moose literature has several indices for Europe and North America that are likely useful (Hepinstall et al. 1996; Koitzsch 2002; Dussault et al. 2006; Tendeng et al. 2016). The aquatic invertebrate literature is also has many potentially useful habitat suitability indices (Jowett and Davey 2007; Tomsic et al. 2007; Theodoropoulos et al. 2018). Developing and using habitat suitability indices is especially important with aquatic invertebrates as these species form the critical link between primary production and upper level predators (Hornung and Foote 2006). Understanding and quantifying how beaver dams affect these lower trophic levels can inform work regarding upper trophic levels which, in turn, often garner project funding and support. Conversely, I found the river otter habitat suitability literature lacking, with most studies focused on European river otter (*Lutra lutra*) as opposed to its North American cousin (Ottino et al. 1995; Kiesow and Dieter 2005). Therefore, research considering North American river otter habitat suitability would prove useful as these mustelids are often considered species of concern.

4.1.4 Project Recommendations

4.1.4.1 Beaver and Ungulate Competition

Beaver and elk competition has been thoroughly examined across many parts of these species' ranges whereas work concerning beaver and moose is just beginning. I suggest future beaver and moose studies consider examining the effects described in Section 3.3 outside of Isle Royale or Yellowstone National Parks to study the generality of results. Another needed investigation is to model at what moose densities beaver can persist similar to Baker et al.'s (2012) work with beaver and elk. Such models give managers a starting point to compare ungulate densities and to determine appropriate actions. Moreover, more complex research projects and models that examine the interactions of elk, moose, and beaver would prove especially useful to managers and researchers working where all three species coexist.

I have shown that browsing by wild ungulates, especially at high densities, can hamper beaver colony longevity as well as beavers' ability to reestablish (see Section 3.3). As such, in areas with high browsing levels, I suggest managers consider surrounding BDAs with browse exclosures to allow the BDAs time to render their full effects on local abiotic and biotic processes (Despain 1989). Such exclosures should encompass at least 100 m around BDAs as most beaver browsing occurs within 100 m of the pond (Masslich et al. 1988; Macfarlane et al. 2017). Furthermore, studies examining how ungulate browsing affects BDAs for perhaps 3 – 10 years post-installation would prove useful in addressing uncertainty surrounding BDAs as restoration tools with high ungulate populations. Such a study could track some of the dam effects described above (see Section 3.2) pre- and post-installation in a Before-After-Control-Impact (BACI) design for dams in browsed and unbrowsed areas.

4.1.4.2 Beavers and Climate Change

An additional area of future research is how beavers and BDAs influence climate change, especially at regional or national scales. Beaver activities alter biogeochemical cycles within their ponds and across the floodplain, including increased carbon retention and methanogenesis which can be important for climate change (see Sections 3.2.1.10 and 3.2.1.11). In recent years, beavers have been expanding north into the Arctic tundra, where their impoundments decrease the extent of permafrost (Jones et al. 2020). Although the Arctic tundra is far from the Southern Rocky Mountains, these same effects may begin appearing at lower latitudes in alpine ecosystems. Studies examining how these phenomena at large spatial scales may influence climate change could elucidate how carbon processes in and around beaver impoundments (i.e., carbon storage, methanogenesis, and the effects of decreased permafrost on floodplain carbon storage) and would likely prove useful for future restoration and climate mitigation projects.

The beaver impoundment literature would benefit from studies examining the extent of North American beaver influence over the past several hundred years. Butler and Malanson (2005) estimated the number of beaver ponds as well as the amount of sediment in those ponds across North America pre- and post-European arrival. These authors calculated that, prior to colonization, North America housed 15 – 250 million beaver ponds and that these ponds contained 3 – 125 billion m^3 of sediment. Post-European arrival, Butler and Malanson (2005) calculated that North America housed 1.5 – 7.7 million ponds with 750 million to 3.85 billion m^3 of sediment. Butler and Malanson's (2005) calculations could be used as a starting point to examine the extent of beaver-influenced water retention and groundwater recharge from pre-colonial times. Such a study could give managers a reference condition to compare their current systems with. These findings would be particularly useful in the arid western U.S. where water retention is a constant issue and may become increasingly so as climate change progresses.

Several of the reviewed papers considered how beaver impoundments act as water filters (Maret et al. 1987; Błędzki et al. 2011). Meanwhile, another publication examined how beaver-influenced habitats resist wildfires (Fairfax and Whittle 2020). Future researchers may examine these aspects in more detail as well as how they may act in concert. For instance, do beaver impoundments maintain better water quality in fire affected areas as compared to when BDAs or no dams are present? Moreover, Maret et al. (1987) suggest encouraging beaver dams close to reservoirs to take full advantage of the dams' water filtration effects; would following this suggestion make a substantial difference in water quality as compared to when no dams are present or when dams are located farther upstream? Answers to these questions can inform management decisions regarding BDAs and may prove especially useful if wildfires do indeed become more common and severe due to climate change.

There are several studies in the beaver impoundment literature that examine how beavers influence various, specific hydrological (i.e., overbank flows, hyporheic and groundwater exchange) and carbon storage aspects at the floodplain scale (see Section 3.2.1). However, there are not yet studies that examine how beavers influence a stream's overall water balance or carbon budget at the reach scale. Along with the above projects, such studies could inform how beavers or BDAs may influence water and carbon storage, and ultimately climate change, at larger spatial scales.

4.1.4.3 Beaver Management

Given the results of this review, I suggest state wildlife and land management agencies within the Southern Rocky Mountains develop beaver management plans for reintroducing beavers and using dams as restoration tools. Beaver management plans should account for large ungulate competition to ensure that managers are aware of the additional considerations involved when large ungulates are present. Of the four Southern Rocky Mountain states, only Utah has published a beaver management plan (Bassett et al. 2010). Utah's plan details management objectives and guidelines for reintroducing beavers and installing BDAs, however, the plan makes no mention of ungulates. Colorado Parks and Wildlife has an extended beaver fact sheet with guidance on how to handle nuisance beavers (i.e., those causing property damage), but the document makes no reference to beaver restoration strategies or competition with wild ungulates (Fenwick 2005). Wyoming Game and Fish Department's website makes passing references to the Department installing BDAs and encouraging beaver reintroductions, but I could find no management plan or guidance concerning beavers or BDAs (WGFD 2019). The New Mexico Department of Game and Fish website contains a beaver natural history fact sheet as well as hunting and trapping regulations, none of which mention beaver restoration strategies or wild ungulate competition (NMGF 2020). I suggest these agencies consider the Oregon Department of Fish and Wildlife, the Washington Department of Fish and Wildlife and the West Coast Division of the National Marine Fisheries Service which have been active in providing guidance for introducing and promoting beaver restoration strategies as well as streamlining BDA permitting processes (Pollock et al. 2015). Moreover, the websites for all three agencies are replete with useful information and guidance regarding their beaver restoration and relocation projects (ODFW 2020; NOAA 2021; WDFW 2021). As beaver restoration techniques gain traction in the Southern Rockies, I hope this review dispels some of the dogma and stigma that often accompany beaver and that beaver restoration strategies receive due consideration within natural resource agencies in the Southern Rocky Mountains and beyond.

5. CASE STUDY: ROCKY MOUNTAIN NATIONAL PARK

5.1 Background

Rocky Mountain National Park, hereafter RMNP or the Park, lies in north-central Colorado, U.S.A., and ranges from about 2,380 m to over 4,300 m in elevation. RMNP sits on Precambian crystalline rocks with formerly glaciated and unglaciated valleys that consist of glacial alluvium and spatially variated bedrock, respectively (Laurel and Wohl 2019). The Park consists of montane, subalpine, and alpine environments and is home to beaver, elk, and moose. Top level predators, such as the gray wolf and grizzly bear, have been absent from the Park since the 1910s (Singer et al. 1998; Polvi and Wohl 2012). For this case study, I focus on three valleys on the Park's east side (i.e., Moraine Park, Beaver Meadows, and Horseshoe Park) around the town of Estes Park, Colorado. These three valleys make up the elk winter range and support 200 – 300 elk during winter (October – April) and have increasingly been home to moose since 2015 (Zeigenfuss et al. 2015; N. Bartush, personal observation). I note that the Park only tracks winter elk population numbers and, while it is assumed there are more elk during the remainder of the year, exact numbers are not known. These three valleys show evidence of beaver dating back thousands of years (Polvi and Wohl 2012). Wohl (2013) found that historic beaver meadows make up about 25% of the length of these valleys while Polvi Pilgrim (2011) and Kramer et al. (2012) found that 30 – 50% of the valleys' sediments are associated with historic beaver activity.

Beavers have been in the Park throughout its recorded history, although their numbers have decreased substantially since trapping began in earnest in the 1800s (Peinetti et al. 2002). On the elk winter range, the Big Thompson River in Moraine Park, was estimated to contain 315 beavers in 1947 (Packard 1947). Stevens and Christianson (1980) estimated there were 12 beavers in Moraine Park and surveys from 2015 – 2019 found zero resident beavers (N. Bartush, personal observation). Packard (1947) also estimated that Beaver Creek in Beaver Meadows, contained 36 beavers while surveys from 2015 – 2019 found only one beaver inside a browse exclosure in 2018 (N. Bartush, personal observation). Fall River in Horseshoe Park, was estimated to have 96 beavers in 1947 (Packard 1947). Recent surveys found three active colonies of unknown size in Horseshoe Park and only one of these predates 2018 (N. Bartush, personal observation).

Elk were eradicated from the Park in the 1880s, but were reintroduced in the 1910s after wolves and grizzly bears were exterminated (Peinetti et al. 2002). Lacking their primary predators, the elk population grew quickly, and National Park Service (NPS) staff began actively managing the herd in 1944. This active management gave way to hands-off regulation in 1969 which led to the herd reaching unprecedented densities in the 1990s (Zeigenfuss et al. 2011). Elk numbers in the Park have since declined, possibly due to ongoing management actions detailed below.

Moose, however, never established a resident population in RMNP or Colorado. Rather, moose dispersed into the Park's west side after being introduced by the Colorado Division of Wildlife, now Colorado Parks and Wildlife, near Walden, Colorado in 1978 (Dungan and Wright 2005). Anecdotal evidence suggests that the moose population in the Park has grown substantially since 2015 from only being west of the Continental Divide to inhabiting every major drainage in the Park. As such, managers began investigating the population size, composition, and distribution of moose in the Park in 2017 via GPS collars and aerial population counts. This demographic work is ongoing; however, the results of this review indicate that a burgeoning moose population could have large impacts on RMNP's riparian restoration efforts (see Section 3.3).

Singer and Zeigenfuss (2002) conducted a series of studies in the 1990s to understand elk browsing effects in RMNP. These studies indicated that elk browsing had removed willow and aspen regeneration from the winter range and caused many remaining plants to assume a short and stunted growth form. Singer and Zeigenfuss (2002) speculated that the cumulation of these effects over decades contributed to the beaver population decline in the Park. The loss of beaver, in turn, transferred the system from a collection of beaver meadows to elk grasslands (Laurel 2019). These elk grasslands can be seen along the streams on the elk winter range which are often incised by a meter or more (N. Bartush, personal observation). As a result, large portions of the Big Thompson River, Fall River, and Beaver Brook are now disconnected from their former floodplains and devoid of woody riparian vegetation. Instead, the former riparian meadows on the elk winter range are largely covered by grasses (e.g., *Poa* spp., *Stipa* spp.), sedges, and upland shrubs (e.g., *Potentilla fruticosa*), leaving little suitable vegetation for dispersing beavers (Singer and Zeigenfuss 2002; N. Bartush, personal observation). Whether moose browsing, both on and off the elk winter range, is compounding the difficulty in reestablishing beaver remains unclear. Even if moose browsing effects are not evident yet, my results indicate that managers can expect a decrease in the smaller size classes of woody riparian vegetation leading to relatively open meadows dominated by grasses and unpalatable woody species, i.e., a spruce-moose savanna, in areas that have not already transferred to elk grasslands (see Section 3.3).

The studies by Singer and Zeigenfuss (2002) laid the groundwork for RMNP's Elk and Vegetation Management Plan (EVMP), an adaptive management plan with objectives and monitoring standards for restoring the elk winter range to a series of beaver meadows (Zeigenfuss et al. 2011). I note that the EVMP does not address moose for, at the time of the plan's adoption, moose rarely occurred on the elk winter range (Zeigenfuss et al. 2011). In accordance with the EVMP, the NPS installed 26 exclosures from 2008 – 2014 to protect remaining willow and aspen stands on the winter range from elk browsing. Quantitative vegetation surveys conducted in 2013 revealed that these exclosures have helped riparian vegetation, especially aspen, to recover in terms of height, stem density, and regeneration. However, the rate and extent of willow recovery was variable, i.e., high in some locations (namely Horseshoe Park) but low in others (namely Beaver Meadows; Zeigenfuss et al. 2015).

5.2 Current Restoration Work

To speed willow and aspen recovery in the lagging sectors, encourage beaver dispersal and establishment and test new restoration strategies, RMNP personnel installed four BDAs, two in a browse exclosure in Beaver Meadows and two outside fencing on Cow Creek, in the fall of 2019. An additional BDA was installed in a browse exclosure in Horseshoe Park in 2020. The BDAs installed on Cow Creek are not located on the elk winter range and experience light levels of elk browsing throughout the year. However, moose are regularly reported in the Cow Creek area and I observed a young female in the area in 2020. I had the opportunity to help install a BDA at Cow Creek and I detail my observations from that day below. I acknowledge the irony in my reporting anecdotal evidence; however, this project's quantitative data is not yet available.

RMNP's BDAs were installed as part of a pilot project to test these restoration tools in the RMNP ecosystem before applying them at a large scale. These "BDAs" do not strictly adhere to the literature definition of a BDA as they are not made of local vegetation (Pollock et al. 2014). Indeed, I note that Park personnel refer to these structures as Simulated Beaver Structures (SBSs) rather than BDAs and I will adhere to this from now on. Park personnel used 15 x 15 cm posts cut to span the stream channel. RMNP personnel opted for this design to limit disturbance to the surrounding vegetation, minimize installation time, and speed water table responses. Posts were dug approximately 30.5 cm into the streambank to make the structure more stable against high flows and to prevent the stream from cutting around the dam. Once enough sediment had been removed from the streambanks and bed to cover half of the first post and ensure the post lay flat on the streambed, additional posts were stacked on top of the first and fastened together using carriage bolts. Posts were stacked until the top of the dam was flush with the streambank; a total of seven posts were used. A notch measuring about 8 cm deep by 15 cm wide by 1 m long was cut in the top post to encourage excess stream flow to go over rather than around the dam. This SBS took about four hours to install for four people and, within three hours of laying the first post, the water level had risen 6 – 7 cm 15 m upstream.

RMNP's SBSs were installed in a stair-step profile with two structures installed at each site within 100 m of each other; the one SBS in Horseshoe Park was augmented by a recently constructed natural beaver dam. RMNP staff selected these sites as they lie in wide, low-gradient valleys that have a long history of beaver influence and are near enough to roads, within 200 m, to make material transportation and monitoring easy, but far enough away to avoid road damage. I note that RMNP chose to place their SBSs within 200 – 300 stream meters of active beaver colonies, hoping dispersing beavers would stay, rather than reintroducing beavers as managers believe the vegetation is not robust enough to justify translocations; reintroduced beavers would likely leave in search of better habitat (Remillard et al. 1987; Harris 1991; Van Deelen 1991). The hope is that dispersing individuals will find and adopt these SBSs as new colony sites. Another consideration influencing SBS site selection was that monitoring stations were already in place collecting stream depth, temperature, and pH data. RMNP staff also installed four acoustic monitors at the sites a year before the dams were installed to track changes in avian species composition before and after dam installation.

5.3 Future Directions

The Park's current winter elk population, 200 – 300 animals, is well below the EVMP's target range of 600 – 800, therefore active elk herd management has ceased for the time being (Zeigenfuss et al. 2011). I note that the cause of the elk population decrease is unclear, but it appears to be due to the browse exclosures removing their food supply, forcing elk that formerly spent their winters in the Park to travel to lower elevations about 11 km east of the Park for the winter. The Park's initial moose demographic work will finish in 2023 with results and management decisions following. Should the initial SBSs prove successful in terms of Park managers' objectives, more structures will likely be installed across the elk winter range, but, to institute widespread change, at least some SBSs will need to be placed outside the limited fencing. Whether elk and moose browsing will permit the SBSs to render their full effects remains to be seen. Even if the elk population declines, RMNP managers may require more fencing to protect their SBSs from what appears to be a growing moose population.

When planning future SBS restoration, I suggest RMNP managers use the BRAT developed by Wheaton and Macfarlane (2014) to help set management objectives and select SBS sites. Furthermore, if dispersing beavers adopt RMNP's SBSs, or if beavers establish elsewhere, managers may consider installing Post-Lines up and downstream of these sites to encourage beavers to build new dams in desirable locations. To further entice dispersing beavers, managers may wish to stock unprotected restoration sites with beaver food and construction material, at least until vegetation growth becomes self-sustaining (Apple 1985; Bilyeu et al. 2008).

Managers may consider evaluating the effects of future SBSs on the various trophic levels in the RMNP ecosystem beyond the current stream, vegetation, and avian monitoring. As aquatic invertebrates are key food chain components, RMNP managers may want to monitor aquatic invertebrate species and habitat compositions prior to installing SBSs, and for some time after, using the indices mentioned above (see Section 4.1.3.2). Moreover, camera traps may be used to monitor medium-sized mammal (e.g., river otter, muskrat, etc.) use of SBS restoration sites. Using camera traps is a low-cost monitoring option that provides coarse scale data regarding habitat use with the added benefit of generating pictures that can be used to increase project awareness and support. Depending on management objectives as well as resource constraints, managers may also wish to monitor small mammal species compositions at the restoration sites via trapping grids. Findings from such a study would contribute to a sector of the beaver literature that is light on information (see Section 3.2.2.6.3). Additionally, RMNP managers may consider using SBS restoration sites for the direct management of other species. For instance, restoring boreal toad populations is another RMNP management goal and Hossack et al. (2015) found that these amphibians preferentially colonized beaver ponds. Therefore, managers may consider using the SBS sites for boreal toad reintroductions.

Based on the results of this review, RMNP's wild ungulates will be a significant ecosystem component that will demand managers' attention for the foreseeable future. If RMNP's moose population study reveals that moose are indeed increasing in abundance, this introduces a new factor to Park restoration efforts that is not addressed in the EVMP. RMNP managers may consider revising the EVMP to include protocols to monitor moose browsing effects throughout the Park to compensate for the current lack of coverage. Alternatively, RMNP managers may need to develop a new management plan for moose as evidence suggests these ungulates inhabit areas well outside the EVMP's scope. Such a plan could be modeled after the EVMP to include similar, albeit more tailored, management actions for managing moose (e.g., taller browse exclosures to account for the greater jumping ability of moose as compared to elk, aversive conditioning to keep moose out of sensitive areas, and, for extreme cases, culling to reduce moose abundance). The plan could also address thresholds for when such actions would take place and monitoring protocols for tracking moose population and browsing levels across the Park. Regardless, any management plan that RMNP managers adopt should account for elk and moose activities and for the competitive relationship between ungulates and beavers. Finally, with a gray wolf pack recently confirmed about 320 km from RMNP, Park managers may consider how a wolf-influenced trophic cascade would affect the Park ecosystem as part of any new management plan (CPW 2021).

6. TABLES

Table 1: Scientific literature databases searched for source material and the search terms used to search the databases. I used the Boolean operator “and” when searching for publications that examined both BDA and elk or moose effects.

Database Name	Search Terms
Academic Search Premier	Beaver Dam Analog
Aquatic Sciences and Fisheries Abstracts (ASFA)	Beaver Dam Analogue
Biological Abstracts Archive	BDA
BIOSIS Citation Index	Simulated Beaver Structure
CAB Abstracts	SBS
Dissertations and Theses Global (ProQuest Collection)	Artificial Beaver Structure
Fish, Fisheries & Aquatic Biodiversity Worldwide	ABS
GeoRef	Moose
Google Scholar	Alces alces
JSTOR	Alces americanus
ScienceDirect	Elk
Web of Science	Cervus elaphus
Wildlife & Ecology Studies Worldwide	Cervus canadensis
Zoological Record	Wapiti

Table 2: Factors associated with natural and artificial beaver dams that were examined in the 331 reviewed publications.

Considered Factors
Abiotic Factors
Amphibians
Aquatic Invertebrates
Beaver Behavior
Birds
Dam Construction
Beaver Diet
Beaver Disease
Beaver Dispersal
Elk
Fish
Geomorphology
Hydrology
Moose
Beaver Population Dynamics
Riparian Vegetation
Sedimentation
Small Mammals

Table 3: Tallies and percentages from the 80 publications that examined the effects of beaver dams on abiotic ecosystem processes and components with the calculated weighted average and standard error for the effect size as well as the averages of the indicator variables (IVA) described in Section 2. “N/A” indicates less than two publications provided quantitative evidence of this effect and, therefore, no weighted average or standard error were calculated. “I.U.” indicates quantitative evidence for this effect was reported in inconvertible units.

Effect	No. of Articles	Percentage Quantitative	Percentage Anecdotal	Mean (SE) Effect Size	IVA
Flow Rate	3	75	25	44.1% (17.3)	-1.0
Total Suspended Solids Discharge	2	50	50	27% (N/A)	-1.0
Sediment Deposition	15	46.67	53.33	75.57 cm/yr (78.25)	1.0
Sediment Size	1	0	100	N/A	-1.0
Overbank Flow	4	0	100	N/A	1.0
Water Table Depth	1	100	0	0.37 m (N/A)	1.0
Riparian Area Width	1	100	0	23.4 m (N/A)	1.0
Groundwater Mixing	2	0	100	N/A	1.0
Hyporheic Mixing	1	0	100	N/A	1.0
Water Temperature	11	36.4	63.6	6.92°C (7.48)	0.3
pH	3	66.7	33.3	0.19 (0.23)	0.0
Total Phosphorus Discharge	3	100	0	1,359.6 μg/l (1,518.5)	-1.0
Nitrate Retention	4	75	25	0.21 mg/l (0.18)	0.7
Ammonium Retention	4	75	25	0.71 mg/l (0.47)	0.7
Total Nitrogen Discharge	5	100	0	I.U.	-1.0
Nitrogen Fixation	1	0	100	N/A	0.0
Dissolved Oxygen Concentration	3	0	100	N/A	-1.0
Dissolved Organic Carbon Retention	2	50	50	N/A	1.0

Effect	No. of Articles	Percentage Quantitative	Percentage Anecdotal	Mean (SE) Effect Size	IVA
Total Organic Carbon Retention	1	0	100	N/A	-1.0
Methane Evasion	2	100	0	24-fold (9)	1.0
Carbon Turnover	1	100	0	N/A	1.0
Water Quality	3	0	100	N/A	1.0

Table 4: Tallies and percentages from the 89 publications that examined beaver dam effects on biotic ecosystem processes and components with the calculated weighted average and standard error for the effect size as well as the average of the indicator variables (IVA) described in Section 2. “Species” has been abbreviated to “Spp.”. “N/A” indicates less than two publications provided quantitative evidence of an effect and, therefore, no weighted average or standard error was calculated. “I.U.” indicates quantitative evidence for this effect was reported in inconvertible units.

Effect	No. of Articles	Percentage Quantitative	Percentage Anecdotal	Mean (SE) Effect Size	IVA
Vegetation					
Spp. Richness	2	50	50	N/A	-1.0
Removed Invasive Spp.	1	0	100	N/A	1.0
Aquatic Production	1	100	0	N/A	1.0
Herbaceous Standing Crop	1	0	100	N/A	-1.0
Willow Production	2	0	100	N/A	0.5
Aquatic Invertebrates					
Spp. Diversity	10	60	40	I.U.	0.1
Production	3	100	0	I.U.	0.7
Density	1	100	0	N/A	1.0
Habitat Quality	2	0	100	N/A	0.0
Fish					
Density	2	100	0	502 fish/100 m^2 (487)	1.0
Survival	1	100	0	N/A	1.0
Production	5	100	0	I.U.	1.0
Spp. Richness	1	100	0	N/A	1.0
Diversity	4	75	25	I.U.	1.0
Habitat Quality	8	12.5	87.5	N/A	1.0
Abundance	1	100	0	N/A	1.0
Movement Barriers	5	0	100	N/A	0.2

Effect	No. of Articles	Percentage Quantitative	Percentage Anecdotal	Mean (SE) Effect Size	IVA
Amphibians					
Wood Frog Production	3	100	0	2.98-fold (1.42)	1.0
Occurrence	4	75	25	I.U.	1.0
Birds					
Spp. Richness	7	71.4	28.6	4.78 spp. (1.63)	0.9
Spp. Diversity	2	100	0	0.64 (0.36)	1.0
Abundance	2	50	50	N/A	1.0
Occurrence	3	0	100	N/A	0.7
Density	3	100	0	I.U.	1.0
Production	1	100	0	N/A	1.0
Mammals					
Muskrat Occurrence	2	0	100	N/A	1.0
Otter Habitat	2	0	100	N/A	1.0
Density	1	100	0	N/A	1.0
Production	1	100	0	N/A	1.0
Spp. Richness	1	100	0	N/A	0.0
Spp. Diversity	1	100	0	N/A	0.0

Table 5: Tallies and percentages from the 42 publications that examined ungulate effects on ecosystem processes and components and ungulate and beaver coactions with the calculated weighted average and standard error for the effect size as well as the average of the indicator variables (IVA) described in Section 2. "Species" has been abbreviated to "Spp.". "N/A" indicates less than two publications provided quantitative evidence of an effect and, therefore, no weighted average or standard error was calculated. "I.U." indicates that quantitative evidence for this effect was reported in inconvertible units.

Effect	No. of Articles	Percentage Quantitative	Percentage Anecdotal	Mean (SE) Effect Size	IVA
Vegetation					
Willow Production	8	62.5	37.5	199.51% g (57)	-0.8
Willow Flowering	5	80	20	34.17% (17.87)	-1.0
Aquatic Production	4	100	0	34.84 g DW/m^2 (15.81)	-1.0
Herbaceous Production	2	100	0	I.U.	0.0
Spp. Diversity	2	0	100	N/A	0.0
Density	3	66.67	33.33	I.U.	0.3
Spp. Richness	1	100	0	N/A	1.0
Biomass	4	75	25	I.U.	-1.0
Birds					
Abundance	1	100	0	N/A	0.0
Diversity	1	100	0	N/A	0.0
Density	1	100	0	N/A	0.0
Small Mammals					
Diversity	1	100	0	N/A	-1.0
Spp. Richness	1	100	0	N/A	-1.0
Production	1	100	0	N/A	-1.0
Beavers and Ungulates					
Beavers Creating Moose Habitat	4	0	100	N/A	1.0

Effect	No. of Articles	Percentage Quantitative	Percentage Anecdotal	Mean (SE) Effect Size	IVA
Vegetation Production	6	50	50	I.U.	-1.0
Ungulates Outcompeting Beaver	5	20	80	N/A	1.0

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