

THESIS

A DAMMING HISTORY: AN ANALYSIS ON THE LEGACY EFFECTS OF BEAVER DAMS ON THE
COMPOSITION AND STRUCTURE OF A MONTANE RIPARIAN ECOSYSTEM

Submitted by

Kara Brunngraber

Department of Forest and Rangeland Stewardship

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Spring 2025

Master's Committee:

Advisor: Jeremy Sueltenfuss

Mark Paschke

Ellen Wohl

Copyright by Kara Brunngraber 2025

All Rights Reserved

ABSTRACT

A DAMMING HISTORY: AN ANALYSIS ON THE LEGACY EFFECTS OF BEAVER DAMS ON THE COMPOSITION AND STRUCTURE OF A MONTANE RIPARIAN ECOSYSTEM

Landscape heterogeneity is widely recognized for its positive influence on ecosystem diversity and stability. As an “ecosystem engineer,” the American beaver (*Castor canadensis*) increases heterogeneity in riparian systems through dam-building activities, resulting in diverse wetland complexes. This study explored the impact that historic, off-channel beaver dams have on the structure and composition of the surrounding vegetative communities. Specifically, I explored how vegetative communities differed in areas of beaver occupancy history, land management impacts, and distance from the river. This study was conducted in the Kawuneeche Valley of Rocky Mountain National Park, Colorado. Field methods focused on vegetative surveys around historic, off-channel beaver dams, the Colorado River, and its major tributaries. Observed beaver sign was classified by age (historic, recent/current, absent), and statistical analysis assessed compositional differences among variables of interest. I found that historic beaver dams supported more wetland-adapted and less disturbance-tolerant plant communities. Notably, shrub cover at historic dams was similar to that of exclosed sites. In contrast, upland, disturbance-adapted species dominated areas of historic beaver activity where dams were not present. Impacts of historic agriculture are still present on the landscape, with higher intensity farming areas dominated by herbaceous species. Finally, the effects of river incision reduced shrub cover within the valley, restricting communities to the river corridor. This study demonstrated that off-channel, historic beaver ponds function as a refuge for wetland plant species in disturbed riparian systems. Incorporating these underutilized

structures already present on the landscape could enhance restoration success by increasing heterogeneity and wetland health.

ACKNOWLEDGEMENTS

I would like to extend my thanks and gratitude to my advisor, Jeremy Sueltenfuss, who has provided help and feedback throughout this journey. Your guidance and encouragement supported me throughout this process. Thank you to my committee, Mark Paschke and Ellen Wohl, for your time and investment in me as a student.

To my friends and family, whose encouragement and belief in me never wavered. Special thanks to my fiancé, Glenn Hoffman, who has been my rock throughout this process. Not only did you provide emotional support, but you were a sounding board for my ideas, and a balm to my insecurities. Your knowledge of ArcGIS, Field Maps, and RStudio was nothing short of magical. Without your help and patient guidance, I would have ended up collecting data for all 400+ plots by hand. You saved me both time and my mental sanity. Without your support I would not be where I am today.

To my field technician, Parker Applegate, your assistance throughout the summer was imperative to our work. Field surveys ran smoothly because of the help you provided. To Marin Oschmann, whose friendship and help throughout this process is greatly appreciated, I wish you all the luck in your own master's degree journey.

I also want to extend a thank you to Ann Hess and the graduate students at the Graybill Statistics and Data Science Laboratory. The insight and assistance provided ensured the quality and accuracy of my data analysis. I also want to extend my greatest thanks to Rocky Mountain Conservancy and Rocky Mountain National Park for providing the funding necessary for this project. Thank you to the NPS employees who have helped along the way.

PREFACE

THE HISTORICAL IMPACT OF THE AMERICAN BEAVER (*CASTOR CANADENSIS*) IN THE UNITED STATES (US)

The American beaver (*Castor canadensis*) is North America's (NA) largest rodent and an ecosystem engineer critical to wetland ecosystem health and integrity (Brazier et al., 2021). Beavers are well-known for their dam-building abilities and can significantly modify the hydrology of their landscape, opening new habitats for a diversity of species to inhabit, significantly increasing heterogeneity and resilience of landscapes (Brazier et al., 2021; Nummi & Holopainen, 2014; Rosell et al., 2005). Historically, many Indigenous nations revered beavers for their landscape-altering abilities and incorporated them into their cultural beliefs (Brady, 2022; U.S. Forest Service, n.d.). However, as Europeans expanded across NA, beavers became valuable for their pelts and castoreum, leading to their near-extinction (Feinstein, 2006; Rosell et al., 2005). The history of the American beaver underscores its vital role in NA's economy, ecology, and culture, emphasizing the necessity to balance human needs with ecosystem conservation.

Historically, beavers covered most of NA, ranging from coast to coast, from the sub-arctic regions of Canada and Alaska to riparian areas of the arid southwest (Baker & Hill, 2003; Wohl, 2021). Estimates place the pre-European beaver population at 60-400 million individuals across NA (Baker & Hill, 2003). During this period, Indigenous tribes shared strong connections with the beaver. For example, the Blackfeet revered the beaver so highly for its ecosystem engineering abilities that it was forbidden to hunt them, and the animal is featured prominently in crests and native legends in other tribal nations (Brady, 2022; U.S. Forest Service, n.d.). Many Indigenous peoples also relied on beavers

as an essential winter food source and used the pelts for clothing (Kuhnlein & Humphries, n.d.). However, it wasn't until the European Fur Trade of the 17th century that beaver populations were exploited at a rate faster than they could recover (Bailey et al., 2019; Baker & Hill, 2003; Tapper & Reynolds, 1996).

During the European fur trade of the 18th and 19th centuries, beavers were extensively hunted in NA for use of their pelts and castoreum in hats and medicine (Baker & Hill, 2003; Feinstein, 2006; Johnston, 2017; Poliquin, 2015; Rosell et al., 2005). During this time, European settlers worked closely with Indigenous Americans, relying heavily on their ecological knowledge and hunting skill sets (Feinstein, 2006), supporting economic trade and alliances between colonists and Indigenous tribes (Feinstein, 2006). Following the over-exploitation of beavers in eastern NA, European settlers and trappers moved west, where the Rocky Mountains and Colorado quickly became the second most important location for continuing the fur trade (Naiman et al., 1988; Reeve, 2016). By 1840, the fur trade in Colorado was over, due to a combination of decimated local beaver populations and changing fashion desires (Reeve, 2016).

Even though the fur trade had ended, beaver populations continued to decline across NA. European expansion brought about an era of landscape changes in the form of wetland draining for cattle grazing and agriculture (Charnley et al., 2020; Fountain, 2014). This significantly altered the land, creating a more homogenous landscape and causing widespread beaver habitat loss and increased human-wildlife conflicts (Charnley et al., 2020; Fountain, 2014). Beavers quickly became a “nuisance species” as they dammed irrigation and drainage ditches, leading to continued trapping and removal (Fountain, 2014).

By the 1920s, federal agencies in the US began recognizing the value of wetlands, and the animals that inhabit them, and instituted the first conservation and reintroduction efforts. While

these initiatives primarily focused on waterfowl and game species, they indirectly benefitted beavers (Fountain, 2014). Wetlands were being protected, preventing these systems from being transformed for agricultural use in the future, and some states even started reintroducing beavers back into these landscapes (Fountain, 2014). Because of this, beaver populations rebounded, though only to an estimated 10% of pre-European levels (Bailey et al., 2019; Naiman et al., 1988). Today, beavers are still perceived as nuisance species in urban and agricultural settings, where their dam-building activities can contribute to economic loss (Fountain, 2014; Gibson & Olden, 2014; Yarmey & Hood, 2020). Management actions, such as removing individuals, fencing off trees, and creating 'beaver-deceivers' to reduce flooding, have been taken to mitigate the perceived impacts of beaver activities, (Yarmey & Hood, 2020). Other management methods focus on mimicking beaver dams to improve wetland restoration efforts (Gibson & Olden, 2014; Pollock et al., 2014), highlighting the continued need for inventive conservation and management strategies supporting education and conflict resolution.

The American beaver is closely intertwined with human culture and history. Beavers' role in establishing and maintaining wetland complexes remains important as these landscapes provide ecological services such as ecosystem resilience and habitat provision. Historical human-beaver interactions act as a warning for today's management efforts and emphasize the need for improved education and management strategies that reduce human-wildlife conflicts in areas of high beaver densities. Landscape managers can ensure continued population expansion and further improve wetland health and restoration by investing in programs that implement conflict resolution and provide education on the ecological benefits of beavers.

TABLE OF CONTENTS

ABSTRACT ii

ACKNOWLEDGEMENTS iv

PREFACE v

LIST OF TABLES..... x

LIST OF FIGURES..... xi

CHAPTER ONE -- A DAMMING HISTORY: AN ANALYSIS ON THE LEGACY EFFECTS OF BEAVER DAMS ON THE COMPOSITION AND STRUCTURE OF A MONTANE RIPARIAN ECOSYSTEM 1

I. Introduction 1

II. Methods 5

 Study Area..... 5

 Habitat Suitability Map 6

 Survey Methods and Plot Design 8

 River Surveys 8

 Historic Dam Surveys 10

 Plots surveyed 11

 Data collection..... 13

 Statistical Analysis 15

 Analyses pertaining to the shrub layer..... 16

 Analyses pertaining to the herbaceous layer 17

 Analyses pertaining to relative percent cover for both herbaceous and shrub communities ... 17

 Analyses pertaining to how distance from the river impacts beaver habitat..... 18

III. Results 18

 How are vegetation communities structured in areas of historic, recent, and current beaver occupancy? 19

 How has historic land management impacted beaver habitat? 24

 How does distance from the river impact beaver habitat? 30

IV. Discussion 34

 Plant community structure and beaver occupancy 34

 Historic land management impacts on beaver habitat 38

 Impacts of distance from the river on beaver habitat 41

V. Management Recommendations..... 44

VI. Conclusion.....	45
APPENDIX A.....	60
APPENDIX B.....	66
APPENDIX C	69
APPENDIX D	72

LIST OF TABLES

Table 1. Shrub health rating	13
Table 2. Accumulated Browsing Index (ABI)	14
Table A1. List of observed shrub species per study location	60
Table A2. List of observed herbaceous species per study location	62
Table B1. List of observed shrub species by agricultural intensity	66
Table B2. List of observed herbaceous species by agricultural intensity	67
Table C1. List of observed shrub species by distance from the river	69
Table C2. List of observed herbaceous species by distance from the river	70
Table D1 List of plot coordinates for historic dam transects	72
Table D2 List of plot coordinates for control transects	74
Table D3 List of plot coordinates for river-associated surveys	75

LIST OF FIGURES

Figure 1. Study area map of the Kawuneeche Valley in Rocky Mountain National Park6

Figure 2 Beaver habitat suitability map8

Figure 3. River survey plot diagram 10

Figure 4. Historic beaver dam survey plot diagram 11

Figure 5. Survey locations and plot layout 12

Figure 6. Accumulated Browsing Index (ABI) 14

Figure 7. Total shrub percent canopy cover by survey group20

Figure 8. Percent canopy cover by height class in each survey group.21

Figure 9. Shrub species richness by survey group22

Figure 10. Total shrub WIS and Mean-C by survey group.....23

Figure 11. Herbaceous canopy cover, WIS , and Mean-C by survey group24

Figure 12. Total shrub percent canopy cover by historic ranching intensity25

Figure 13. Percent canopy cover by height class in each historic ranching intensity.....26

Figure 14. Shrub species richness by historic ranching intensity.....27

Figure 15. Shrub WIS and Mean-C by historic ranching intensity.....28

Figure 16. Herbaceous canopy cover, WIS, and Mean-C by historic ranching intensity.....29

Figure 17. Predicted shrub canopy cover and shrub species richness as distance from the river increased31

Figure 18. Predicted shrub WIS and shrub Mean-C as distance from the river increased32

Figure 19. Predicted herbaceous canopy cover, WIS, Interaction between water and WIS values, and Mean-C as distance from the river increased33

Figure. 20 Aerial photo of the Holzworth historic ranching site in 196541

CHAPTER ONE -- A DAMMING HISTORY: AN ANALYSIS ON THE LEGACY EFFECTS OF BEAVER DAMS
ON THE COMPOSITION AND STRUCTURE OF A MONTANE RIPARIAN ECOSYSTEM

I. Introduction

The influence of landscape heterogeneity on species diversity has been widely accepted as a positive one (Stein & Kreft, 2015). Landscape structure and composition fluctuate over spatial extents (Stein & Kreft, 2015; Malanson & Cramer, 1999) and these fluctuations create variations in habitat types and provide greater access to necessary resources, resulting in increased species diversity across the landscape (Stein & Kreft, 2015; Londe et al., 2020). Highly diverse ecosystems may be more stable and can continue functioning at similar levels after a disturbance (Loreau & de Mazancourt, 2013). Many species of animals, commonly called “ecosystem engineers”, can increase landscape heterogeneity through manipulating some contributing factor to landscape heterogeneity, such as vegetation structure or micro-topographical variations.

The American Beaver (*Castor canadensis*) plays a vital role as an “ecosystem engineer” in the functioning of wetland and riparian systems. Beavers create and manipulate a riparian ecosystem’s abiotic and biotic aspects through a cyclical pattern of dam building, flooding, and abandonment (Rosell et al., 2005; Nummi & Kuuluvainen, 2013; Westbrook, 2021; Brazier et al., 2021), and can create a large wetland complex in as little as ten years (Westbrook, 2021; Brazier et al., 2021). As beavers dam a riverine system, ponding and water retention increase the lateral connectivity with the floodplain, the duration of standing water, and raise the surrounding water table (Brazier et al., 2021; Westbrook, 2021; Hossack et al., 2015). The increased ponding expands habitat for a diversity of aquatic, semi-aquatic, and terrestrial organisms (Brazier et al., 2021; Aznar & Desrochers, 2008; Hood et al., 2021; Nummi & Holopainen, 2014; Hossack et al., 2015; Rosell et

al., 2005; Nummi et al., 2019; Fedyń et al., 2022) and leads to a community shift towards aquatic vegetation (Hossack et al., 2015; Westbrook, 2021; Gibson & Olden, 2014). Through their cyclical process of dam establishment and abandonment, beavers increase landscape heterogeneity and species diversity within the greater wetland complex over both spatial and temporal scales.

Beavers also play a prominent role in the structure and function of willow communities. Willows are a primary food and building source for beavers and have co-evolved to benefit from beaver utilization. Willows display increased growth rate and cover after being foraged by beavers (Westbrook, 2021; Gibson & Olden, 2014; Baker & Cade, 1995) and cuttings have evolved to rapidly root in areas of exposed sediment, such as along dams or on point bars downstream of beaver-occupied sites (Westbrook, 2021; Levine & Meyer, 2019; Gibson & Olden, 2014). The spatial and structural heterogeneity of willow communities is increased by beavers through their selective foraging of stems (Peinetti et al., 2009; Baker et al., 2005).

Historically, beavers covered much of North America, extending coast to coast and north-south from the subarctic regions of North America down into the contiguous United States and northern regions of Mexico (Baker & Hill, 2003; Wohl, 2021). Beaver populations in North America were estimated to be between 60 – 400 million before European settlement (Seton, 1929, as cited by Baker & Hill, 2003; Bailey et al., 2019). After European settlement, beaver populations experienced a considerable reduction in numbers from overexploitation from the fur trade as well as habitat loss and continued trapping due to homesteading activities across the West (Baker & Hill, 2003; Bailey et al., 2019). By the 1920s, beaver populations were near extinct, causing federal conservation agencies to implement protection and reintroduction efforts in the U.S. (Fountain, 2014; Naiman et al., 1988; Rosell et al., 2005). However, populations are still only estimated to be between 6 – 12 million, with more recent estimates stating that only 10% of historical populations remain (Naiman et al., 1988; Bailey et al., 2019).

Loss of beavers in an ecosystem initiates cascading changes that influence almost every aspect of a landscape. When beaver populations decline, dams breach and riverine systems shift from a multi-threaded wetland complex to a single-channel system that is often incised and disconnected from the floodplain, leading to lower groundwater tables (Scamardo et al., 2022; Pollock et al., 2014). For example, in Colorado, loss of beavers on a landscape results in about a 40% reduction in surface water (Scamardo et al., 2022). As water tables recede, riparian vegetation starts to die back, contributing to additional habitat loss (Neff, 1957; Wohl, 2021). As a result, the diversity of wildlife decreases, especially for aquatic and semi-aquatic species dependent on ponds such as breeding waterfowl, fish, and aquatic invertebrates (Neff, 1957; M. Pollock et al., 2004; Nummi et al., 2021; Wohl, 2021; Scamardo et al., 2022).

Abandoned beaver dams can last for several decades (Neff, 1957; Rosell et al., 2005; Wright et al., 2003) and can continue to function and retain water for years after abandonment. Abandoned beaver dams still connected to a riparian corridor can promote new stream meanders and increase riparian heterogeneity and diversity (Levine & Meyer, 2019). The literature establishes that historic and abandoned beaver dams still influence the surrounding landscape, but their effects vary depending on the environment. However, these studies focus on historic beaver dams still connected to the riverine system, there is limited research on how dams separated from a river influence vegetative communities of wetland and riparian landscapes.

The Kawuneeche Valley (KV) in Rocky Mountain National Park is a model system to study the long-term landscape impacts of abandoned beaver dams that are no longer connected to the riparian system. The KV has experienced many land use changes over recent centuries, from being inhabited by Indigenous peoples, to gold, silver, and lead mining and homesteading and ranching in the 1800s and then the incorporation into the National Park Service (Tanismore, 2022; National Park Service, n.d.). These land use changes and increased human-beaver conflicts resulted in the

reduction of beavers across the valley (Baker et al., 2004; Brown & Fouty, 2011; Fountain, 2014; NPS - RMNP, 2024). Up until the early 2000s, beavers were present and maintaining dams across the valley (Westbrook et al., 2006). As the KV is a glacial valley with many lateral groundwater inputs, many of these dams were built along these inputs rather than the Colorado River (Woods et al., 2006). However, compounding land use changes reduced the amount of quality habitat in the area. This caused the remaining beaver population to vacate the KV, leaving behind numerous historical beaver dams that are separated from the riverine system.

This research explored if historic beaver structures within the KV influence vegetation communities. Specifically, I ask: 1) How are communities structured in areas of historic, recent, and current beaver occupancy; 2) how has historic land management impacted beaver habitat; and 3) how does distance from the river's edge impact beaver habitat? I hypothesized that both herbaceous and willow communities will differ across the valley, with more hydrophilic herbaceous species and a higher cover of willows present in areas where historic beaver dams are still visible on the landscape compared to areas of the KV that have seen more land use changes. The occurrence of exotic invasive species will be more common in valley areas that have seen more anthropogenic disturbances and no longer have beaver dams in the area. I also hypothesized that beaver dams will support a more hydric herbaceous composition compared to the riparian areas due to sustained ponding behind many of the dams. Due to historic ponding, I expected to see a higher willow density along the dam and downstream of the dam. However, I expected to see a lower willow density at the historic dam sites compared to areas near the river due to increased propagule distribution and access to higher water tables for river plots.

II. Methods

Study Area

This study was conducted in the Kawuneeche Valley (KV) within Rocky Mountain National Park. The KV is located on the western portion of Rocky Mountain National Park and is located within the Upper Colorado River Basin. It is surrounded by mountain ranges with the Continental Divide to the east and The Never Summer range to the west. This study focused on surveying the Colorado River and its tributaries within the KV. Survey elevations ranged from 2602 m to 3280 m and annual precipitation averages 507 mm per year (NPS- RMNP, n.d.). Survey areas were largely confined to the valley and the Grand Ditch, a century-old water diversion ditch that still provides water to the Poudre and South Platte Rivers (Atkins, 1976; Colorado State University, n.d.; Visty, 2008). Additionally, some subalpine wetlands west of the Grand Ditch were included in the surveys.

Starting in the 1980s, several exclosures were established throughout the KV to reduce herbivory pressure on the willow population by ungulates. Only one exclosure was incorporated in this study, as it is the only one with entry points and is currently situated on the Colorado River. Areas of the KV that were impacted by the 2020 East Troublesome Fire were not included in the survey.

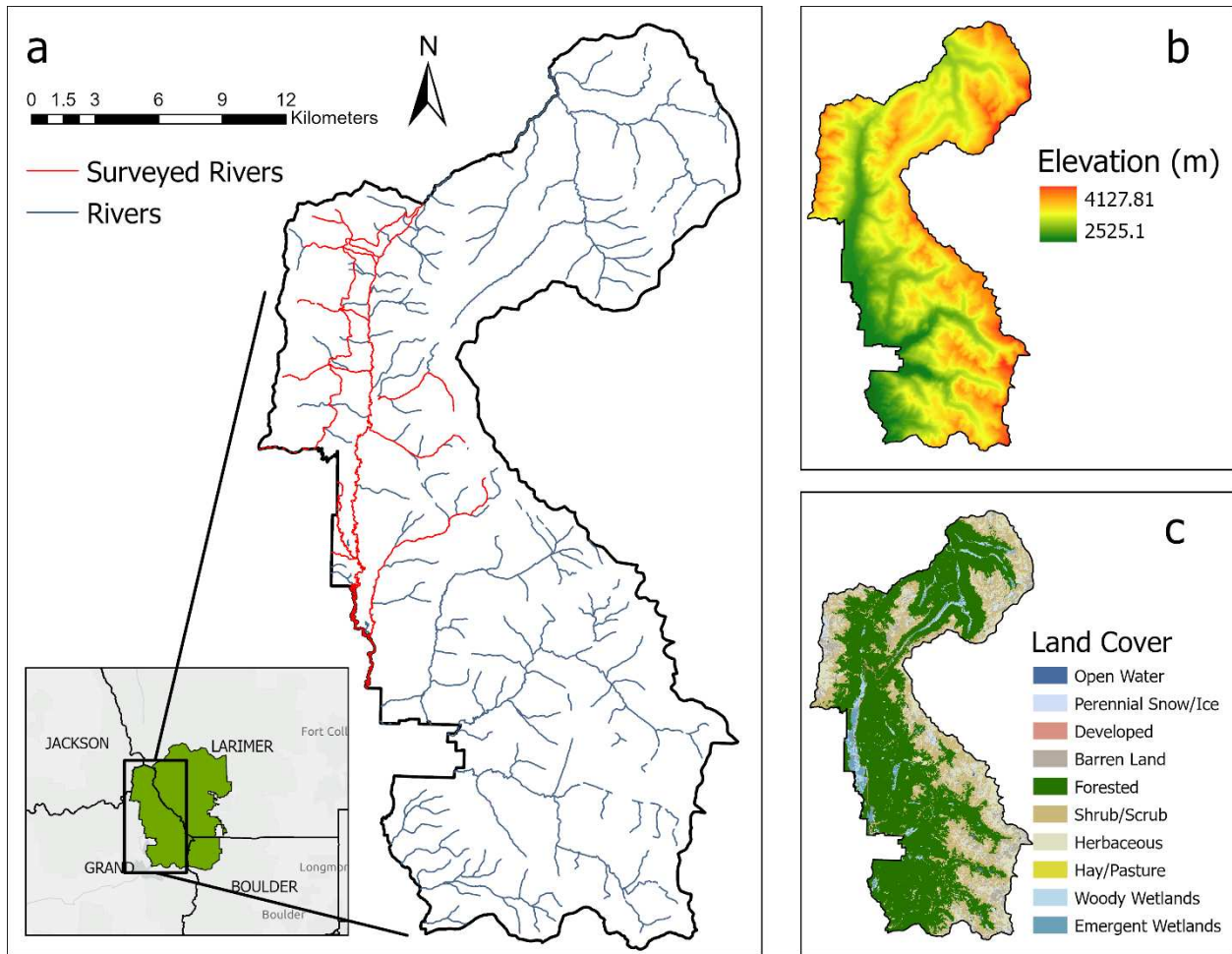


Figure 1. Study area map of the Kawuneeche Valley in Rocky Mountain National Park. Surveyed rivers and streams are shown in red (a). With elevation (b) and land cover (c) shown in the panels to the right.

Habitat Suitability Map

A beaver habitat suitability map was developed prior to field surveys and was used to determine high value habitat areas to prioritize field surveys within the western portion of Rocky Mountain National Park. The suitability map was created using ArcGIS Pro version 3.1.2. Data and sources utilized in the creation of the map comprised of 3DEP elevation data for the park and NHD+ data in vector format obtained from USGS Download Manager, park roads and boundary in vector format obtained from RMNP Open Data, and an NLCD landcover raster obtained from NRCS Data

Gateway. The NHD flowline was the only layer of the NHD+ data used to create the suitability map (Figure 2).

Underground pipelines were removed from the data so that only aboveground waterbodies remained. Next, a 200-m buffer was created around the NHD flowline data and dissolved into one polygon layer. Two-hundred meters was chosen as the buffer based on previous literature stating that is the maximum distance beavers have been observed to travel from the river to forage (USFS, n.d.). The NLCD data were then masked to the river buffer and the land cover types were reclassified and weighted so that herbaceous or woody wetlands and open water were classified as optimal habitat with a weight of 3, followed by shrub/scrub as good habitat and a weight of 2. All other land cover types were classified as poor habitat type with a weight of 1. Slope was calculated using the elevation DEM and was reclassified and weighted into groups; 0-3% slope was optimal for beaver establishment and had a weight of 3, 3-6% was the next highest group with a weight of 2, followed by 6-15% with a weight of 1, and slopes above 15% were excluded from analysis as these slopes cannot support beaver establishment (Boyle & Owens, 2007; Dittbrenner et al., 2018). A weighted overlay was then used to create the habitat suitability map using the reclassified elevation raster and reclassified buffered NLCD raster. Land cover was weighted heavier (65%) than slope (35%) based on previous literature stating that vegetation availability is more important than slope when determining beaver establishment (Boyle & Owens, 2007).

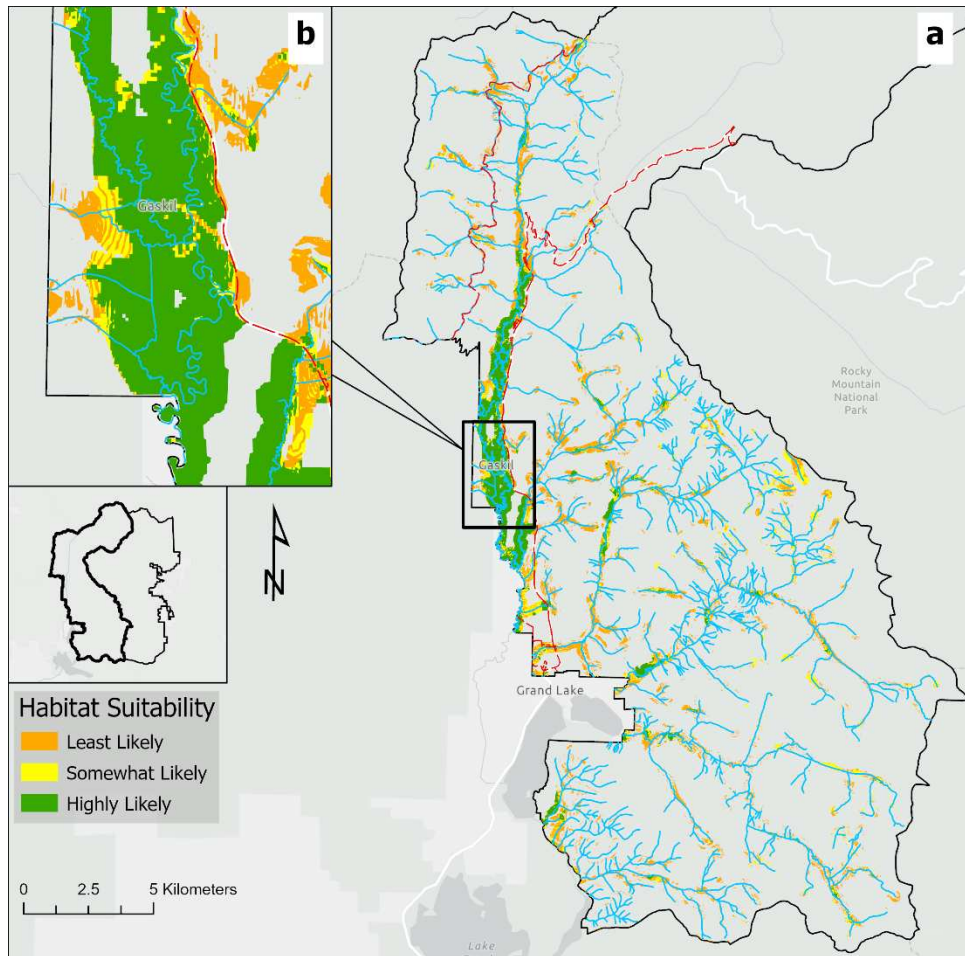


Figure 2 (a.) Beaver habitat suitability map for Kawuneeche Valley in Rocky Mountain National Park, CO. This map was used to determine priority survey areas for the summer of 2023. (b.) Zoomed in section of the southern portion of Kawuneeche Valley showing a detailed image of the suitability ratings. Park Roads are indicated by the red dotted lines.

Survey Methods and Plot Design

River Surveys

River surveys were conducted along the length of the Colorado River in Kawuneeche Valley, as well as its major tributaries. Surveyors walked along the riverbank, one near the river's edge and the other spaced about 20 meters further into the valley and surveyed for current or historic beaver sign utilizing methodology adapted from Campbell-Palmer et al. (2020), Small et al. (2016), and Graham et al. (2022). Beaver sign included browse marks on woody plants, dams, lodges or bank

dens, large felled trees, food caches, scent mounds, or animal observations. Once beaver sign had been observed, a GPS point was collected and data associated with the type of sign, age of sign (historic, recent, current), and an image of the observed sign was recorded. Beaver sign age was determined visually in the field.

Historic browse sign was identified by the beveled edge typical of beaver browsing and the stem consisted of dead grey wood lacking bark. Historic dams were identified by their distinct elevated structure and asymmetric shape, oriented perpendicular to the river. These dams typically also had willows and other shrubs growing from the sides and base of the structure. Recent beaver sign consisted of beaver browse marks. Stems that were recently chewed exhibited brown living wood that was starting to discolor and darken. Current beaver sign consisted mostly of fresh browse marks on shrubs, indicated by light brown, living wood, with fresh woodchips scattered at the base of the plant. Current chewed stems were also determined by sap visibly seeping from the browse site.

Vegetation transects were then established near the river's edge closest to the observation point, where the vegetation was starting to establish at the channel bank. Transects were aligned so that they were roughly perpendicular to the length of the valley and extended 40 m into it. Three vegetation plots were established along the transect, one at the 0 m mark, another at 20 m, and the last at 40 m. Plots were 2-m x 2-m and were aligned along the transect so that the tape was bisecting the plot. New transects were placed every 80 m for as long as beaver sign continued to be observed. Once beaver sign was no longer observed within the 80 m distance, a final control transect was placed 100 m from the previous transect as long as no further beaver sign had been observed within the additional 20 m (Figure 3). When the first vegetation transect was established, surveyors would backtrack 100 m and establish an additional control transect. Vegetation transects were grouped by

a conceptual baseline, called feeding lines, so that those within the pairs of control transects shared the same baseline ID.

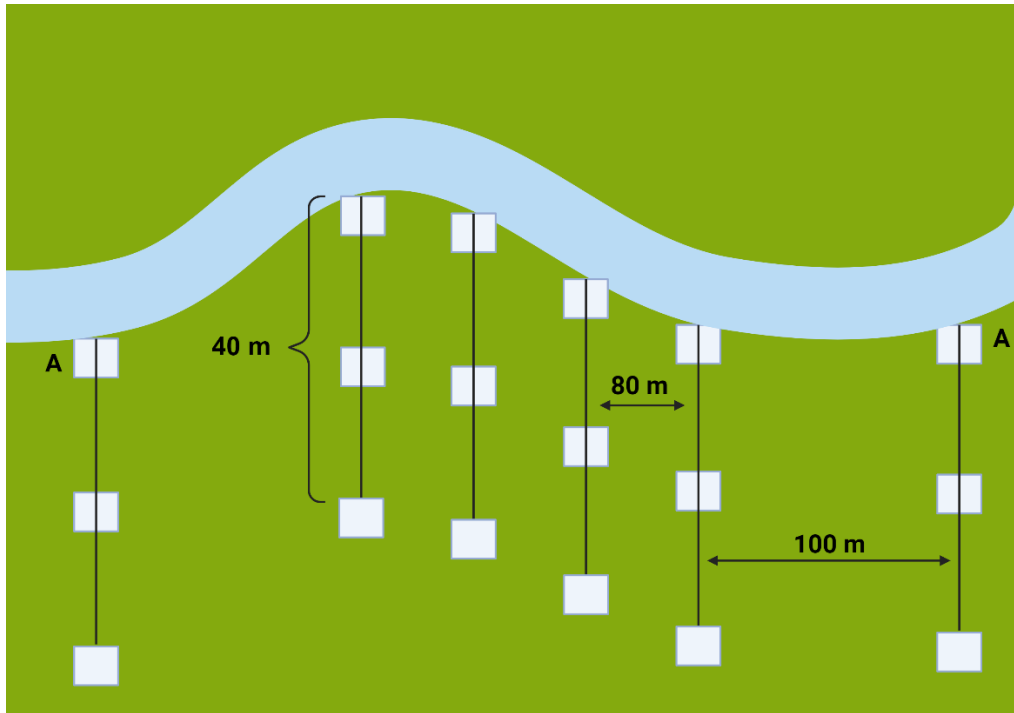


Figure 3. Diagram of transect and plot arrangement. Black vertical lines represent transects, with those marked "A" representing control transects. Plots are represented by the squares.

Historic Dam Surveys

Historical beaver dams within the KV were determined using historical and present-day aerial imagery as well as personal communications. Dams were numbered randomly and selected for surveys using a random number generator. Dams were then ground-truthed to confirm that the structure was a historic beaver dam and vegetation surveys were conducted. Surveys were similar in structure to river vegetation surveys with the main differences being that the "feeding line" described for the river surveys was a 40-m line established parallel to the valley flow at the end of the observable dam, and 40-m transects were extended from this baseline at the 0-m, 20-m, and 40-m marks perpendicular to the feeding line. The end of the dam was located 20 m along the baseline, so that the middle transect would

capture vegetation along or near to the dam itself (Figure 4). Plot setup and data collection along the transects were the same as the river surveys.

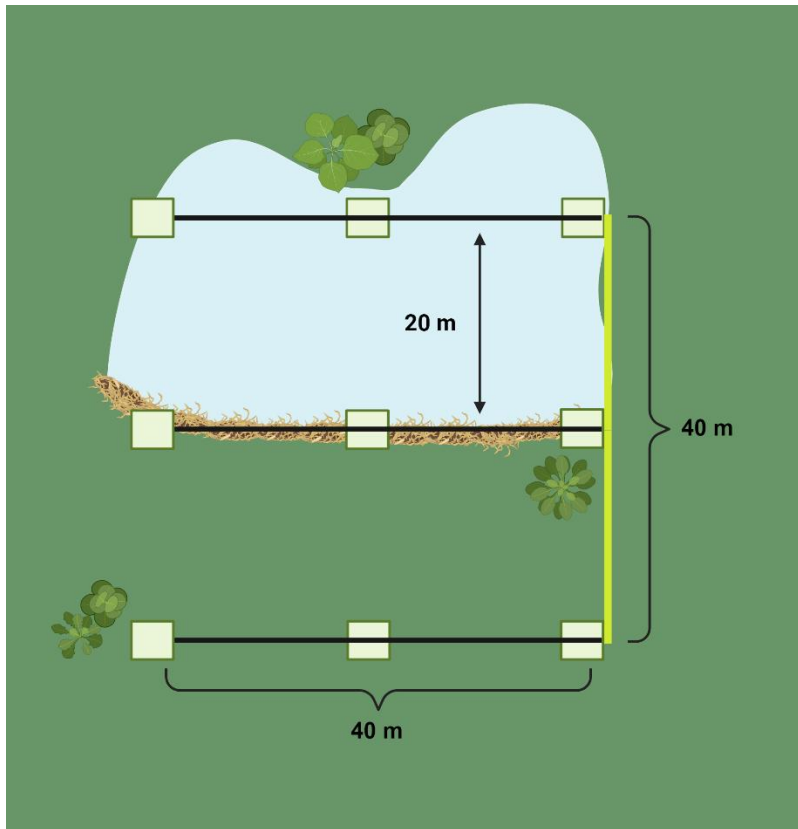


Figure 4. Image of the arrangement for historical beaver dam vegetation surveys. The yellow line is the 40-m baseline that established the locations of three transects represented as black lines. Squares indicate vegetation plots.

Plots surveyed

The survey area was separated into two historic agricultural intensities, low and high, based on visual observations and historic aerial imagery. The southern portions of the KV were identified as high historic farming as these areas have been denuded of shrubby vegetation for farming and ranching purposes. High farming extended north to the Holzworth historic site. North of Holzworth was identified as low intensity, as this portion of the valley had consistent shrub cover throughout historic aerial imagery (Figure 5).

A total of 449 river associated plots were surveyed. One hundred and fifty of those were in low intensity farming and 299 were in high intensity farming locations. A total of 13 historic dams were surveyed, 12 of which were in low farming intensity locations, and one was within high farming intensity (Figure 5). Coordinates for the first plot of each transect can be found in Tables D1, D,2, and D3 in appendix D.

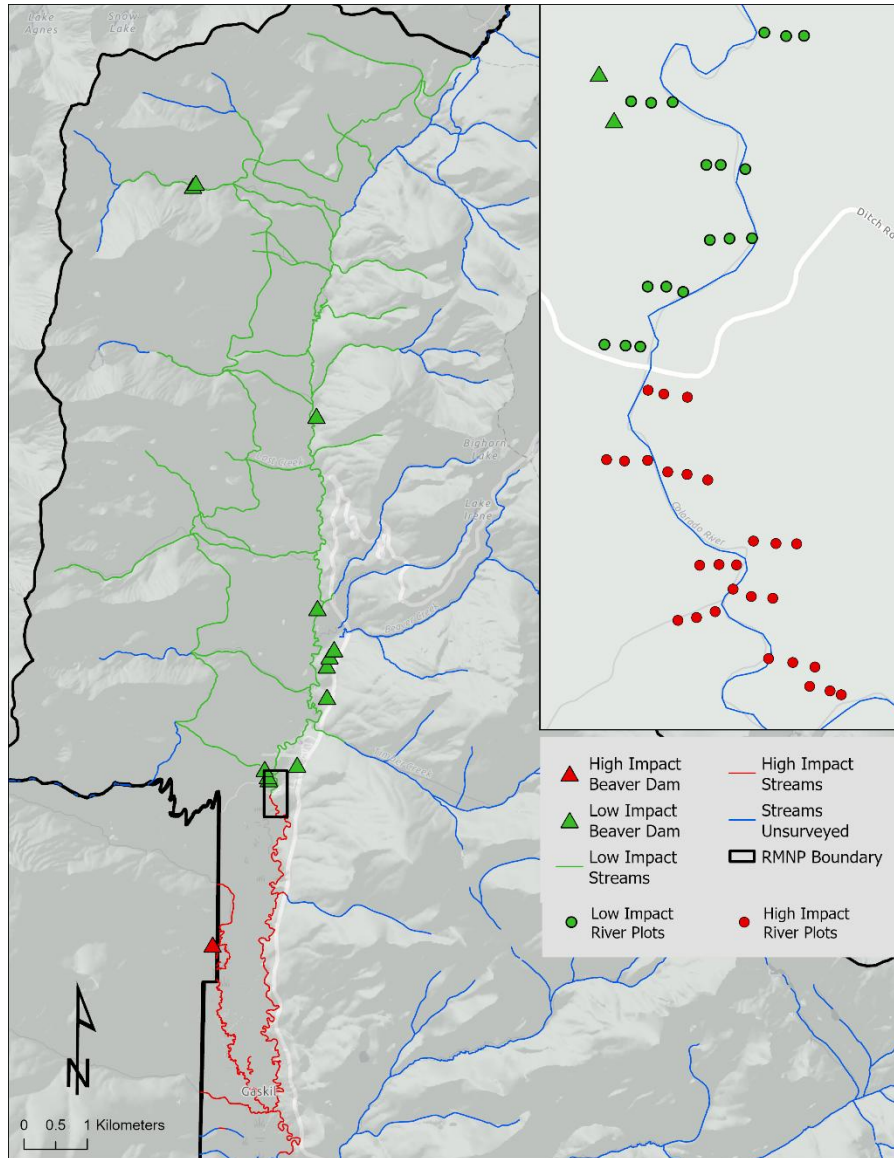


Figure 5. Survey locations and plot layout. Historic dams are indicated by triangle icons, there were 9 plots for each dam. River survey plots are indicated by circle icons, with three plots per transect.

Data collection

All data were collected from late June to late August of 2023 using ESRI Field Maps version 23.3.0. Data collected within each plot included vegetation composition within the plot, browsing intensity of elk, moose, and beaver, and indicators of beaver presence and its age (historic, recent, or current). Vegetation composition data included the percent canopy cover of the three dominant herbaceous species and the percent canopy cover of all shrub species, shrub health, and browsing intensity. Percent canopy cover, health, and browsing intensity were collected for three shrub height classes: short (<1 m height), medium (1-2 m height), and tall (>2 m height). Percent cover was also collected for standing water and bare ground, and the type of bare ground was recorded (sand/sediment, rock, gravel, mix). Cover was collected so that all values totaled 100%. Protocols for surveys were adapted from previous literature, primarily from Campbell-Palmer et al. (2020), and Small et al. (2016).

Shrub health data was collected for each of the three height classes, following a framework by Schindler et al. (2020) shown below (Table 1).

Table 1. Brief summary of shrub health rating descriptions and their corresponding numerical values.

Rating	Description
1	Plant dead
2	Strong sign of stress, mostly unhealthy, all leaves damaged or dead
3	Signs of stress, leaves not fully developed, >50% of leaves are damaged
4	Mild signs of stress, mostly healthy, all leaves developed, <50% of leaves are damaged
5	Very healthy plants, no signs of stress, all leaves without damage

Browsing pressure was collected for each of the shrub height classes, as well as individually for beaver, moose, and elk, using an accumulated browsing index (ABI) of 0-3 adapted from a study

done by the NPS and University of Michigan exploring competition between moose and beaver in Isle Royale National Park (Crane et al., 2022; Mathisen et al., 2017). ABI is a unitless qualitative measurement used to estimate the browsing intensity of ungulates on trees and shrubs. Scores and their meanings are listed in Table 2 with a visual representation shown in Figure 6.

Table 2. Accumulated browsing index (ABI) numerical values and the corresponding descriptions.

Rating	Description
0	No previous browsing
1	Previous browsing, but structure and growth form have not been impacted
2	Browsing has visibly changed the structure and growth form of the plant
3	Browsing has greatly changed the structure and growth form of the plant

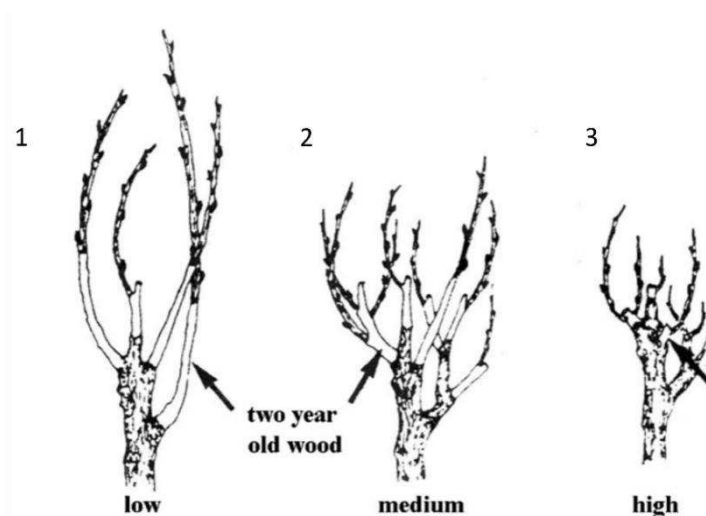


Figure 6. Examples of Accumulated Browsing Index (ABI) used for determining browsing severity of elk, moose, and beaver. ABI is a categorical variable ranging from 0-3, 0 indicating no previous browsing, 1 indicating that there has been previous browsing but no impact to growth form or canopy. 2 indicates that browsing has caused some changes to the growth form and canopy. 3 indicates that browse has greatly impacted the canopy and growth form. [Image adapted from Hood & Bayley, 2009].

Statistical Analysis

The relationship of beaver sign, shrub communities, herbaceous communities, and how distance from the river changes these two communities were evaluated with analyses of covariance (ANCOVA), analyses of variance (ANOVA), generalized linear mixed effects models, Kruskal-Wallis tests, and Poisson generalized mixed models. Dominant herbaceous plants and shrub species were analyzed by their Wetland Indicator Status (WIS), the probability that a plant would occur in a wetland versus an upland ecosystem, and Mean coefficients of conservatism (Mean-C). Coefficients of conservatism (C-values) are a numerical value between 0-10 that is assigned to an individual representing that plant species' ability to withstand an anthropogenically disturbed environment (Smith et al., 2020). High values are reserved for species that are more likely to occur in unaltered conditions, while lower values indicate species that can tolerate human disturbance (Smith et al., 2020). Mean-C values are simply the average of all the C-values within a defined area. For a plant community to be considered a wetland community, WIS values typically are comprised of values of three or less. Other dependent variables included shrub species richness and relative percent cover for the herbaceous layer, and shrub layer for three different height classes (short <1 m, medium 1-2 m, and tall >2 m). Independent variables represented historic farming intensity (high and low), such as hay production, transect location within or outside an enclosure, and survey group. Survey groups consisted of historic dams (off-channel abandoned beaver dams), and three types of river associated surveys (historic beaver floodplains, active beaver floodplains, and non-beaver floodplains).

Prior to analysis, data preparation included removing plots within burned areas of the East Troublesome Fire using an ArcGIS online layer of soil burn severity (Woodward, 2022). Data points within high and medium soil burn severity areas were removed from analysis, and those within low burn severity remained in the study. Individual plots were assigned plot numbers ranging from 1-3,

where 1 indicated the closest plot to the river, 2 was 20 m away, and 3 was the farthest plot away at 40 m. For transects that fell alongside the river, rather than perpendicular to, each plot was renumbered so that all plots were labeled as 1. Mean-C, WIS values, and relative percent cover for surface water and all vegetation layers were calculated by averaging across transects for all analyses except those pertaining to how distance from the river impacts beaver habitat. In this case, these variables were averaged per plot. Shrub species richness was totaled across transects or within plots, depending on the analysis.

Analyses pertaining to the shrub layer

The relationship between age of beaver sign and shrub species richness was explored with an ANCOVA comparing between survey groups. An ANOCVA was used to control potential confounding factors that may influence these variables, including farming intensity and relative surface water cover. Shrub WIS and Mean-C were both heavily tailed so a non-parametric Kruskal-Wallis test was employed for each analysis. Dunn's test with a Bonferroni correction was used for pairwise comparisons when results were significant.

When comparing the effect of historic farming impacts on beaver habitat, a Kruskal-Wallis test was used, with an interaction between location in the enclosure and farming intensity, to test for differences within shrub richness and WIS. Dunn's tests with a Bonferroni correction were used for pairwise comparisons when results were significant. Shrub Mean-C was tested using an ANCOVA. Covariates were the same as above, with the inclusion of mean herbaceous cover and mean shrub cover. Farming intensity was removed from the ANCOVA as it had already been included in the interaction.

Analyses pertaining to the herbaceous layer

To evaluate how Mean-C and WIS values changed in relation to age of beaver sign, an ANCOVA was used to analyze differences in these variables between the survey groups. An ANCOVA was used to control potential confounding factors that may influence these variables, including farming intensity, relative surface water cover, mean shrub cover, and mean herbaceous cover. Pairwise comparisons on statistically significant results were made using a Tukey correction. When comparing the impact of historical farming intensity on WIS and Mean-C values, a Kruskal-Wallis test was employed with an interaction between farming intensity and the plots located in the enclosure.

Analyses pertaining to relative percent cover for both herbaceous and shrub communities

The relationship of beaver activity with percent cover was explored in a similar fashion for both the herbaceous and shrub layers. Percent cover data was heavily tailed for both layers, and all subsequent analyses thus consisted of nonparametric tests to account for non-normal distributions. A Kruskal-Wallis test followed by a Dunn's test with a Bonferroni correction was utilized to analyze differences between the study groups' herbaceous cover and shrub cover (by height class and total). Kruskal-Wallis tests with an interaction between enclosure presence and farming intensities, followed by a Dunn's test with a Bonferroni correction, were applied to analyze the effects on herbaceous and shrub (total and by height class) covers.

Analyses pertaining to how distance from the river impacts beaver habitat

The influence of distance from the river's edge on variables of interest were analyzed in several ways. For analyses concerning WIS, Mean-C, and total percent cover for both the herbaceous and shrub layers, linear mixed-effects models (LMM) were used. Shrub and herbaceous percent cover, and shrub WIS values were heavily tailed, so data were transformed using a square root transformation prior to analysis. Since shrub richness was heavily tailed but consisted of count data, a generalized linear mixed-effects model (GLMM) with a Poisson distribution was employed to analyze changes in richness as distance from the river increased. In all models, transects and feeding lines were used as nested random effects. Plot number, survey group, percent surface water, and farming impact intensities were fixed effects. Plot number was used as a proxy for distance in these analyses, with the variables of interest either being averaged (WIS, Mean-C, percent cover), or totaled (species richness) by plot.

All statistical analyses were performed in RStudio (version 4.2.3).

III. Results

The ungulate enclosure within the Kawuneeche Valley was the only location that had recent and current beaver sign. This beaver sign was found primarily within the enclosure, with only one browsed tree outside of the fence line late in the summer. This indicates that beavers were only present within the enclosure and did not venture far outside of the fence line for food or building resources. The enclosure will be referenced as active beaver floodplains in text and "River-Current" in figures. The rest of the river survey area consisted of historic beaver sign or lacked beaver sign entirely. Portions of the river that had historic beaver sign will be referred to as historic beaver floodplains in text and "River-Historic" in figures, while portions of the river that lacked beaver sign

will be referred to as non-beaver floodplains in text and “River-Absent” in figures. Historic dams were all off-channel dams and were primarily located at the northern portion of the valley, with a few along the southern end.

Lists of observed species for each research question can be found in tables A1, A2, B1, B2, C1, and C2 in appendices A, B, and C.

How are vegetation communities structured in areas of historic, recent, and current beaver occupancy?

Floodplains with active beaver had significantly higher shrub canopy cover than both non-beaver floodplains and floodplain areas with historic beaver sign ($p = 0.0018$ and 0.047 , respectively, Figure 7). However, active beaver floodplains were only marginally different from historic dams ($p = 0.054$, Figure 7, $\chi^2 = 16.46$, $p = 0.0009$, $df = 3$).

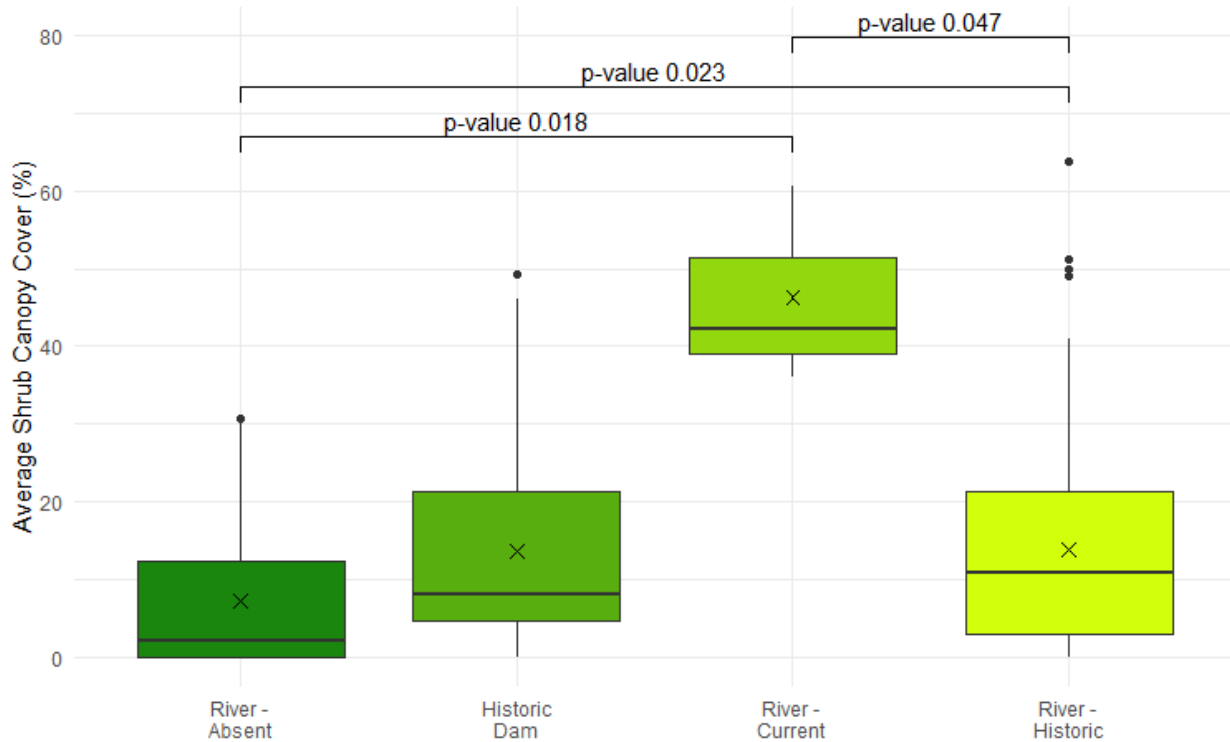


Figure 7. Comparison of shrub percent canopy cover by location. A Kruskal-Wallis test was used to assess significance ($\chi^2 = 16.46$, $p = 0.0009$, $df = 3$), followed by Dunn's pairwise comparisons with Bonferroni corrections. Adjusted p-values for significant comparisons ($\alpha=0.05$) are shown in the plot. Sample sizes were $n = 22$ river – absent, $n = 39$ historic dams, $n = 3$ river – current, and $n = 130$ river – historic. Group means are indicated by an 'X' in the plot.

The active beaver floodplain was the only location that had consistent medium and tall shrub cover, as all other sites had only short shrubs. For the medium height class, active beaver floodplains had significantly higher percent cover compared to non-beaver floodplains, historic dams, and floodplains with historic beaver sign ($p < 0.0001$ for all comparisons, Figure 8b, $\chi^2 = 38.17$, $p < 0.0001$, $df = 3$). The tall height class had similar results, with active beaver floodplains having significantly higher percent cover compared to all groups ($p < 0.0001$ for all comparisons, Figure 8c, $\chi^2 = 58.49$, $p < 0.0001$, $df = 3$). Floodplains with historic beaver sign had similar vegetation characteristics to non-beaver floodplains in all metrics other than short shrub canopy cover. Floodplains with historic beaver sign had more short shrub canopy cover than non-beaver floodplains ($p = 0.021$, Figure 8a, $\chi^2 = 9.02$, $p = 0.03$, $df = 3$).

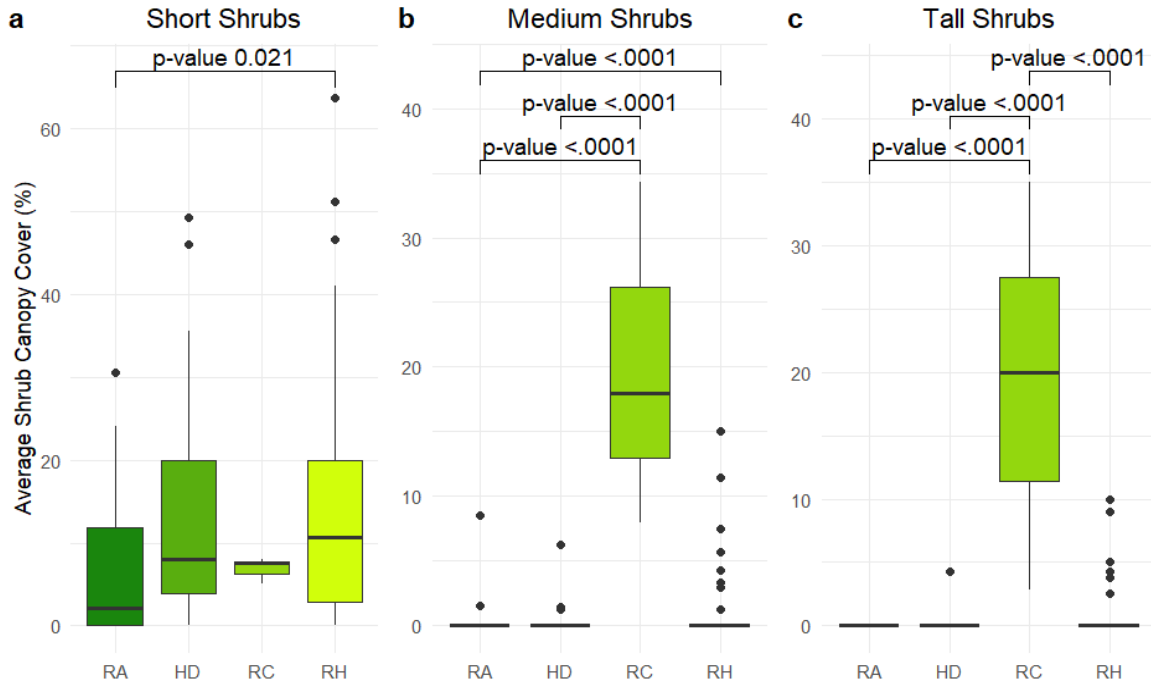


Figure 8. Comparison of average percent canopy cover for three height classes by location. Kruskal-Wallis tests were used to assess significance (plot a: $\chi^2 = 9.02$, $p = 0.03$, $df = 3$, plot b: $\chi^2 = 38.17$, $p < 0.0001$, $df = 3$, and plot c: $\chi^2 = 58.49$, $p < 0.0001$, $df = 3$), followed by Dunn's pairwise comparisons with Bonferroni corrections. Adjusted p -values for significant comparisons ($\alpha = 0.05$) are shown in the plots. Sample sizes were $n = 22$ river – absent (RA), $n = 39$ historic dams (HD), $n = 3$ river – current (RC), and $n = 130$ river – historic (RH). Group means are indicated by an 'X' in the plots.

Unlike shrub percent cover, shrub richness was only marginally different between study groups $F(3, 188) = 2.40$, $p = 0.07$ (Figure 9). Active beaver floodplains had the highest average shrub species richness (5.33 ± 1.53), followed by floodplains with historic beaver sign (3.42 ± 1.80), historic dams (3.23 ± 1.44), and finally, non-beaver floodplains with the lowest average richness (2.64 ± 2.46).

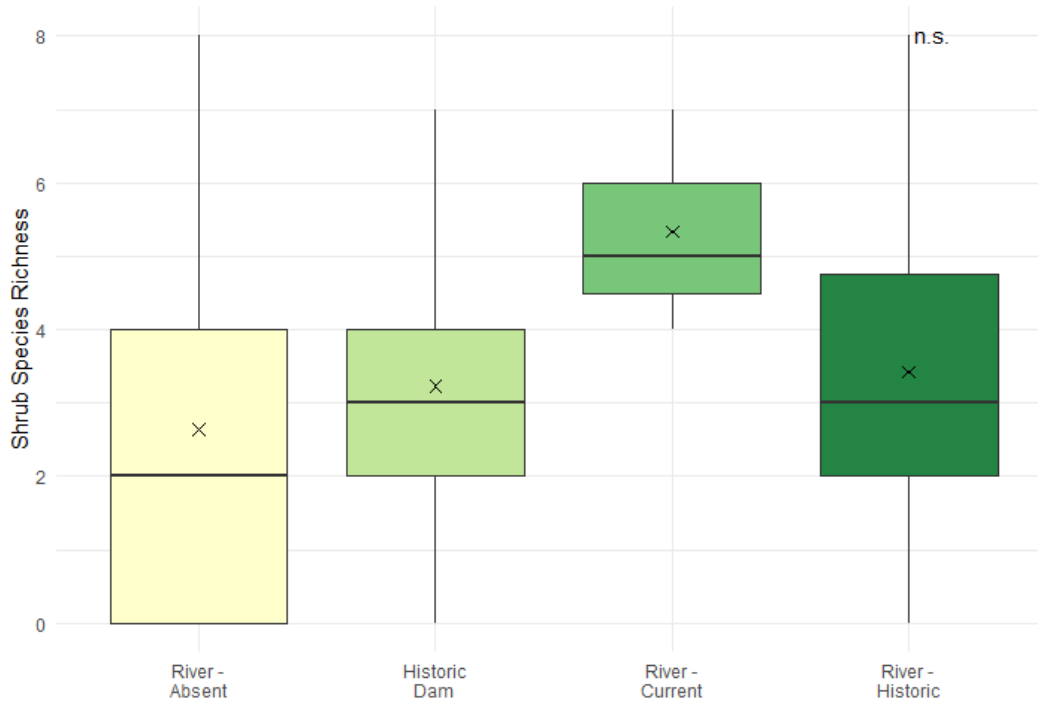


Figure 9. Comparison of shrub species richness by location. An ANCOVA was used to assess significance ($F(3, 188) = 2.40, p = 0.07$), indicating no statistically significant differences among groups ($\alpha = 0.05$). Sample sizes were $n = 22$ river - absent, $n = 39$ historic dams, $n = 3$ river - current, and $n = 130$ river - historic. Group means are indicated by an 'X' in the boxplots.

Historic dams had significantly lower (wetter) shrub WIS values than floodplains with historic beaver sign, indicating a more wetland adapted community associated with historic dams ($p = 0.02$, Figure 10a). Interestingly, no other comparison was significant ($p > 0.05$, $\chi^2 = 10.56, p = 0.014, df = 3$).

Historic dams had higher shrub Mean-C values compared to both non-beaver floodplains and floodplains containing historic beaver sign ($p = 0.008$ and < 0.0001 , respectively, Figure 10b). Indicating a shrub community less tolerant of disturbance. No other comparisons were significant ($\chi^2 = 26.38, p = < 0.0001, df = 3$).

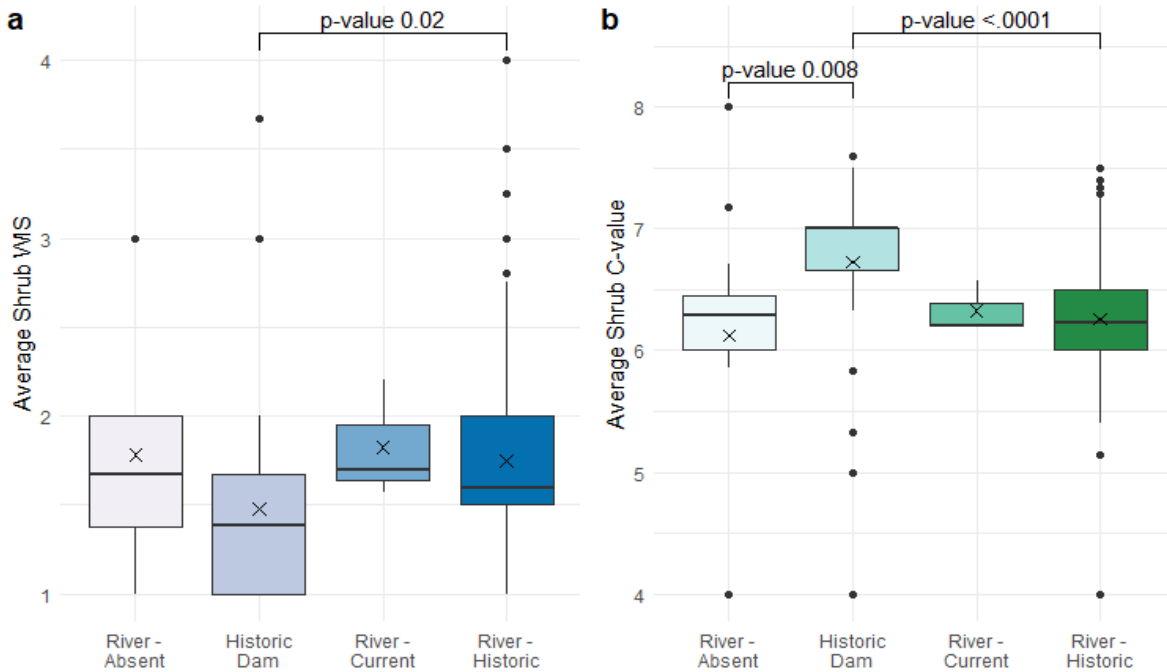


Figure 10. Comparison of shrub WIS values (a) and shrub Mean-C (b) by location. Kruskal-Wallis tests were used to assess significance (plot a: $\chi^2 = 10.56$, $p = 0.014$, $df = 3$, plot b: $\chi^2 = 26.38$, $p = <0.0001$, $df = 3$), followed by Dunn's pairwise comparisons with Bonferroni corrections. Adjusted p -values for significant comparisons ($\alpha = 0.05$) are shown in the plots. Sample sizes for both tests were $n = 15$ river - absent, $n = 36$ historic dam, $n = 3$ river - current, and $n = 118$ river - historic. Group means are indicated by an 'X' in the boxplots.

In contrast to the findings from shrub percent cover, herbaceous percent cover was higher in non-beaver floodplains compared to active and historic beaver floodplains ($p = 0.003$, and 0.04 , respectively, Figure 11a). Active beaver floodplains had a marginal trend of less herbaceous cover compared to both historic dams and historic beaver floodplains ($p = 0.08$ and 0.06 , respectively. $\chi^2 = 15.17$, $p = 0.002$, $df = 3$).

Historic beaver floodplains had significantly higher (drier) herbaceous WIS values compared to historic dams ($p < 0.0001$, Figure 11b), indicating that historic beaver floodplains have an herbaceous community that is more adapted to drier soils. These floodplains also had marginally higher WIS values compared to non-beaver floodplains ($p = 0.07$). Active beaver floodplains were not significantly different from any comparison ($p > 0.05$, $F(3, 186) = 9.94$, $p = < 0.0001$).

Herbaceous mean-C values associated with historic dams were significantly higher than values associated with historic beaver floodplains ($p = 0.005$, Figure 11c). This indicates that historic beaver dams support an herbaceous community that is less tolerant to human disturbance. No other comparisons were significant ($p > 0.05$, $F(3, 186) = 4.09$, $p = 0.008$).

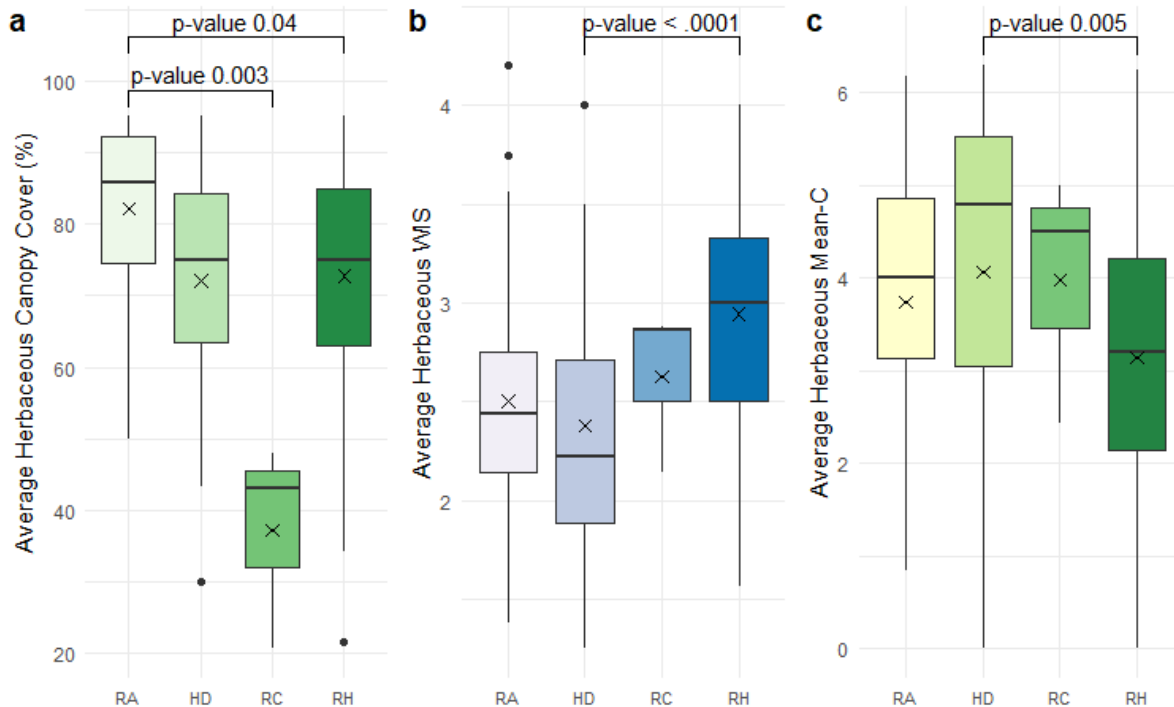


Figure 11. Comparison of herbaceous canopy cover (a), WIS (b), and Mean-C (c) by location. A Kruskal-Wallis test was used to assess significance for herbaceous cover ($\chi^2 = 15.17$, $p = 0.002$, $df = 3$), followed by a Dunn's pairwise comparison with a Bonferroni correction. ANCOVAs were used to assess significance for WIS and Mean-C (plot b: $F(3, 186) = 9.94$, $p = < 0.0001$, plot c: $F(3, 186) = 4.09$, $p = 0.008$), followed by Tukey pairwise comparisons. Adjusted p-values are shown on the plot ($\alpha = 0.05$). Sample sizes for all tests were $n = 22$ river-absent (RA), $n = 39$ historic dam (HD), $n = 3$ river-current (RC), and $n = 130$ river-historic (RH). Group means are indicated by an 'X' in the boxplots.

How has historic land management impacted beaver habitat?

Shrub cover was significantly higher within the active beaver floodplain exposed to low farming intensity than historical beaver landscapes regardless of farming intensity ($p = 0.04$ and 0.007 for low and high intensity, respectively, Figure 12, $\chi^2 = 13.02$, $p = 0.001$, $df = 2$).

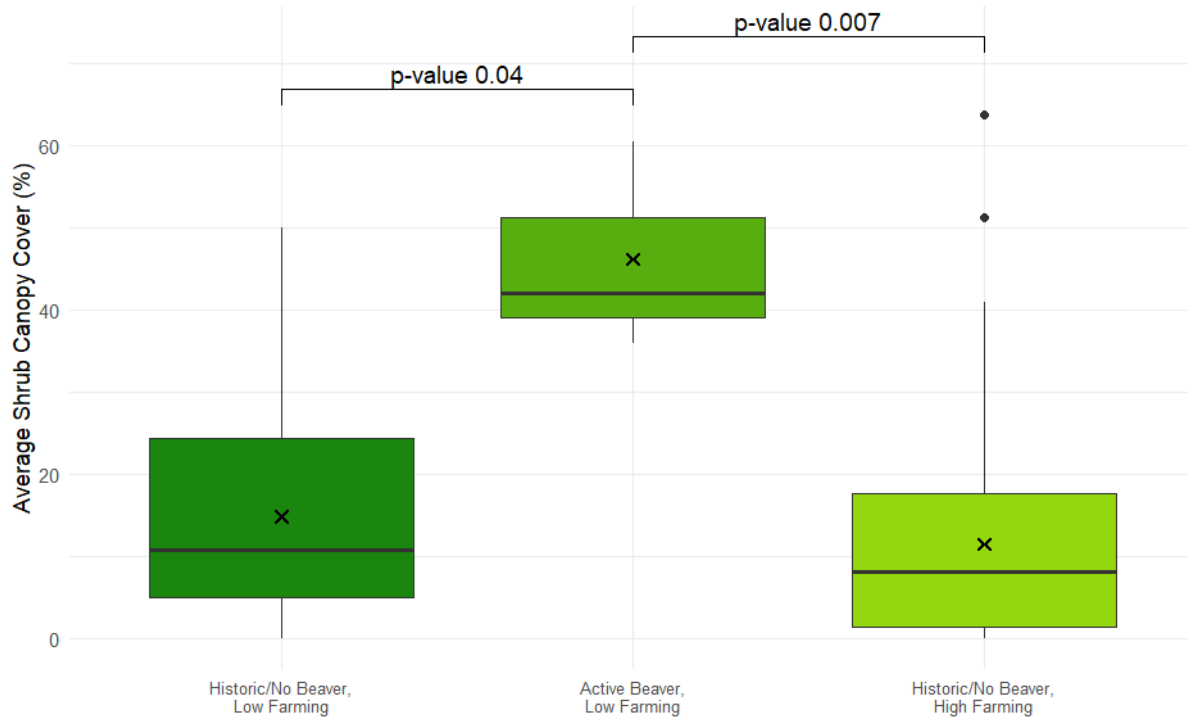


Figure 12. Comparison of total shrub percent canopy cover by historic farming intensity. A Kruskal-Wallis test was used to assess significance ($\chi^2 = 13.02$, $p = 0.001$, $df = 2$), followed by Dunn's pairwise comparisons with a Bonferroni correction. Adjusted p -values for significant comparisons ($\alpha=0.05$) are shown on the plot. Sample sizes were $n = 85$ for historic/no beaver and low farming, $n = 3$ active beaver and low farming, and $n = 106$ historic/no beaver and high farming. Group means are indicated by an 'X' in the boxplots

The active beaver landscape that experienced low farming intensity had significantly higher percent cover for both the medium and tall height class analyses ($p < 0.0001$, for all comparisons of both analyses, Figure 13b and c respectively. $\chi^2 = 40.67$, $p = < 0.0001$, $df = 2$ for the analysis of medium shrub cover and $\chi^2 = 57.86$, $p = < 0.0001$, $df = 2$ for the analysis of tall shrub cover). Short shrub canopy cover was only marginally different between historical farming intensity areas ($p = 0.08$, Figure 13a), indicating that cover was relatively consistent between analysis groups ($\chi^2 = 4.95$, $p = 0.08$, $df = 2$).

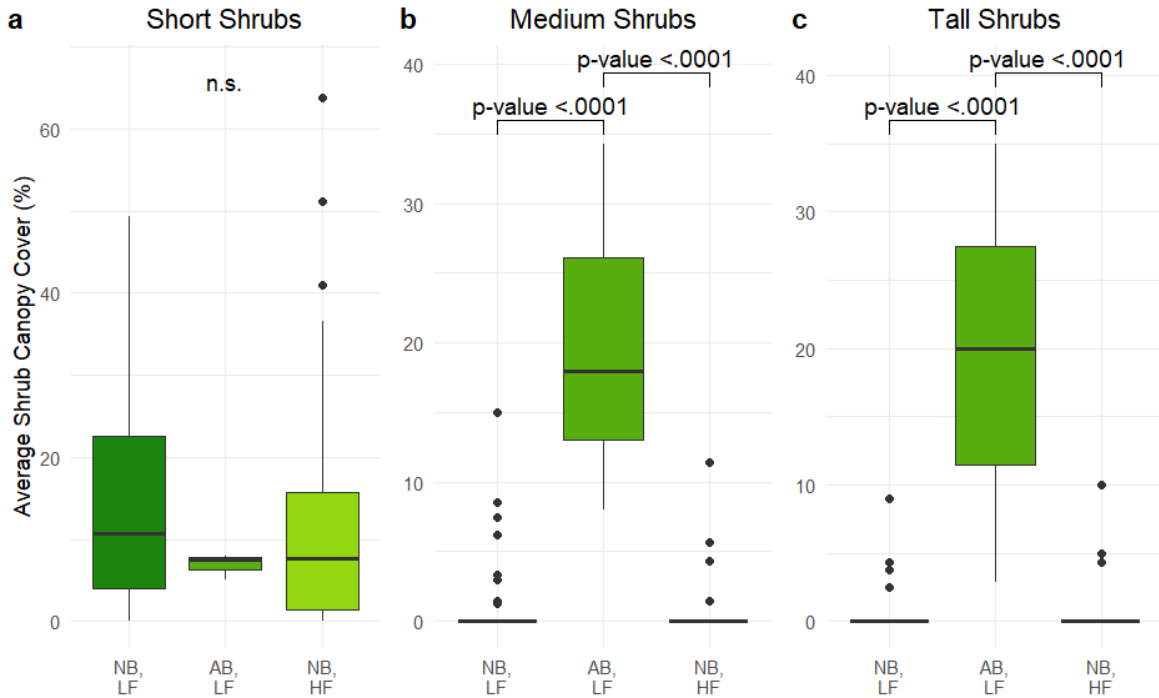


Figure 13. Comparison of percent canopy cover for the short (a), medium (b), and tall (c) height classes by historic farming intensity. Kruskal-Wallis tests were used to assess significance (plot a: $\chi^2 = 4.95$, $p = 0.08$, $df = 2$, plot b: $\chi^2 = 40.67$, $p = < 0.0001$, $df = 2$, plot c: $\chi^2 = 57.86$, $p = < 0.0001$, $df = 2$), followed by Dunn's pairwise comparisons with Bonferroni corrections. Adjusted p-values for significant comparisons ($\alpha=0.05$) are shown in the plots. NB - no/historic beaver activity, AB - active beaver activity, LF- low farming intensity, HF - high farming intensity. Sample sizes for all tests were $n = 85$ NB, LF; $n = 3$ AB, LF; and $n = 106$ NB, HF.

Unlike total shrub cover, shrub species richness was not significantly different between areas within active beaver floodplains that experienced low farming intensity, historic beaver landscapes that experienced low intensity, and historic beaver landscapes that experienced high farming intensity ($\chi^2 = 3.77$, $p = 0.15$, $df = 2$, Figure 14).

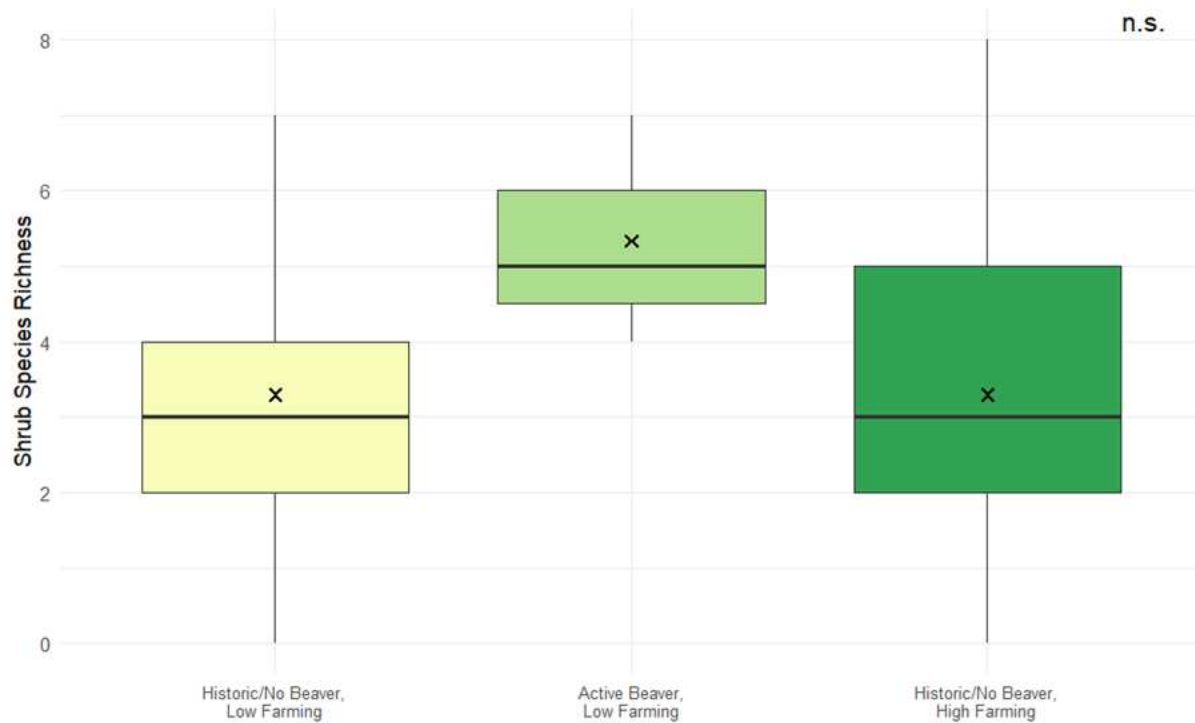


Figure 14. Comparison of shrub species richness by historic farming intensity. A Kruskal-Wallis test was used to assess significance ($\chi^2 = 3.77$, $p = 0.15$, $df = 2$), followed by Dunn's pairwise comparisons with a Bonferroni correction. Adjusted p -values for significant comparisons ($\alpha = 0.05$) are shown on the plot. Sample sizes were $n = 85$ for historic/no beaver and low farming, $n = 3$ active beaver and low farming, and $n = 106$ historic/no beaver and high farming. Group means are indicated by an 'X' in the boxplots

WIS values for the shrub layer were not significantly different between farming intensity areas ($\chi^2 = 2.11$, $p = 0.35$, $df = 2$, Figure 15a). Average shrub WISs were similar for all groups, with values around 2.

Shrub Mean-C values were not significantly different between analysis groups ($p > 0.05$, Figure 15b). The main effects of farming intensity and age of beaver activity was examined and found to not have significant effects of shrub Mean-C ($F(2, 164) = 1.12$, $p = 0.33$), indicating that the interaction of historical farming intensity and time of beaver activity may not have any impact on C-values associated with the shrub layer.

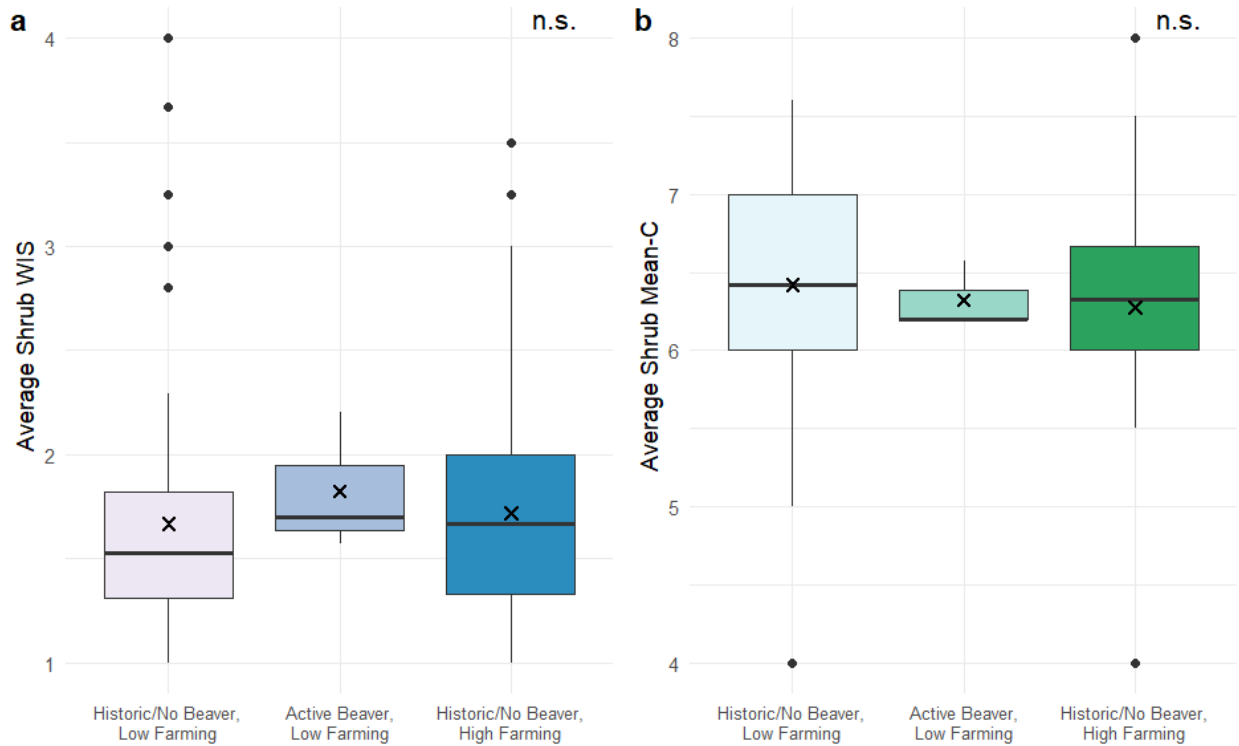


Figure 15. Comparison of Shrub WIS values (a) and Mean-C (b) by historic farming intensity. A Kruskal-Wallis test was used to assess significance for the WIS analysis ($\chi^2 = 2.11$, $p = 0.35$, $df = 2$) while an ANCOVA was used to assess significance for Mean-C values ($F(2, 164) = 1.12$, $p = 0.33$). Results indicated no statistically significant differences among groups for either analysis ($\alpha = 0.05$). Sample sizes for both tests were $n = 80$ for historic/no beaver and low farming, $n = 3$ active beaver and low farming, and $n = 89$ historic/no beaver and high farming. Group means are indicated by an 'X' in the boxplots

Herbaceous percent cover was significantly higher in historic beaver landscapes in high farming intensity compared to both active beaver landscapes and historic beaver landscapes in low farming intensities ($p = 0.009$ and 0.03 , respectively, Figure 16a). While not significant, there was a marginal trend showing that active beaver landscapes in low farming intensity had lower herbaceous percent cover than historic beaver landscapes in the same farming intensity ($p = 0.06$). Suggesting that historical farming activities may have left long term effects on the community composition of the floodplains ($\chi^2 = 14.07$, $p = 0.0009$, $df = 2$).

Herbaceous WIS values were not different between analysis groups ($F(2, 186) = 0.09$, $p = 0.92$, Figure 16b). This is not surprising, as all analysis groups had similar mean WIS values. Overall,

the herbaceous community within these floodplains tended to be comprised of facultative species that are equally found in wetland and non-wetland communities.

Similar to herbaceous WIS, there was no significant difference in herbaceous Mean-C values between any of the analysis groups ($\chi^2 = 2.19$, $p = 0.33$, $df = 2$, Figure 16c). Mean-C values for all analysis groups averaged around 3.5, indicating communities common to disturbed areas.

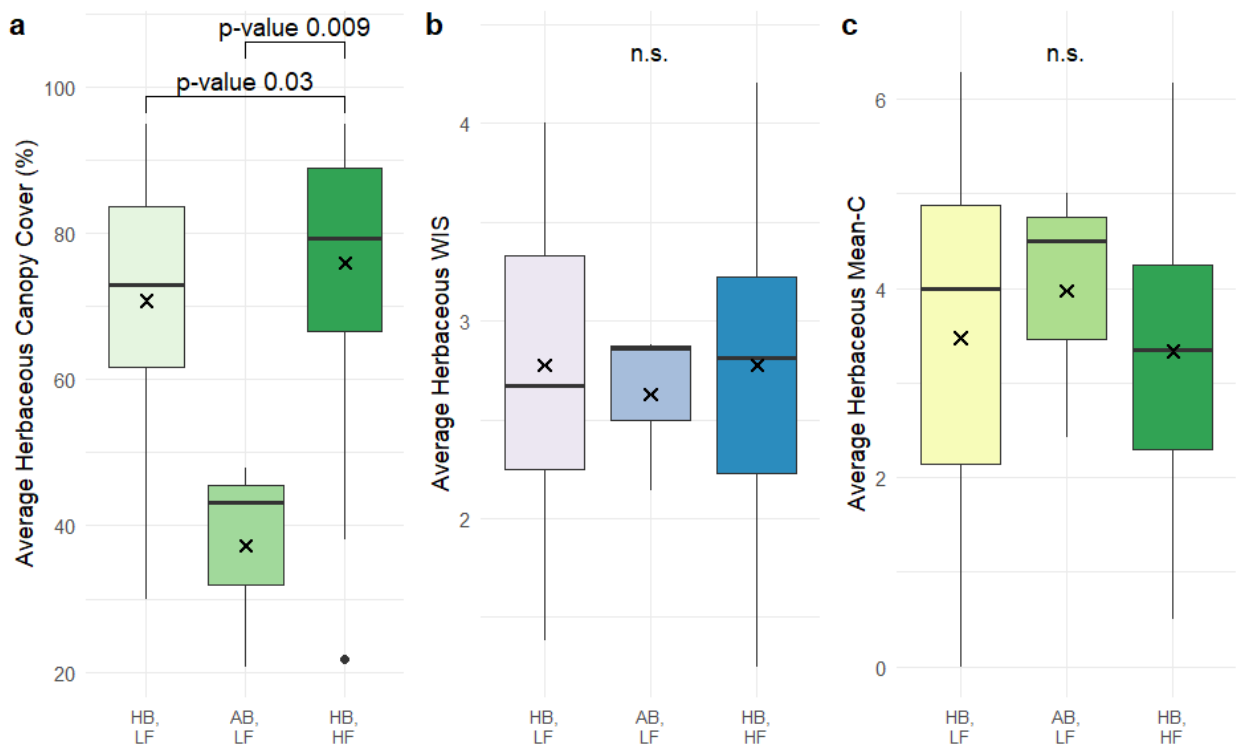


Figure 16. Comparison of herbaceous canopy cover (a), WIS (b), and Mean-C by historic farming intensity. Kruskal-Wallis tests were used to assess significance for herbaceous cover and Mean-C (plot a: $\chi^2 = 14.07$, $p = 0.0009$, $df = 2$, plot c: $\chi^2 = 2.19$, $p = 0.33$, $df = 2$), followed by a Dunn's pairwise comparison with a Bonferroni correction when significant. An ANCOVA was used to assess significance for herbaceous WIS (plot b, $F(2, 186) = 0.09$, $p = 0.92$), indicating no statistical significant differences among groups. Adjusted p -values are shown on the plot ($\alpha = 0.05$). NB - no/historic beaver activity, AB - active beaver activity, LR - low farming intensity, HR - high farming intensity. Sample sizes for all tests were $n = 85$ NB, LF; $n = 3$ AB, LF; and $n = 106$ NB, HF. Group means are indicated by an 'X' in the boxplots.

How does distance from the river impact beaver habitat?

Historic beaver browse extended beyond the 40-m transects throughout the study area. The glacial valley of our study area was historically a large beaver wetland complex that allowed access to food and building resources far from the current river's edge. Additionally, hillside groundwater inputs from the lateral moraines allowed beavers to build dams and forage across the valley, independent of the main river channel. In contrast to that historic landscape, willows today are largely constrained to the channel margins, and fresh beaver sign remained within 40 m of the river's edge.

Distance from the river significantly influenced shrub cover ($p < 0.001$). Shrub cover in both the second and third vegetation plots was significantly lower than in the first plot (estimate = -0.63, -0.97, and $p = 0.002$, < 0.0001 , for second and third plots respectively), showing a reduction in shrub cover as distance increased (Figure 17a). The other fixed effects did not have a significant effect on shrub cover ($p > 0.05$).

Shrub species richness decreased as distance from the river increased ($F = 16.28$, Figure 17b), with significant decreases in both plot two and plot three when compared to the first plot (estimate = -0.36 for plot two, estimate = -0.58 for plot three, $p = 0.0004$, and $< .0001$ for plot two and three respectively). Percent surface water, historic beaver floodplains, and ranching intensity did not significantly affect species richness ($p > 0.05$). However, active beaver floodplains had significantly higher shrub richness ($p = 0.04$).

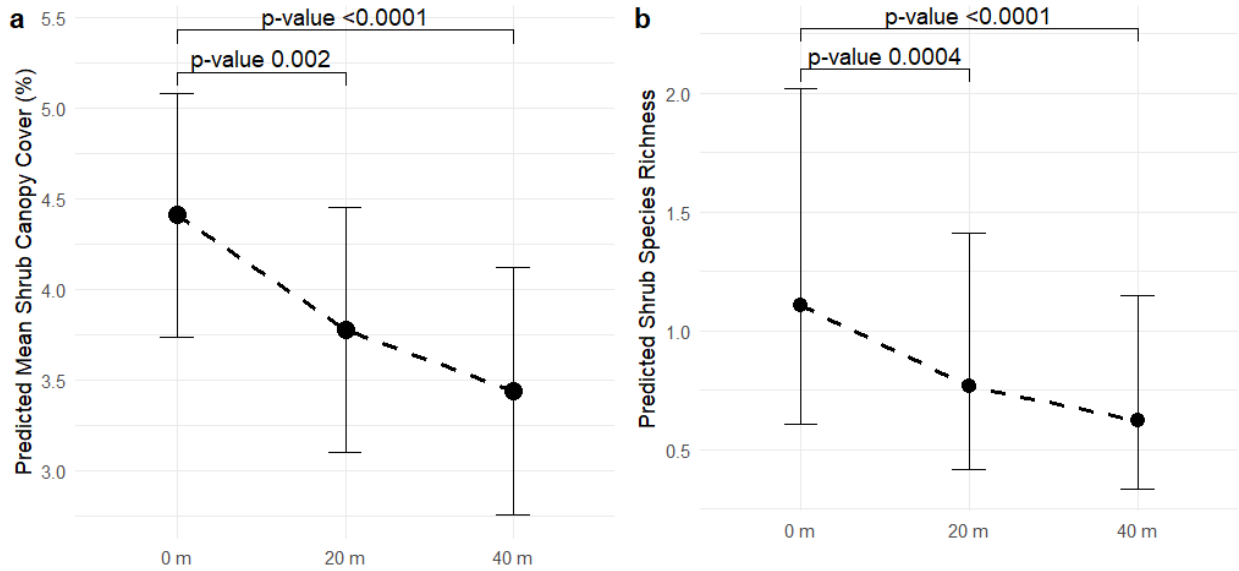


Figure 17 Predicted shrub canopy cover (a), and species richness (b) as a function of distance from the river. Predictions were determined using a linear mixed-effects model (a) and generalized linear mixed-effects model (b), with significance tested using ANOVA followed by a Tukey pairwise comparison ($\alpha = 0.05$). The dotted line represents model-predicted values, and the vertical lines represent the 95% confidence intervals. Adjusted p-values from the Tukey test are shown on the plot. Sample sizes for both tests were $n = 167$ for 0 m, $n = 146$ for 20 m, and $n = 136$ for 40 m.

Although not statistically significant at the conventional significance level of 0.05 (model $p = 0.08$), there was a marginal difference in shrub WIS between the first and third plots (Estimate = 0.08, $p = 0.07$, Figure 18a). This trend suggests that shrub WIS increased slightly as distance from the river increased. No other fixed effects influenced shrub WIS ($p > 0.05$).

Similar to shrub WIS, shrub Mean-C did not significantly change as distance from the river increased ($p > 0.05$, Figure 18b). Regardless of plot location, shrub Mean-C values were all around 6.3, indicating shrub communities that are consistently found in both non-disturbed and disturbed areas. No fixed effects had a significant influence on shrub Mean-C values ($p > 0.05$).

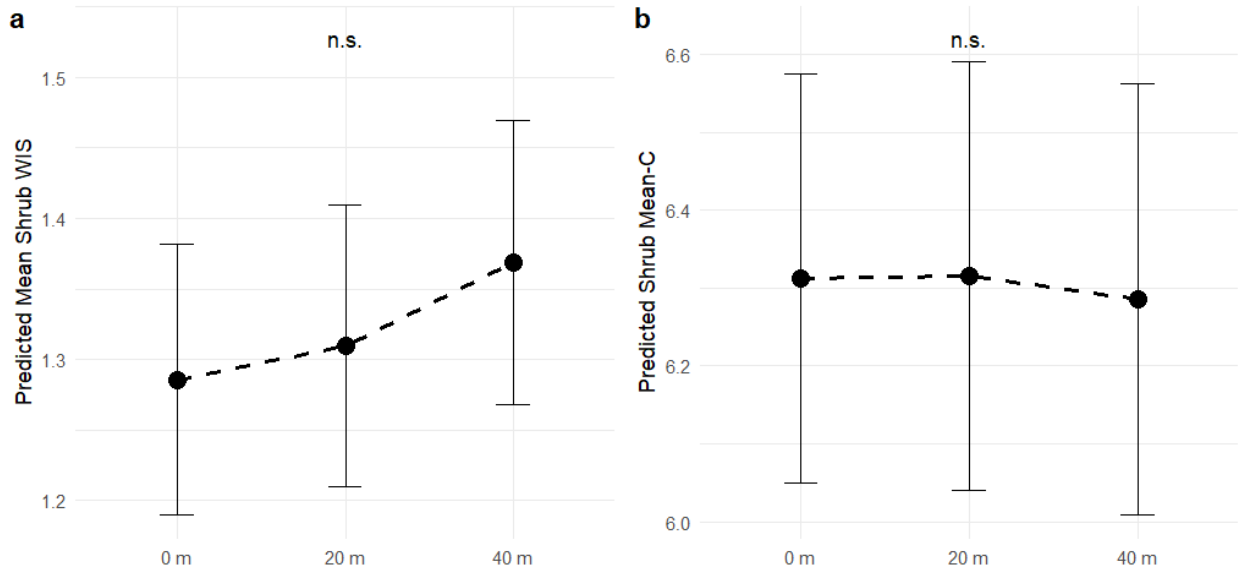


Figure 18. Predicted shrub WIS (a) and Mean-C (b) as a function of distance from the river. Predictions were determined using linear mixed-effects models (LMMs), with significance tested using ANOVA ($\alpha = 0.05$). The dotted line represents the model-predicted values, and the vertical lines represent the 95% confidence intervals. Sample sizes for both tests were $n = 125$ plot one, $n = 89$ plot two, and $n = 74$ plot three.

Herbaceous cover did not significantly change as distance from the river increases ($p = 0.4$; Figure 19a). Surface water cover had a significant effect on herbaceous cover (Estimate = -0.35 , $p < 0.001$). Suggesting that increasing surface water cover results in decreasing herbaceous cover. Active beaver floodplains had significantly lower herbaceous cover (Estimate = -2.31 , $p = 0.0008$).

Average herbaceous WIS values did not change significantly as distance from the river increased ($p = 0.11$). However, there were some marginally significant trends displaying a slight increase in average WIS values in the third plot, to less wetland adapted herbaceous plants, when compared to the first plot (estimate = 0.18 , and $p = 0.05$, Figure 19b). This is due to the significant interaction between distance to the river and surface water cover ($p = 0.03$), where in the third plot, increased standing water resulted in a sharper decrease in WIS values than any other plot (Figure 19c). This result suggests that by 40 m away from the river, increasing surface water cover plays a more prominent role in supporting an herbaceous community that is more wetland adapted. No other fixed effect had any influence on herbaceous WIS ($p > 0.05$).

Similarly to herbaceous WIS values, herbaceous Mean-C values showed no significant changes as distance from the river increased ($p = 0.9$, Figure 19d). Across the three plots, herbaceous Mean-C values averaged around 4, indicating herbaceous communities that are commonly found in both non-disturbed and disturbed environments. No other fixed effects had a significant impact on Mean-C values ($p > 0.05$).

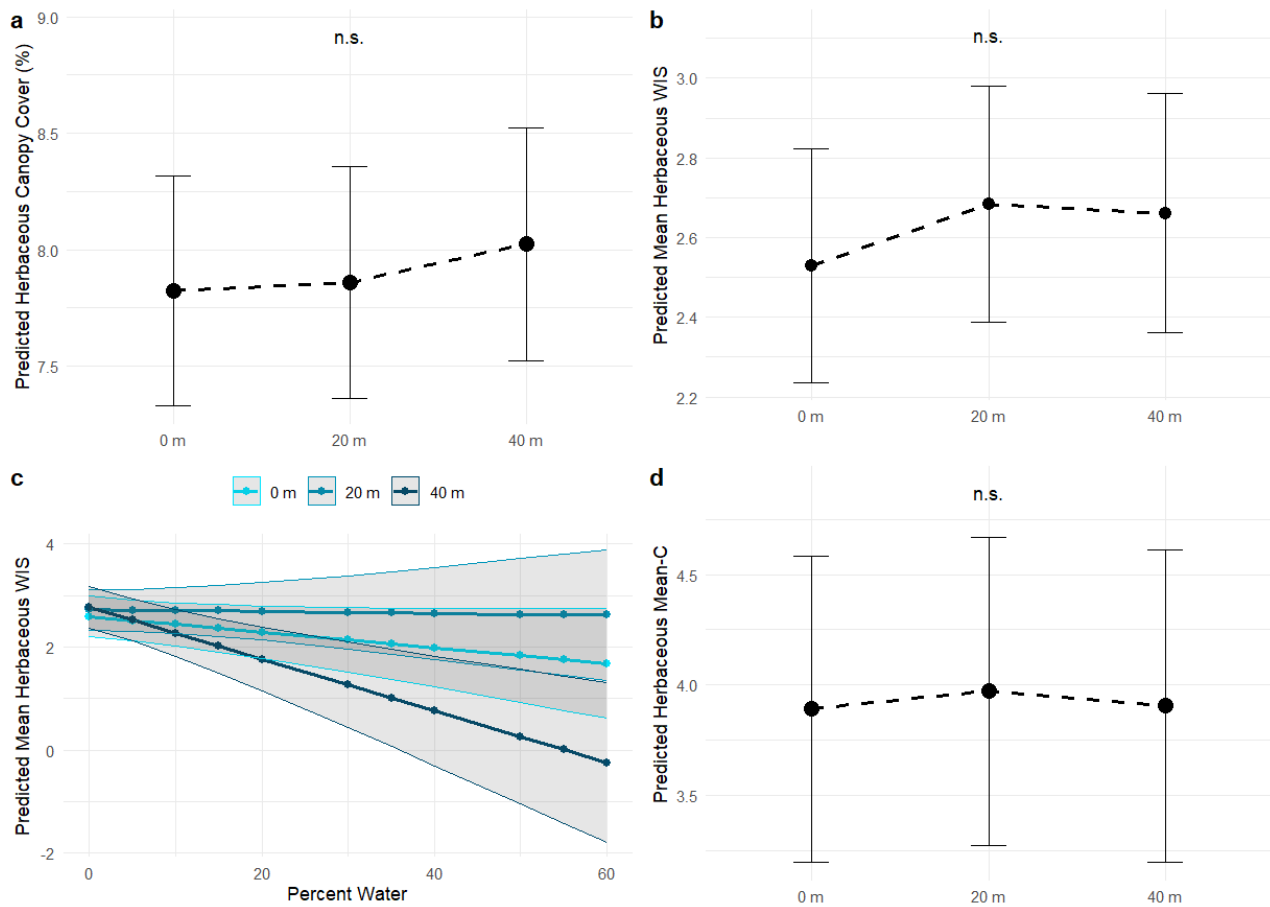


Figure 19. Predicted herbaceous canopy cover (a), herbaceous WIS (b), Interaction showing the influence that increasing water has on WIS values (c) and Mean-C (d) as a function of distance from the river. Predictions were determined using linear mixed-effect models (LMMs), with significance testing using ANOVA ($\alpha = 0.05$). The dotted line represents the model-predicted value, and the vertical lines represent the 95% confidence intervals. Sample sizes for herbaceous percent cover were $n = 167$ plot one, $n = 146$ plot two, and $n = 136$ plot three. WIS and Mean-C sample sizes were $n = 163$ for the plot one, $n = 146$ for plot two, and $n = 133$ for plot three.

IV. Discussion

Plant community structure and beaver occupancy

The patterns of shrub cover across the study area partially confirmed the hypothesis regarding beaver influence on canopy cover. Shrub canopy cover was highest and dominated by taller height classes in floodplain areas with active beaver activity, confirming the hypothesis. However, shrub cover did not differ significantly between areas with historic beaver sign and historic beaver dams, and short shrub cover was ubiquitous across the entire study area, not supporting the hypothesis. Both shrub and herbaceous WIS and Mean-C values supported the hypotheses, with historic dams fostering vegetative communities more wetland-adapted and less disturbance-tolerant. Contrary to expectations, shrub species richness was unaffected by the age of beaver activity, and herbaceous canopy cover was unexpectedly higher in floodplains lacking beaver sign rather than in areas with historic dams.

In the right environmental conditions, abandoned beaver dams can last for several decades on the landscape and can impart variable impacts on the landscape (Neff, 1957; Rosell et al., 2005; Wright et al., 2002). If the dam does not breach fully, these structures can retain water for decades after abandonment and can continue to provide valuable habitat to a variety of species, such as semi-aquatic invertebrates and mammals (Rosell et al., 2005). There is, however, a gap in our understanding of off-channel, abandoned beaver ponds and the influence they impart on maintaining wetland conditions in montane valleys with incised streams.

This study found that historic, off-channel, beaver dams supported more wetland and less disturbance-adapted species in both the shrub and herbaceous layers, differing from historic beaver floodplains. Historic, off-channel dams supported communities consisting of a facultative wet species, *Calamagrostis canadensis*, and two obligate wetland species, *Carex aquatilis* and *Carex*

utriculata, in the herbaceous layer (Table A2). In contrast, historic beaver floodplains had more mesic communities typical of a disturbed environment, consisting of several non-natives as well, *Taraxacum officinale* (FACU), *Fragaria virginiana* (FACU), and *Alopecurus pratensis* (FAC, Table A2). Shrub communities throughout the study area were more consistent, with *Salix* species being the most observed shrub. Non-beaver, historic, and active beaver floodplains had *Salix* spp. as the three most observed shrubs, while *Betula glandulosa* (OBL) and *Dasiphora fruticosa* (FAC) was present in historic dams (Table A1). Historic dams also supported similar total shrub cover as active beaver floodplains. This is an interesting result, as the active beaver floodplain was within an enclosure, and therefore had additional protection from ungulate browse, allowing the shrub community within to reach medium and tall height classes. These findings suggest that abandoned beaver dams may provide beneficial environmental factors that support the continuation of wetland communities in a disturbed wetland environment.

Many of these historic beaver ponds retained water throughout the study period, and this likely contributed to these results. Within the same study area, Westbrook et al. (2006), found that portions of the valley where beavers had built dams and increased sedimentation in the past transitioned quickly to drier upland ecosystems after the dam breached. The loss of dams reduced lateral connectivity of the river to the surrounding valley and increased river incision, altering flooding and groundwater disturbance dynamics, shifting vegetative communities to disturbed upland compositions (Westbrook et al., 2006; Scamardo et al., 2022). While riparian shrubs are able to adapt to lowering water tables by extending their root system (Naumburg et al., 2005; Bau' et al., 2021), herbaceous species are more sensitive to soil saturation and groundwater changes (Lite & Stromberg, 2005; Škarpich et al., 2016). The water table alterations due to historic beaver abandonment and river incision likely caused the herbaceous vegetation to shift towards the composition seen in historic beaver floodplains, resulting in invaded, upland compositions with

lower Mean-C values. Meanwhile, the consistent presence of water provided by historic dams may have provided a buffer against a drying riparian wetland valley, sustaining a more natural wetland community when the rest of the study area could not.

The localized ponding provided by historic dams may have also supported enhanced shrub growth, allowing total shrub cover to match that of active beaver floodplains within the enclosure. In riparian valleys with incised channels, like the study area, riparian shrubs can adapt to lowered water tables to an extent. However stable ground water provision is necessary to support healthy communities and sustain growth (Lite & Stromberg, 2005; Hultine et al., 2010; Stromberg et al., 2013). Ponding associated with historic beaver dams may provide the necessary water requirements and access to a higher water table throughout the growing season, thereby supporting equivalent cover of shrubs in the enclosure. Additionally, historic beaver dams are often invaded by shrubs as they start to break down (Aznar & Desrochers, 2008; Neff, 1957), potentially contributing to similar shrub cover. However, active beaver floodplains were the only location that supported taller shrubs, likely attributable to the enclosure fencing, which reduces ungulate browsing pressure and supports shrub growth to heights that are conducive for beaver activity (Bilyeu et al., 2008; Contento, 2021; Marshall et al., 2013). Outside of the enclosure, shrubs were stunted by repeated ungulate browsing, suggesting that without the protection of the enclosure fencing, the area may not be able to support beaver reestablishment, as they require taller shrubs for food and building activities (Gibson & Olden, 2014; Boyle & Owens, 2007; Baker et al., 2005; Contento, 2021).

Species with Mean-C values of 4-6 typically are common species that form the foundation of many ecosystems (Taft et al., 1997). This suggests that the shrub community has been relatively resilient to reduced beaver activity in the valley, albeit at reduced densities, and with appropriate restoration measures may be able to be restored to its historic state. Restoration thresholds based on Mean-C values indicate that landscapes with values above 3.5 retain sufficient ecological

integrity to support successful restoration (Wilhelm and Masters, 1995, as cited by Rocchio, 2006). However, because these thresholds were developed for wetlands in the Midwest, further research is needed to determine whether they apply to the Southern Rocky Mountains. If these thresholds are consistent across regions, then communities surrounding historic dams, which had a Mean-C of 4.1, are more likely to experience successful restoration compared to other areas of the valley.

The evidence presented in this study suggests that historic, off-channel beaver dams are acting as a refuge for higher quality, wetland vegetative communities. Land managers should consider incorporating these structures into future restoration projects to increase project success and ensure efficient use of project funding. Exclosures have been shown to be effective for riparian shrub establishment and growth (Bilyeu et al., 2008; Marshall et al., 2013), incorporating these historic dams into future exclosures could increase the speed of successful restoration. By reducing ungulate browsing, shrub communities surrounding these historic dams will be able to reach the necessary heights for successful restoration, and the higher soil saturation and local water table around the dams may increase the rate of shrub growth as these individuals are not water limited. Additionally, these historic dams can act as seed sources and increase the rate of establishment for these communities.

Future research should focus on establishing a methodology for evaluating the viability of historic dams for restoration. This methodology, paired with existing exclosure techniques, will increase project success and reduce unnecessary spending by prioritizing historic dams that have higher quality vegetative communities associated with them. Since these historic dams are benefiting wetland communities, Beaver Pond Analogs (BPAs) could be explored as restoration tools in disturbed riparian areas where historic dams are no longer intact or present. Additionally, this study was conducted in a single montane riparian valley. Replicating this study in other locations

with varying levels of beaver and exclosure presence would create a more robust dataset, ensuring the consistency of patterns, and increase the generalizability of the findings.

Historic land management impacts on beaver habitat

Shrub cover was highest and dominated by taller classes in the active beaver floodplain with low farming intensity, aligning with the hypothesis that exclosures and lower farming would promote higher cover. However, shrub cover in historic beaver landscapes did not differ significantly between low and high intensities, contrary to expectations. Herbaceous cover was greater in historic beaver landscapes with high farming intensity than in active and historic landscapes with low farming, supporting the proposed hypothesis. In contrast to initial expectations, historic farming intensity did not influence shrub species richness, WIS and Mean-C values for both the shrub and herbaceous layers.

Globally, wetlands and riparian systems have experienced major land-use alterations to support agriculture or grazing practices throughout human history (Blann et al., 2009; Burkett & Kusler, 2000; Xu et al., 2019). In the Western U.S., these systems have undergone several modifications, including wetland draining, vegetation removal, and water diversions (Andrews, 2011; Charnley et al., 2020; Freilich et al., 2003). Wetlands were drained to access the fertile soil, causing widespread habitat loss (Blann et al., 2009; Charnley et al., 2020). Overgrazing has caused alterations to vegetation structure and composition, favoring the replacement of native herbaceous species with introduced grasses (Poff et al., 2011; Freilich et al., 2003). Soil compaction from cattle and other domestic ungulates caused alterations to vegetation structure and composition and in severe cases even caused de-vegetation within riparian systems, leading to erosion and increased incision rates (Ohmart, 1996; Poff et al., 2011). These landscape alterations resulted in an ecosystem

shift from diverse, beaver-wetland complexes with high heterogeneity, to homogenous hay meadows with a single-stream riparian system (Freilich et al., 2003; Blann et al., 2009).

The impacts of historic farming within the study area are still prevalent today. Portions of the study area that experienced higher levels of farming were still dominated by herbaceous species (Figure 20). *A. pratensis* was the most observed species in these areas (Table B2), a relic of farming and haying activities from the 1800s. These communities were comprised of a mix of disturbance-tolerant native and non-native species. Observationally, shrub communities were less present on these landscapes compared to low farming areas, a pattern that is supported by previous research completed in the study area (Contento, 2021). The only location that had taller shrubs and higher cover values was the active beaver landscape within the enclosure, indicating, again, that enclosure fencing provides the necessary protection to support increased shrub growth (Kay & Bartos, 2000; Brookshire et al., 2002; Nopp-Mayr et al., 2024). This study, along with the findings presented by Contento (2021), highlight the long-lasting impacts of historic farming activities when they are left to passive restoration. The agricultural changes imparted to the landscape have led to homogenized communities dominated by generalist herbaceous species with minimal shrub cover that is reduced in stature (Blann et al., 2009; Freilich et al., 2003; Burcham, 1981; Baker et al., 2005; Poff et al., 2011; Small et al., 2016; Kauffman et al., 2022).

Management efforts are currently focused on reestablishing healthy riparian shrub communities and beaver populations. However, land modifications associated with historic agricultural impacts more than just the vegetative community (Poff et al., 2011; Freilich et al., 2003; Ohmart, 1996). Understanding the extent of changes to soil nutrient cycling, compaction, and soil microbiota should be explored, as these factors may limit vegetative restoration (Bhaduri et al., 2022; Coban et al., 2022; Gaertig et al., 2002; Keller et al., 2021). Understanding how these factors influence the current and future vegetative community can provide insights on the correct restoration

pathway to take for reestablishing wetland shrub communities, supporting more successful beaver reestablishment.

It's important to note that this study prioritized areas with visible beaver habitation (historic or current) rather than the extent of historical agricultural impacts. As a result, these findings do not fully capture the broader effects of historic farming on vegetative communities across the landscape. Future research should focus on better understanding the successional pathway of abandoned agricultural fields by focusing more on areas that were farmed, regardless of shrub presence, and explore potential confounding factors that may reduce restoration potential. Nonetheless, the results offer insights into how historic agriculture and beaver activity influence vegetation, though they should be cautiously interpreted when applied more broadly.



Figure. 20 Aerial photo of the Holzworth historic ranching site in 1965, marked by a star. Ranching impacts can be seen in the photo, where dominant vegetation are mostly comprised of homogenous herbaceous species to the south of the site. Drainage tiling is present within the hay fields. Vegetation north of the Holzworth access road was more heterogeneous, with several beaver dams and a large population of willow and riparian shrubs [Photo courtesy of RMNP].

Impacts of distance from the river on beaver habitat

Vegetative composition patterns across the study area supported several hypotheses regarding changes as distance from the river increased. Total shrub cover and species richness declined in plots farther from the river, consistent with the hypotheses. However, shrub WIS and Mean-C, herbaceous cover, and herbaceous Mean-C values did not change significantly with

distance, contrary to expectations. Herbaceous WIS values were unaffected by distance alone, although standing water cover had a significant effect on herbaceous WIS values in the third plot, indicating that herbaceous composition there was more influenced by water availability.

The loss of beavers in riparian systems can cause cascading effects on the landscape. When beaver presence declines, dams tend to degrade and breach, causing the ponds to drain. Reductions in ponded water results in a shift from multithreaded wetland complexes to single threaded stream systems, causing rivers to incise, lowering the water table, and disconnecting it from the floodplain (Scamardo et al., 2022; Škarpich et al., 2016; Wohl, 2021). River incision has drastic effects on the surrounding vegetation, constricting riparian vegetation to the river corridor, therefore reducing overall cover. This causes a shift to mesic and upland communities and reduces landscape heterogeneity (Pollock et al., 2014; Škarpich et al., 2016).

These findings emphasize the critical role that proximity to the river plays in shaping shrub community cover and composition within incised floodplain environments. Access to shallow groundwater plays a large role in determining shrub distribution in mountain valleys (Lite & Stromberg, 2005; Škarpich et al., 2016; Stromberg et al., 2013). In the study area, shrub cover and richness decreased in plots 20 – 40 m from the river’s edge, suggesting that riparian shrubs may not have access to the water table further away from the river and that shrubs in the study area rely on river-associated water tables and propagule dispersal mechanisms. Similar patterns have been noted in disturbed wetland valleys, where wetland shrubs are often restricted to river edges with accessible groundwater (Lite et al., 2005; Škarpich et al., 2016; Johaneman et al., 2023).

Previous studies found that WIS values for both herbaceous and shrub communities shift as distance increases from the river channel. In these studies, vegetation shifted from wetland adapted species close to the river, to xeric and upland communities as distance increased and water tables

dropped (Lite et al., 2005; Škarpich et al., 2016). While I did not see the same patterns in our plant communities, both shrub and herbaceous WIS values displayed a marginal trend showing an increase in WIS by 40 m from the river, this potentially reflects patterns like those in the literature. Future research should determine if these patterns remain true to the study area. Herbaceous plants also showed a strong interaction between standing water and the presence of wetter-adapted species in the farthest plot. Herbaceous and shallow-rooted plants have more nuanced responses to water availability, and can be strongly influenced by soil saturation rather than access to the water table (Lite et al., 2005). Lite et al. (2005) found that herbaceous plants shifted towards wetter communities after monsoonal rains, regardless of distance from the river. Additionally, reductions in surface water has been seen to reduce the presence of wetland-adapted herbaceous species (Stromberg et al., 2013). The patterns observed in previous studies could account for the strong response of wetter herbaceous communities to an increase in surface water at 40 meters from the river. Riparian shrub's ability to extend roots to follow a lowering water table may impart some amount of resilience to river incision and may explain the lack of significant findings (Bau' et al., 2021; Naumburg et al., 2005). Additionally, previous research studied vegetational changes across the width of entire floodplains, whereas I did not. Extending transect lengths may uncover similar vegetational patterns and should be studied further.

Land managers should consider reducing river incision, as this can increase the success of restoration efforts focused on increasing riparian shrub cover. Without addressing incision impacts, riparian shrubs may not be able to be restored far from the river's edge. Including off-channel historic dams into exclosure fencing may be able to mitigate some of the water table disconnect from river incision, supporting increased shrub growth and heterogeneity, but these are localized areas and may not support growth far from the pond. Beaver Dam Analogs (BDAs) have been used in similar restoration projects and have shown promise in restoring riparian connectivity (Bouwes et al., 2016;

Davee et al., 2017; Pollock et al., 2014; Wolf, 2023) . Employing a combination of enclosure fencing around both small streams and historic beaver ponds, as well as implementing BDAs to increase riparian connectivity, may hasten restoration time and improve landscape heterogeneity by increasing wetland communities.

Future research should focus on determining the best methodology for prioritizing high impact areas for restoring riparian connectivity and wetland communities. Determining water table depth thresholds can improve restoration success by setting distinct goals. For example, Lite and Stromberg (2005) determined that native *Populus* and *Salix* communities could not survive in areas where water tables were more than 2.6 meters deep. Supporting this, several studies found that water tables more than 1m deep reduced the growth of riparian shrubs (Bilyeu et al., 2008; Marshall et al., 2013; Zeigenfuss et al., 2002). Determining vegetation patterns in relation to these thresholds could improve restoration success by determining areas where water tables are lower than threshold levels, allowing for prioritization of sites.

V. Management Recommendations

Historic dams and ponds are underutilized structures currently on the landscape that can work in compliment to the enclosure fencing and BDA work that is currently being implemented through the Kawuneeche Valley Restoration Collaborative (KVRC). Historic beaver dams and ponds support similar shrub cover to that inside of the enclosure fencing, albeit of shorter stature due to ungulate browsing. Ponds and dams also support herbaceous communities that are comprised of more wetland-adapted and less non-native species than those near the river corridor. Making sure to include these legacy structures in future or existing fencing could expedite restoration by providing access to seed and propagule sources and by increasing the initial heterogeneity of the restoration

area. Future management should prioritize developing a methodology to select historic dams based on feasibility of inclusion in an enclosure and the quality of the surrounding vegetative community.

Historic agriculture has significantly altered the landscape, and its effects are still seen today in the form of reduced shrub cover and homogenized plant communities. While some historic dams are still present in Kawuneeche Valley, many are restricted to the edge of the valley or do not retain water throughout the growing season. Such dams may not provide many benefits to restoration projects in the central valley. In this situation, implementing Beaver Pond Analogs (BPAs), depressional wetlands mimicking beaver ponds, paired with vegetation management can increase the heterogeneity of the landscape and support a healthier and denser riparian shrub community. Dams should closely mimic off-channel beaver ponds, so depth, nutrient cycling and storage, and microtopographic changes should be identified in historic ponds. Methods should also be established to monitor the success of wetland vegetation establishment in these locations.

Restoration projects that increase the heterogeneity of the landscape tend to have higher success rates. By utilizing or imitating the legacy structures left by beavers, success of current and future restoration projects can be increased while limiting additional costs. While implementing BPAs will add complexity, they may be necessary tools to increase the heterogeneity and improve the wetland community within historic agricultural areas of the Kawuneeche Valley.

VI. Conclusion

The findings presented in this study emphasize the critical role that historic beaver structures play in shaping and sustaining montane riparian ecosystems. Even after years of abandonment, these structures support wetland-adapted vegetation and provide refuge for native shrub and herbaceous communities in a disturbed, uniform landscape. The sustained hydrological effects

these dams provide mitigate the impact of river incision and historic land-use alterations by acting as isolated islands of wetland communities and providing some heterogeneity in an otherwise homogenous landscape. Historic beaver dams may provide beneficial attributes for restoration efforts. Including these dams in exclosure fencing can increase shrub growth and seed dispersal, increasing overall ecosystem resilience. However, the impacts of historic ranching and other anthropogenic disturbances can pose challenges to restoration, as these activities have homogenized much of the landscape, resulting in areas of reduced shrub cover dominated by non-native grasses. Future efforts should focus on integrating historic beaver dams into management strategies and employing a combination of restoration activities, such as exclosure fencing and BDAs, to improve restoration success. Further research into vegetative quality and hydrological thresholds will improve restoration methodologies and aid in prioritizing high-impact sites. By leveraging the ecological benefits of historic beaver dams already on the landscape, land managers can improve restoration success and contribute to the long-term resilience of montane riparian systems.

REFERENCES

- Andrews, T. G. (2011). *An Environmental History of the Kawuneeche Valley and the Headwaters of the Colorado River, Rocky Mountain National Park*. The National Park Service.
- Atkins, D. F. (1976). *Grand River Ditch (National Register of Historic Places Inventory—Nomination Form)*. National Park Service. <https://npshistory.com/publications/romo/nr-grand-river-ditch.pdf>
- Aznar, J.-C., & Desrochers, A. (2008). Building for the future: Abandoned beaver ponds promote bird diversity. *Écoscience*, *15*(2), 250–257.
- Bailey, D. R., Dittbrenner, B. J., & Yocom, K. P. (2019). Reintegrating the North American beaver (*Castor canadensis*) in the urban landscape. *WIREs Water*, *6*(1), e1323. <https://doi.org/10.1002/wat2.1323>
- Baker, B. W., & Cade, B. S. (1995). Predicting Biomass of Beaver Food from Willow Stem Diameters. *Journal of Range Management*, *48*(4), 322. <https://doi.org/10.2307/4002484>
- Baker, B. W., Ducharme, H. C., Mitchell, D. C. S., Stanley, T. R., & Peinetti, H. R. (2004). Why aren't there more beaver in Rocky Mountain National Park? *Proceedings of the Annual Conference of the Colorado Riparian Association*, *17*, 85–90.
- Baker, B. W., Ducharme, H. C., Mitchell, D. C. S., Stanley, T. R., & Peinetti, H. R. (2005). INTERACTION OF BEAVER AND ELK HERBIVORY REDUCES STANDING CROP OF WILLOW. *Ecological Applications*, *15*(1), 110–118. <https://doi.org/10.1890/03-5237>
- Baker, B. W., & Hill, E. P. (2003). Beaver (*Castor canadensis*). In *Wild Mammals of North America: Biology, management, and conservation* (2nd ed., pp. 288–310). Johns Hopkins University Press.

- Bau, V., Borthwick, A. G. L., & Perona, P. (2021). Plant Roots Steer Resilience to Perturbation of River Floodplains. *Geophysical Research Letters*, *48*(9), e2021GL092388.
<https://doi.org/10.1029/2021GL092388>
- Bhaduri, D., Sihi, D., Bhowmik, A., Verma, B. C., Munda, S., & Dari, B. (2022). A review on effective soil health bio-indicators for ecosystem restoration and sustainability. *Frontiers in Microbiology*, *13*. <https://doi.org/10.3389/fmicb.2022.938481>
- Bilyeu, D. M., Cooper, D. J., & Hobbs, N. T. (2008). Water Tables Constrain Height Recovery of Willow on Yellowstone's Northern Range. *Ecological Applications*, *18*(1), 80–92.
<https://doi.org/10.1890/07-0212.1>
- Blann, K. L., Anderson, J. L., Sands, G. R., & Vondracek, B. (2009). Effects of Agricultural Drainage on Aquatic Ecosystems: A Review. *Critical Reviews in Environmental Science and Technology*, *39*(11), 909–1001. <https://doi.org/10.1080/10643380801977966>
- Bouwes, N., Weber, N., Jordan, C. E., Saunders, W. C., Tattam, I. A., Volk, C., Wheaton, J. M., & Pollock, M. M. (2016). Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). *Scientific Reports*, *6*(1), 28581. <https://doi.org/10.1038/srep28581>
- Boyle, S., & Owens, S. (2007). *North American Beaver (Castor canadensis): A Technical Conservation Assessment*. BIO-Logic Environmental.
- Brady, A. (2022, December 1). *How Beavers Shaped America, from Capitalism to Climate Change*. Scientific American. <https://doi.org/10.1038/scientificamerican1222-74>
- Brazier, R. E., Puttock, A., Graham, H. A., Auster, R. E., Davies, K. H., & Brown, C. M. L. (2021). Beaver: Nature's ecosystem engineers. *WIREs Water*, *8*(1), e1494.
<https://doi.org/10.1002/wat2.1494>

- Brookshire, J. E., Kauffman, B. J., Lytjen, D., & Otting, N. (2002). Cumulative effects of wild ungulate and livestock herbivory on riparian willows. *Oecologia*, 132(4), 559–566.
<https://doi.org/10.1007/s00442-002-1007-4>
- Brown, S. T., & Fouty, S. (2011). Beaver Wetlands. *Lakeline*, 34–38.
- Burcham, L. T. (1981). California Rangelands in Historical Perspective. *Rangelands*, 3(3).
- Burkett, V., & Kusler, J. (2000). Climate Change: Potential Impacts and Interactions in Wetlands of the United States¹. *JAWRA Journal of the American Water Resources Association*, 36(2), 313–320. <https://doi.org/10.1111/j.1752-1688.2000.tb04270.x>
- Campbell-Palmer, R., Puttock, A., Wilson, K. A., Leow-Dyke, A., Graham, H. A., Gaywood, M. J., & Brazier, R. E. (2021). Using field sign surveys to estimate spatial distribution and territory dynamics following reintroduction of the Eurasian beaver to British river catchments. *River Research and Applications*, 37(3), 343–357. <https://doi.org/10.1002/rra.3755>
- Charnley, S., Gosnell, H., Davee, R., & Abrams, J. (2020). Ranchers and Beavers: Understanding the Human Dimensions of Beaver-Related Stream Restoration on Western Rangelands☆. *Rangeland Ecology and Management*, 73(5), 712–723.
<https://doi.org/10.1016/j.rama.2020.04.008>
- Coban, O., De Deyn, G. B., & Van Der Ploeg, M. (2022). Soil microbiota as game-changers in restoration of degraded lands. *Science*, 375(6584), abe0725.
<https://doi.org/10.1126/science.abe0725>
- Colorado State University. (n.d.). *Grand River Ditch*. CSU - Public and Environmental History Center. Retrieved January 9, 2025, from https://pehc.colostate.edu/digital_projects/dp/poudre-river/moving-storing/ditches-dams-diversions/grand-river-ditch/

- Contento, T. E. (2021). *WILLOW GROWTH RESPONSE TO ALTERED DISTURBANCE REGIMES IN ROCKY MOUNTAIN NATIONAL PARK: HERBIVORY, WATER LEVELS, AND HAY PRODUCTION*. Colorado State University.
- Crane, A., December, K., Dowker, T., & Skowronek, L. (2022). *Evaluation of Competitive Moose-Beaver Herbivory on Isle Royale National Park*. <https://doi.org/10.7302/4336>
- Davee, R., Charnley, S., & Gosnell, H. (2017). *Silvies Valley Ranch, Oregon: Using Artificial Beaver Dams to Restore Incised Streams*.
- Dittbrenner, B. J., Pollock, M. M., Schilling, J. W., Olden, J. D., Lawler, J. J., & Torgersen, C. E. (2018). Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation. *PLOS ONE*, *13*(2), e0192538. <https://doi.org/10.1371/journal.pone.0192538>
- Fedyń, I., Przepióra, F., Sobociński, W., Wyka, J., & Ciach, M. (2022). Eurasian beaver – A semi-aquatic ecosystem engineer rearranges the assemblage of terrestrial mammals in winter. *Science of The Total Environment*, *831*, 154919. <https://doi.org/10.1016/j.scitotenv.2022.154919>
- Feinstein, K. (2006). *A brief history of the beaver trade*. Fashionable Felted Fur: The Beaver Hat in 17th Century English Society. <https://humwp.ucsc.edu/cwh/feinstein/A%20brief%20history%20of%20the%20beaver%20trade.html>
- Fountain, S. M. (2014). Ranchers' Friend and Farmers' Foe: Reshaping Nature with Beaver Reintroduction in California. *Environmental History*, *19*(2), 187–430. <https://doi.org/10.1093/envhis/emu003>

- Freilich, J. E., Emlen, J. M., Duda, J. J., Freeman, D. C., & Cafaro, P. J. (2003). Ecological Effects of Ranching: A Six-Point Critique. *BioScience*, 53(8), 759–765. [https://doi.org/10.1641/0006-3568\(2003\)053\[0759:EEORAS\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0759:EEORAS]2.0.CO;2)
- Gaertig, T., Schack-Kirchner, H., Hildebrand, E. E., & Wilpert, K. v. (2002). The impact of soil aeration on oak decline in southwestern Germany. *Forest Ecology and Management*, 159(1), 15–25. [https://doi.org/10.1016/S0378-1127\(01\)00706-X](https://doi.org/10.1016/S0378-1127(01)00706-X)
- Gibson, P. P., & Olden, J. D. (2014). Ecology, management, and conservation implications of North American beaver (*Castor canadensis*) in dryland streams. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24(3), 391–409. <https://doi.org/10.1002/aqc.2432>
- Graham, H. A., Puttock, A., Chant, J., Elliott, M., Campbell-Palmer, R., Anderson, K., & Brazier, R. E. (2022). Monitoring, modelling and managing beaver (*Castor fiber*) populations in the River Otter catchment, Great Britain. *Ecological Solutions and Evidence*, 3(3), e12168. <https://doi.org/10.1002/2688-8319.12168>
- Hood, G. A., & Bayley, S. E. (2009). A comparison of riparian plant community response to herbivory by beavers (*Castor canadensis*) and ungulates in Canada's boreal mixed-wood forest. *Forest Ecology and Management*, 258(9), 1979–1989. <https://doi.org/10.1016/j.foreco.2009.07.052>
- Hood, G. A., McIntosh, A. C. S., & Hvenegaard, G. T. (2021). Ecological Compromise: Can Alternative Beaver Management Maintain Aquatic Macroinvertebrate Biodiversity? *Wetlands*, 41(8), 1–17. <https://doi.org/10.1007/s13157-021-01494-7>
- Hossack, B. R., Gould, W. R., Patla, D. A., Muths, E., Daley, R., Legg, K., & Corn, P. S. (2015). Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. *Biological Conservation*, 187, 260–269. <https://doi.org/10.1016/j.biocon.2015.05.005>

- Hultine, K. R., Bush, S. E., & Ehleringer, J. R. (2010). Ecophysiology of riparian cottonwood and willow before, during, and after two years of soil water removal. *Ecological Applications: A Publication of the Ecological Society of America*, 20(2), 347–361.
<https://doi.org/10.1890/09-0492.1>
- Johaneman, T. M., Lininger, K. B., Schook, D. M., Pitlick, J., & Martin, M. (2023). The Influence of Knickpoint Development and Channel Incision on Riparian Vegetation in Semi-Arid River Corridors. *Water Resources Research*, 59(10), e2023WR034872.
<https://doi.org/10.1029/2023WR034872>
- Johnston, C. A. (2017). Legacy of Beaver–Human Interaction. In C. A. Johnston (Ed.), *Beavers: Boreal Ecosystem Engineers* (pp. 1–11). Springer International Publishing.
https://doi.org/10.1007/978-3-319-61533-2_1
- Kauffman, J. B., Coleman, G., Otting, N., Lytjen, D., Nagy, D., & Beschta, R. L. (2022). Riparian vegetation composition and diversity shows resilience following cessation of livestock grazing in northeastern Oregon, USA. *PLOS ONE*, 17(1), e0250136.
<https://doi.org/10.1371/journal.pone.0250136>
- Kay, C. E., & Bartos, D. L. (2000). Ungulate herbivory on Utah aspen: Assessment of longterm exclosures. *JOURNAL OF RANGE MANAGEMENT*, 53(2).
- Keller, T., Colombi, T., Ruiz, S., Schymanski, S. J., Weisskopf, P., Koestel, J., Sommer, M., Stadelmann, V., Breitenstein, D., Kirchgessner, N., Walter, A., & Or, D. (2021). Soil structure recovery following compaction: Short-term evolution of soil physical properties in a loamy soil. *Soil Science Society of America Journal*, 85(4), 1002–1020.
<https://doi.org/10.1002/saj2.20240>

- Kuhnlein, H. V., & Humphries, M. M. (n.d.). *Beaver*. Traditional Animal Foods of Indigenous Peoples of Northern North America - Animals - Mammals - Furbearers. Retrieved November 1, 2023, from <http://traditionalanimalfoods.org/mammals/furbearers/page.aspx?id=6142>
- Levine, R., & Meyer, G. A. (2019). Beaver-generated disturbance extends beyond active dam sites to enhance stream morphodynamics and riparian plant recruitment. *Scientific Reports*, 9(1), Article 1. <https://doi.org/10.1038/s41598-019-44381-2>
- Lite, S. J., Bagstad, K. J., & Stromberg, J. C. (2005). Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA. *Journal of Arid Environments*, 63(4), 785–813. <https://doi.org/10.1016/j.jaridenv.2005.03.026>
- Lite, S. J., & Stromberg, J. C. (2005). Surface water and ground-water thresholds for maintaining Populus–Salix forests, San Pedro River, Arizona. *Biological Conservation*, 125(2), 153–167. <https://doi.org/10.1016/j.biocon.2005.01.020>
- Londe, D. W., Dwayne Elmore, R., Davis, C. A., Fuhlendorf, S. D., Luttbeg, B., & Hovick, T. J. (2020). Structural and compositional heterogeneity influences the thermal environment across multiple scales. *Ecosphere*, 11(11), e03290. <https://doi.org/10.1002/ecs2.3290>
- Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, 16(s1), 106–115. <https://doi.org/10.1111/ele.12073>
- Malanson, G. P., & Cramer, B. E. (1999). Landscape Heterogeneity, Connectivity, and Critical Landscapes for Conservation. *Diversity and Distributions*, 5(1/2), 27–39.
- Marshall, K. N., Hobbs, N. T., & Cooper, D. J. (2013). Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. *Proceedings. Biological Sciences*, 280(1756), 20122977. <https://doi.org/10.1098/rspb.2012.2977>

- Mathisen, K. M., Milner, J. M., & Skarpe, C. (2017). Moose–tree interactions: Rebrowsing is common across tree species. *BMC Ecology*, *17*, 12. <https://doi.org/10.1186/s12898-017-0122-3>
- Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of North American Streams by Beaver. *Bioscience*, *38*(11), 753–762. <https://doi.org/10.2307/1310784>
- National Park Service, [NPS]. (n.d.). *Brief Park History—Rocky Mountain National Park*. National Park Service. Retrieved November 6, 2023, from <https://www.nps.gov/romo/learn/historyculture/brief.htm>
- Naumburg, E., Mata-gonzalez, R., Hunter, R. G., Mclendon, T., & Martin, D. W. (2005). Phreatophytic Vegetation and Groundwater Fluctuations: A Review of Current Research and Application of Ecosystem Response Modeling with an Emphasis on Great Basin Vegetation. *Environmental Management*, *35*(6), 726–740. <https://doi.org/10.1007/s00267-004-0194-7>
- Neff, D. J. (1957). Ecological Effects of Beaver Habitat Abandonment in the Colorado Rockies. *The Journal of Wildlife Management*, *21*(1), 80–84. <https://doi.org/10.2307/3797684>
- Nopp-Mayr, U., Lechner, W., Reimoser, S., & Reimoser, F. (2024). Long-term surveys of ungulates' effects on tree and shrub species in mountainous forests –outcomes and potential limits. *Environmental Management*. <https://doi.org/10.1007/s00267-024-02063-4>
- NPS - RMNP. (2024, September 13). *Beaver Occupancy in Rocky Mountain National Park (U.S. National Park Service)*. National Park Service. <https://www.nps.gov/articles/beaver-occupancy-in-rocky-mountain-national-park.htm>
- NPS- RMNP. (n.d.). *All About Weather—Rocky Mountain National Park (U.S. National Park Service)*. Rocky Mountain National Park. Retrieved January 8, 2025, from <https://www.nps.gov/romo/planyourvisit/all-about-weather.htm>

- Nummi, P., & Holopainen, S. (2014). Whole-community facilitation by beaver: Ecosystem engineer increases waterbird diversity. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 24(5), 623–633. <https://doi.org/10.1002/aqc.2437>
- Nummi, P., & Kuuluvainen, T. (2013). Forest disturbance by an ecosystem engineer: Beaver in boreal forest landscapes. *Boreal Environment Research*, 18, 13–24.
- Nummi, P., Liao, W., Huet, O., Scarpulla, E., & Sundell, J. (2019). The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. *Global Ecology and Conservation*, 20, e00701. <https://doi.org/10.1016/j.gecco.2019.e00701>
- Nummi, P., Liao, W., van der Schoor, J., & Loehr, J. (2021). Beaver creates early successional hotspots for water beetles. *Biodiversity and Conservation*, 30(10), 2655–2670. <https://doi.org/10.1007/s10531-021-02213-8>
- Ohmart, R. (1996). Chapter 16: Historical and Present Impacts of Livestock Grazing on Fish and Wildlife Resources in Western Riparian Habitats. In *Rangeland Wildlife*. The Society for Range Management.
- Peinetti, H. R., Baker, B. W., & Coughenour, M. B. (2009). Simulation modeling to understand how selective foraging by beaver can drive the structure and function of a willow community. *Ecological Modelling*, 220(7), 998–1012. <https://doi.org/10.1016/j.ecolmodel.2009.01.009>
- Poff, B., Koestner, K. A., Neary, D. G., & Henderson, V. (2011). Threats to Riparian Ecosystems in Western North America: An Analysis of Existing Literature. *JAWRA Journal of the American Water Resources Association*, 47(6), 1241–1254. <https://doi.org/10.1111/j.1752-1688.2011.00571.x>
- Poliquin, R. (2015). *Beaver*. Reaktion Books.

- Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N., & Volk, C. (2014). Using Beaver Dams to Restore Incised Stream Ecosystems. *BioScience*, 64(4), 279–290. <https://doi.org/10.1093/biosci/biu036>
- Pollock, M., Pess, G., Beechie, T., & Montgomery, D. (2004). The Importance of Beaver Ponds to Coho Salmon Production in the Stillaguamish River Basin, Washington, USA. *North American Journal of Fisheries Management*, 24, 749–760. <https://doi.org/10.1577/M03-156.1>
- Reeve, H. (2016, August 1). *Beaver* [Text]. Colorado Encyclopedia. <https://coloradoencyclopedia.org/article/beaver>
- Rocchio, J. (2006). *Rocky Mountain Alpine-Montane Wet Meadow Ecological System, Ecological Integrity Assessment*. Colorado Natural Heritage Program.
- Rosell, F., Bozsér, O., Collen, P., & Parker, H. (2005). Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, 35(3–4), 248–276. <https://doi.org/10.1111/j.1365-2907.2005.00067.x>
- Scamardo, J. E., Marshall, S., & Wohl, E. (2022). Estimating widespread beaver dam loss: Habitat decline and surface storage loss at a regional scale. *Ecosphere*, 13(3). <https://doi.org/10.1002/ecs2.3962>
- Schindler, M., Jungmann, L., Donath, T. W., & Ludewig, K. (2020). Influence of flooding duration and aeration on saplings of ten hardwood floodplain forest species. *PLoS ONE*, 15(6), e0234936. <https://doi.org/10.1371/journal.pone.0234936>
- Škarpich, V., Horáček, M., Galia, T., Kapustová, V., & Šála, V. (2016). The effects of river patterns on riparian vegetation: A comparison of anabranching and single-thread incised channels. *Moravian Geographical Reports*, 24(3), 24–31. <https://doi.org/10.1515/mgr-2016-0014>

- Small, B. A., Frey, J. K., & Gard, C. C. (2016). Livestock grazing limits beaver restoration in northern New Mexico. *Restoration Ecology*, 24(5), 646–655. <https://doi.org/10.1111/rec.12364>
- Smith, P., Doyle, G., & Lemly, J. (2020). *Revision of Colorado's Floristic Quality Assessment Indices*. Colorado Natural Heritage Program.
- Stein, A., & Kreft, H. (2015). Terminology and quantification of environmental heterogeneity in species-richness research. *Biological Reviews*, 90(3), 815–836. <https://doi.org/10.1111/brv.12135>
- Stromberg, J. C., McCluney, K. E., Dixon, M. D., & Meixner, T. (2013). Dryland Riparian Ecosystems in the American Southwest: Sensitivity and Resilience to Climatic Extremes. *Ecosystems*, 16(3), 411–415. <https://doi.org/10.1007/s10021-012-9606-3>
- Taft, J. B., Wilhelm, G. S., Ladd, D. M., & Masters, L. A. (1997). *FLORISTIC QUALITY ASSESSMENT FOR VEGETATION IN ILLINOIS A METHOD FOR ASSESSING VEGETATION INTEGRITY*.
- Tanismore, E. (2022). Rocky Mountain National Park: An Indigenous History. *Rocky Mountain Conservancy*. <https://rmconservancy.org/rocky-mountain-national-park-an-indigenous-history/>
- Tapper, S., & Reynolds, J. (1996). The wild fur trade: Historical and ecological perspectives. In V. J. Taylor & N. Dunstone (Eds.), *The Exploitation of Mammal Populations* (pp. 28–44). Springer Netherlands. https://doi.org/10.1007/978-94-009-1525-1_3
- U.S. Forest Service. (n.d.). *Nez Perce National Historic Trail—Nature & Science*. North American Beaver. Retrieved November 1, 2023, from <https://www.fs.usda.gov/wps/portal/fsinternet3/cs/detail/npnht/learningcenter/nature-science/>
- USFS. (n.d.). *Castor canadensis*. Retrieved November 13, 2023, from <https://www.fs.usda.gov/database/feis/animals/mammal/caca/all.html#2>

- Visty, J. (2008, January). *Effects of the Grand Ditch (U.S. National Park Service)*. National Park Service. <https://www.nps.gov/articles/effects-of-the-grand-ditch.htm>
- Westbrook, C. J. (2021). Beaver as agents of plant disturbance. In E. A. Johnson & K. Miyanishi (Eds.), *Plant Disturbance Ecology* (2nd ed., pp. 489–528). Academic Press. <https://doi.org/10.1016/B978-0-12-818813-2.00014-9>
- Westbrook, C. J., Cooper, D. J., & Baker, B. W. (2006). Beaver dams and overbank floods influence groundwater–surface water interactions of a Rocky Mountain riparian area. *Water Resources Research*, 42(6). <https://doi.org/10.1029/2005WR004560>
- Wohl, E. (2021). Legacy effects of loss of beavers in the continental United States. *Environmental Research Letters*, 16(2), 025010. <https://doi.org/10.1088/1748-9326/abd34e>
- Wolf, J. (2023). Analyzing the Impacts of Beaver Dam and Beaver Dam Analog Complexes to Stream Ecology Within the Intermountain West. *All Graduate Theses and Dissertations, Fall 2023 to Present*. <https://doi.org/10.26076/8178-3aac>
- Woods, S. W., MacDonald, L. H., & Westbrook, C. J. (2006). HYDROLOGIC INTERACTIONS BETWEEN AN ALLUVIAL FAN AND A SLOPE WETLAND IN THE CENTRAL ROCKY MOUNTAINS, USA. *Wetlands*, 26(1), 230–243. [https://doi.org/10.1672/0277-5212\(2006\)26\[230:HIBAAF\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2006)26[230:HIBAAF]2.0.CO;2)
- Woodward, C. (2022). *East Troublesome Fire Soil Burn Severity v1 (Version 1)* [Geospatial dataset]. <https://www.arcgis.com/sharing/rest/content/items/6425ccc20c5d492aa5d152786d46c2f7>
- Wright, J. P., Flecker, A. S., & Jones, C. G. (2003). LOCAL VS. LANDSCAPE CONTROLS ON PLANT SPECIES RICHNESS IN BEAVER MEADOWS. *Ecology*, 84(12), 3162–3173. <https://doi.org/10.1890/02-0598>

Wright, J. P., Jones, C. G., & Flecker, A. S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, 132(1), 96–101.

<https://doi.org/10.1007/s00442-002-0929-1>

Xu, T., Weng, B., Yan, D., Wang, K., Li, X., Bi, W., Li, M., Cheng, X., & Liu, Y. (2019). Wetlands of International Importance: Status, Threats, and Future Protection. *International Journal of Environmental Research and Public Health*, 16(10), Article 10.

<https://doi.org/10.3390/ijerph16101818>

Yarmey, N., & Hood, G. (2020). Resident Perceptions of Human–Beaver Conflict in a Rural Landscape in Alberta, Canada. *Human–Wildlife Interactions*, 14(3).

<https://doi.org/10.26077/0c80-ab0a>

Zeigenfuss, L. C., Singer, F. J., Williams, S. A., & Johnson, T. L. (2002). Influences of herbivory and water on willow in elk winter range. *Journal of Wildlife Management*, 66(3), 788–795.

<https://doi.org/10.2307/3803143>

APPENDIX A

Table A1. Shrub species observations by study location. Non-beaver floodplains are river associated surveys where beaver sign was not observed. Historic dams were abandoned, off channel beaver dams. Active beaver floodplains are river surveys within the enclosure, and historic beaver floodplains were associated with river surveys that had observed historic beaver sign. Floodplains are indicated as FP in the table.

Species	Location Type				Species	Location Type			
	Non-beaver FP	Historic Dam	Active Beaver FP	Historic Beaver FP		Non-beaver FP	Historic Dam	Active Beaver FP	Historic Beaver FP
<i>Alnus incana</i>	6	2	1	22	<i>Salix drummondiana</i>	10	6	3	77
<i>Arctostaphylos uva-ursi</i>	-	-	-	1	<i>Salix exigua</i>	-	-	1	-
<i>Betula glandulosa</i>	2	23	1	12	<i>Salix geyeriana</i>	3	8	4	66
<i>Dasiphora fruticosa</i>	5	16	1	32	<i>Salix irrorata</i>	-	-	-	2
<i>Juniperus communis</i>	-	-	-	6	<i>Salix lasiandra</i>	-	-	-	1
<i>Kalmia microphylla</i>	-	1	-	-	<i>Salix ligulifolia</i>	-	-	1	3
<i>Lonicera involucreta</i>	2	1	-	3	<i>Salix lucida</i>	-	-	-	1
<i>Mahonia repens</i>	-	-	-	1	<i>Salix lutea</i>	2	-	2	4
<i>Populus tremuloides</i>	-	-	-	1	<i>Salix melanopsis</i>	-	7	-	5
<i>Ribes inerme</i>	-	-	-	1	<i>Salix monticola</i>	11	15	1	100
<i>Rosa woodsii</i>	1	2	-	6	<i>Salix planifolia</i>	16	45	3	88
<i>Rubus deliciosus</i>	-	-	-	4	<i>Salix wolfii</i>	6	5	-	24
<i>Rubus idaeus</i>	-	-	-	1	<i>Shepherdia canadensis</i>	-	1	-	1

Species	Location Type				Species	Location Type			
	Non-beaver FP	Historic Dam	Active Beaver FP	Historic Beaver FP		Non-beaver FP	Historic Dam	Active Beaver FP	Historic Beaver FP
<i>Salix bebbiana</i>	1	2	1	14	<i>Vaccinium myrtillus</i>	-	2	-	7
<i>Salix boothii</i>	-	-	3	13	<i>Vaccinium scoparium</i>	-	-	-	2
<i>Salix brachycarpa</i>	-	-	-	1	Unknown	-	2	-	1

Table A2. Herbaceous species observations by study location. Non-beaver floodplains are river associated surveys where beaver sign was not observed. Historic dams were abandoned, off channel beaver dams. Active beaver floodplains are river surveys within an enclosure, and historic beaver floodplains were associated with river surveys that had observed historic beaver sign. Floodplains are indicated as FP in the table.

Species	Location Type				Species	Location Type			
	Non-beaver FP	Active Beaver FP	Historic Beaver FP	Historic Dam		Non-beaver FP	Active Beaver FP	Historic Beaver FP	Historic Dam
<i>Achillea millefolium</i>	1	1	12	-	<i>Galium boreale</i>	1	-	-	2
<i>Agrimonia sp.</i>	1	-	10	6	<i>Geranium richardsonii</i>	-	1	4	3
<i>Agrostis gigantea</i>	-	-	6	6	<i>Geum macrophyllum</i>	5	-	17	7
<i>Agrostis idahoensis</i>	-	-	1	-	<i>Glyceria sp.</i>	-	-	2	-
<i>Agrostis sp.</i>	2	-	-	3	<i>Glyceria striata</i>	3	-	1	-
<i>Alopecurus aequalis</i>	-	-	-	1	<i>Heracleum maximum</i>	-	-	3	1
<i>Alopecurus magellanicus</i>	-	-	-	1	<i>Juncus arcticus</i>	-	-	3	-
<i>Alopecurus pratensis</i>	20	-	119	1	<i>Juncus ensifolius</i>	4	-	-	-
<i>Anaphalis margaritacea</i>	-	-	1	-	<i>Juncus sp.</i>	1	-	5	-
<i>Angelica pinnata</i>	-	-	1	-	<i>Koeleria macrantha</i>	1	-	-	-
<i>Antennaria parvifolia</i>	-	-	4	-	<i>Ligusticum tenuifolium</i>	-	-	1	-
<i>Arnica cordifolia</i>	-	-	2	-	<i>Lupinus argenteus</i>	-	-	1	-
<i>Astragalus alpinus</i>	-	-	1	-	<i>Lupinus sp.</i>	-	-	1	-

Species	Location Type				Species	Location Type			
	Non-beaver FP	Active Beaver FP	Historic Beaver FP	Historic Dam		Non-beaver FP	Active Beaver FP	Historic Beaver FP	Historic Dam
<i>Astragalus flexuosus</i>	-	-	4	-	<i>Luzula parviflora</i>	-	-	1	-
<i>Astragalus sp.</i>	-	-	1	1	<i>Luzula sp.</i>	-	-	-	2
<i>Bromus inermis</i>	2	-	9	5	<i>Maianthemum racemosum</i>	-	-	5	-
<i>Calamagrostis canadensis</i>	19	2	95	47	<i>Maianthemum stellatum</i>	-	-	1	-
<i>Caltha leptosepala</i>	2	-	-	-	<i>Mertensia ciliata</i>	1	-	6	3
<i>Cardamine cordifolia</i>	1	-	1	-	<i>Myriophyllum sibiricum</i>	-	-	-	1
<i>Carex aquatilis</i>	28	4	102	42	<i>Oxytropis sp.</i>	1	-	-	-
<i>Carex aurea</i>	-	-	1	-	<i>Pedicularis groenlandica</i>	-	1	-	-
<i>Carex buxbaumii</i>	-	-	-	1	<i>Phalaris arundinacea</i>	5	-	32	3
<i>Carex egglestonii</i>	-	-	1	1	<i>Phleum pratense</i>	2	-	6	2
<i>Carex emoryi</i>	-	-	-	3	<i>Poa compressa</i>	-	-	1	-
<i>Carex nebrascensis</i>	-	-	-	3	<i>Poa palustris</i>	-	-	1	-
<i>Carex praegracilis</i>	-	-	1	-	<i>Poa pratensis</i>	6	2	39	14
<i>Carex sp.</i>	9	-	70	32	<i>Poa sp.</i>	1	1	38	9
<i>Carex utriculata</i>	13	1	46	31	<i>Polemonium foliosissimum</i>	-	-	-	1
<i>Chamerion angustifolium</i>	1	-	3	1	<i>Polemonium occidentale</i>	1	-	5	1

Species	Location Type				Species	Location Type			
	Non-beaver FP	Active Beaver FP	Historic Beaver FP	Historic Dam		Non-beaver FP	Active Beaver FP	Historic Beaver FP	Historic Dam
<i>Cirsium arvense</i>	3	-	26	13	<i>Potentilla pulcherrima</i>	6	-	11	-
<i>Cirsium clavatum</i>	-	-	1	-	<i>Potentilla sp.</i>	2	-	2	-
<i>Cirsium scariosum</i>	-	-	1	-	<i>Pseudoroegneria spicata</i>	1	-	3	-
<i>Cirsium sp.</i>	-	-	1	-	<i>Puccinellia nuttalliana</i>	-	-	-	2
<i>Cirsium vulgare</i>	-	-	1	-	<i>Pyrola asarifolia</i>	-	-	2	-
<i>Danthonia intermedia</i>	-	-	5	-	<i>Ranunculus gmelinii</i>	-	-	-	1
<i>Deschampsia cespitosa</i>	-	-	-	2	<i>Rhodiola rhodantha</i>	-	-	1	2
<i>Eleocharis sp.</i>	-	-	1	-	<i>Rhodiola sp.</i>	-	-	-	1
<i>Elymus elymoides</i>	-	-	-	1	<i>Senecio bigelovii</i>	1	-	7	6
<i>Elymus trachycaulus</i>	2	-	11	-	<i>Senecio hydrophilus</i>	1	-	4	2
<i>Epilobium hornemannii</i>	1	-	-	-	<i>Senecio sp.</i>	-	-	1	1
<i>Epilobium sp.</i>	-	-	-	1	<i>Senecio triangularis</i>	-	-	2	8
<i>Equisetum arvense</i>	7	3	50	10	<i>Solidago sp.</i>	-	1	3	-
<i>Equisetum variegatum</i>	-	-	2	-	<i>Spiranthes diluvialis</i>	-	-	-	1
<i>Erigeron glabellus</i>	-	-	1	3	<i>Taraxacum officinale</i>	12	4	127	9
<i>Erigeron sp.</i>	3	-	1	1	<i>Thalictrum dasycarpum</i>	-	1	3	4

Species	Location Type				Species	Location Type			
	Non-beaver FP	Active Beaver FP	Historic Beaver FP	Historic Dam		Non-beaver FP	Active Beaver FP	Historic Beaver FP	Historic Dam
<i>Eriogonum umbellatum</i>	1	-	1	-	<i>Trifolium pratense</i>	4	-	29	-
<i>Festuca idahoensis</i>	-	-	2	-	<i>Trifolium repens</i>	1	-	2	-
<i>Festuca sp.</i>	-	-	1	-	<i>Trifolium sp.</i>	1	3	11	1
<i>Fragaria virginiana</i>	11	2	123	14	Unknown	-	-	12	9

APPENDIX B

Table B1. Shrub species observations by farming intensity. High farming intensity areas are located in the southern portion of the Kawuneeche Valley, south of the Holzworth access road. The low farming intensity areas are located in the northern portion of the Kawuneeche Valley, north of the Holzworth access road.

Species	Farming Intensity		Species	Farming Intensity	
	High	Low		High	Low
<i>Alnus incana</i>	17	14	<i>Salix drummondiana</i>	67	29
<i>Arctostaphylos uva-ursi</i>	1	-	<i>Salix exigua</i>	-	1
<i>Betula glandulosa</i>	10	28	<i>Salix geyeriana</i>	40	41
<i>Dasiphora fruticosa</i>	29	25	<i>Salix irrorata</i>	1	1
<i>Juniperus communis</i>	5	1	<i>Salix lasiandra</i>	1	-
<i>Kalmia microphylla</i>	-	1	<i>Salix ligulifolia</i>	2	2
<i>Lonicera involucrata</i>	3	3	<i>Salix lucida</i>	1	-
<i>Mahonia repens</i>	1	-	<i>Salix lutea</i>	4	4
<i>Populus tremuloides</i>	1	-	<i>Salix melanopsis</i>	1	11
<i>Ribes inerme</i>	-	1	<i>Salix monticola</i>	70	57
<i>Rosa woodsii</i>	6	3	<i>Salix planifolia</i>	80	72
<i>Rubus deliciosus</i>	1	3	<i>Salix wolfii</i>	29	6
<i>Rubus idaeus</i>	-	1	<i>Shepherdia canadensis</i>	1	1
<i>Salix bebbiana</i>	4	14	<i>Vaccinium myrtillus</i>	4	5
<i>Salix boothii</i>	9	7	<i>Vaccinium scoparium</i>	2	-
<i>Salix brachycarpa</i>	-	1	Unknown	1	2

Table B2. Herbaceous species observations by farming intensity. High farming intensity areas are located in the southern portion of the Kawuneeche Valley, south of the Holzworth access road. The low farming intensity areas are located in the northern portion of the Kawuneeche Valley, north of the Holzworth access road.

Species	Location Type		Species	Location Type	
	High	Low		High	False
<i>Achillea millefolium</i>	7	7	<i>Galium boreale</i>	1	2
<i>Agrimonia sp.</i>	3	14	<i>Geranium richardsonii</i>	2	6
<i>Agrostis gigantea</i>	6	6	<i>Geum macrophyllum</i>	16	13
<i>Agrostis idahoensis</i>	1	-	<i>Glyceria sp.</i>	2	-
<i>Agrostis sp.</i>	2	3	<i>Glyceria striata</i>	4	-
<i>Alopecurus aequalis</i>	-	1	<i>Heracleum maximum</i>	1	3
<i>Alopecurus magellanicus</i>	-	1	<i>Juncus arcticus</i>	2	1
<i>Alopecurus pratensis</i>	134	6	<i>Juncus ensifolius</i>	4	-
<i>Anaphalis margaritacea</i>	-	1	<i>Juncus sp.</i>	6	-
<i>Angelica pinnata</i>	1	-	<i>Koeleria macrantha</i>	1	-
<i>Antennaria parvifolia</i>	3	1	<i>Ligusticum tenuifolium</i>	1	-
<i>Arnica cordifolia</i>	1	1	<i>Lupinus argenteus</i>	1	-
<i>Astragalus alpinus</i>	-	1	<i>Lupinus sp.</i>	1	-
<i>Astragalus flexuosus</i>	3	1	<i>Luzula parviflora</i>	-	1
<i>Astragalus sp.</i>	-	2	<i>Luzula sp.</i>	-	2
<i>Bromus inermis</i>	9	7	<i>Maianthemum racemosum</i>	3	2
<i>Calamagrostis canadensis</i>	90	73	<i>Maianthemum stellatum</i>	1	-
<i>Caltha leptosepala</i>	2	-	<i>Mertensia ciliata</i>	7	3
<i>Cardamine cordifolia</i>	1	1	<i>Myriophyllum sibiricum</i>	-	1
<i>Carex aquatilis</i>	107	69	<i>Oxytropis sp.</i>	1	-
<i>Carex aurea</i>	1	-	<i>Pedicularis groenlandica</i>	-	1
<i>Carex buxbaumii</i>	-	1	<i>Phalaris arundinacea</i>	27	13
<i>Carex egglestonii</i>	-	2	<i>Phleum pratense</i>	4	6
<i>Carex emoryi</i>	-	3	<i>Poa compressa</i>	1	-

Species	Location Type		Species	Location Type	
	High	Low		High	False
<i>Carex nebrascensis</i>	1	2	<i>Poa palustris</i>	1	-
<i>Carex praegracilis</i>	1	-	<i>Poa pratensis</i>	24	37
<i>Carex sp.</i>	23	88	<i>Poa sp.</i>	7	42
<i>Carex utriculata</i>	50	41	<i>Polemonium foliosissimum</i>	1	-
<i>Chamerion angustifolium</i>	4	1	<i>Polemonium occidentale</i>	4	3
<i>Cirsium arvense</i>	14	28	<i>Potentilla pulcherrima</i>	11	6
<i>Cirsium clavatum</i>	1	-	<i>Potentilla sp.</i>	3	1
<i>Cirsium scariosum</i>	1	-	<i>Pseudoroegneria spicata</i>	4	-
<i>Cirsium sp.</i>	-	1	<i>Puccinellia nuttalliana</i>	-	2
<i>Cirsium vulgare</i>	1	-	<i>Pyrola asarifolia</i>	-	2
<i>Danthonia intermedia</i>	5	-	<i>Ranunculus gmelinii</i>	-	1
<i>Deschampsia cespitosa</i>	-	2	<i>Rhodiola rhodantha</i>	-	3
<i>Eleocharis sp.</i>	1	-	<i>Rhodiola sp.</i>	-	1
<i>Elymus elymoides</i>	1	-	<i>Senecio bigelovii</i>	3	11
<i>Elymus trachycaulus</i>	10	3	<i>Senecio hydrophilus</i>	4	3
<i>Epilobium hornemannii</i>	1	-	<i>Senecio sp.</i>	-	2
<i>Epilobium sp.</i>	-	1	<i>Senecio triangularis</i>	-	10
<i>Equisetum arvense</i>	29	41	<i>Solidago sp.</i>	1	3
<i>Equisetum variegatum</i>	2	-	<i>Spiranthes diluvialis</i>	-	1
<i>Erigeron glabellus</i>	1	3	<i>Taraxacum officinale</i>	89	63
<i>Erigeron sp.</i>	4	1	<i>Thalictrum dasycarpum</i>	4	4
<i>Eriogonum umbellatum</i>	1	1	<i>Trifolium pratense</i>	28	5
<i>Festuca idahoensis</i>	2	-	<i>Trifolium repens</i>	-	3
<i>Festuca sp.</i>	1	-	<i>Trifolium sp.</i>	3	13
<i>Fragaria virginiana</i>	102	48	Unknown	4	17

APPENDIX C

Table C1. Shrub species observations as distance from the river increased. Only river survey data is included in this table. Plots were used as a proxy for distance, where the first plot was established at the start of the riverside vegetation (0 m), then the second plot was 20 m away, and the third was 40 m from the river's edge.

Species	Distance From River			Species	Distance From River		
	0 m	20 m	40 m		0 m	20 m	40 m
<i>Alnus incana</i>	27	1	1	<i>Salix exigua</i>	-	1	-
<i>Arctostaphylos uva-ursi</i>	1	-	-	<i>Salix geyeriana</i>	30	30	13
<i>Betula glandulosa</i>	3	6	6	<i>Salix irrorata</i>	2	-	-
<i>Dasiphora fruticosa</i>	13	16	9	<i>Salix lasiandra</i>	-	1	-
<i>Juniperus communis</i>	1	2	3	<i>Salix ligulifolia</i>	3	1	-
<i>Lonicera involucrata</i>	-	2	3	<i>Salix lucida</i>	-	1	-
<i>Mahonia repens</i>	-	-	1	<i>Salix lutea</i>	6	2	-
<i>Populus tremuloides</i>	-	-	1	<i>Salix melanopsis</i>	1	4	-
<i>Ribes inerme</i>	-	-	1	<i>Salix monticola</i>	57	30	25
<i>Rosa woodsii</i>	2	2	3	<i>Salix planifolia</i>	43	38	26
<i>Rubus deliciosus</i>	-	1	3	<i>Salix wolfii</i>	13	10	7
<i>Rubus idaeus</i>	-	-	1	<i>Shepherdia canadensis</i>	1	-	-
<i>Salix bebbiana</i>	9	5	2	<i>Vaccinium myrtillus</i>	2	2	3
<i>Salix boothii</i>	6	7	3	<i>Vaccinium scoparium</i>	-	-	2
<i>Salix brachycarpa</i>	1	-	-	Unknown	-	-	1
<i>Salix drummondiana</i>	40	27	23				

Table C2. Herbaceous species observations as distance from the river increased. Only river survey data is included in this table. Plots were used as a proxy for distance, where the first plot was established at the start of the riverside vegetation (0 m), then the second plot was 20 m away, and the third was 40 m from the river's edge.

Species	Distance From River			Species	Distance From River		
	0 m	20 m	40 m		0 m	20 m	40 m
<i>Achillea millefolium</i>	5	5	4	<i>Geranium richardsonii</i>	-	3	2
<i>Agrimonia sp.</i>	2	3	6	<i>Geum macrophyllum</i>	10	7	5
<i>Agrostis gigantea</i>	1	2	3	<i>Glyceria sp.</i>	1	1	-
<i>Agrostis idahoensis</i>	1	-	-	<i>Glyceria striata</i>	2	1	1
<i>Agrostis sp.</i>	1	-	1	<i>Heracleum maximum</i>	-	2	1
<i>Alopecurus pratensis</i>	55	42	42	<i>Juncus arcticus</i>	-	2	1
<i>Anaphalis margaritacea</i>	1	-	-	<i>Juncus ensifolius</i>	3	-	1
<i>Angelica pinnata</i>	-	1	-	<i>Juncus sp.</i>	3	-	3
<i>Antennaria parvifolia</i>	2	2	-	<i>Koeleria macrantha</i>	-	-	1
<i>Arnica cordifolia</i>	-	1	1	<i>Ligusticum tenuifolium</i>	-	1	-
<i>Astragalus alpinus</i>	1	-	-	<i>Lupinus argenteus</i>	-	1	-
<i>Astragalus flexuosus</i>	2	1	1	<i>Lupinus sp.</i>	-	-	1
<i>Astragalus sp.</i>	-	-	1	<i>Luzula parviflora</i>	-	1	-
<i>Bromus inermis</i>	3	3	5	<i>Maianthemum racemosum</i>	-	2	3
<i>Calamagrostis canadensis</i>	53	36	27	<i>Maianthemum stellatum</i>	-	-	1
<i>Caltha leptosepala</i>	-	-	2	<i>Mertensia ciliata</i>	2	3	2
<i>Cardamine cordifolia</i>	1	-	1	<i>Oxytropis sp.</i>	-	1	-
<i>Carex aquatilis</i>	54	44	36	<i>Pedicularis groenlandica</i>	1	-	-
<i>Carex aurea</i>	1	-	-	<i>Phalaris arundinacea</i>	17	9	11
<i>Carex egglestonii</i>	-	-	1	<i>Phleum pratense</i>	3	1	4
<i>Carex praegracilis</i>	-	-	1	<i>Poa compressa</i>	-	-	1
<i>Carex sp.</i>	24	28	27	<i>Poa palustris</i>	-	1	-
<i>Carex utriculata</i>	19	20	21	<i>Poa pratensis</i>	13	22	12
<i>Chamerion angustifolium</i>	-	3	1	<i>Poa sp.</i>	14	15	11

Species	Distance From River			Species	Distance From River		
	0 m	20 m	40 m		0 m	20 m	40 m
<i>Cirsium arvense</i>	9	8	12	<i>Polemonium occidentale</i>	1	3	2
<i>Cirsium clavatum</i>	-	-	1	<i>Potentilla pulcherrima</i>	2	7	8
<i>Cirsium scariosum</i>	-	-	1	<i>Potentilla sp.</i>	-	1	3
<i>Cirsium sp.</i>	-	-	1	<i>Pseudoroegneria spicata</i>	3	-	1
<i>Cirsium vulgare</i>	1	-	-	<i>Pyrola asarifolia</i>	-	1	1
<i>Danthonia intermedia</i>	1	3	1	<i>Rhodiola rhodantha</i>	-	-	1
<i>Eleocharis sp.</i>	1	-	-	<i>Senecio bigelovii</i>	2	3	3
<i>Elymus trachycaulus</i>	5	6	2	<i>Senecio hydrophilus</i>	-	3	2
<i>Epilobium hornemannii</i>	1	-	-	<i>Senecio sp.</i>	1	-	-
<i>Equisetum arvense</i>	32	18	10	<i>Senecio triangularis</i>	-	1	1
<i>Equisetum variegatum</i>	2	-	-	<i>Solidago sp.</i>	-	2	2
<i>Erigeron glabellus</i>	-	1	-	<i>Taraxacum officinale</i>	40	57	46
<i>Erigeron sp.</i>	-	2	2	<i>Thalictrum dasycarpum</i>	1	2	1
<i>Eriogonum umbellatum</i>	-	-	2	<i>Trifolium pratense</i>	14	12	7
<i>Festuca idahoensis</i>	-	-	2	<i>Trifolium repens</i>	3	-	-
<i>Festuca sp.</i>	-	1	-	<i>Trifolium sp.</i>	7	4	4
<i>Fragaria virginiana</i>	37	54	45	Unknown	2	4	6
<i>Galium boreale</i>	-	1	-				

APPENDIX D

Table D1. Coordinates and transect bearings for historic dams included in the study. Each plot listed is the first plot of the transect, there are three plots per transect and three transects per dam, for a total of nine plots per dam.

Historic Dam ID	Plot Number	Latitude	Longitude	Bearing (°)
HBDL_3	1	40.37367904	-105.8595212	88
	4	40.373828	-105.859581	
	7	40.374016	-105.859481	
HBDL_4	1	40.374101	-105.859682	88
	4	40.374283	-105.859689	
	7	40.37447	-105.85982	
HBDL_5	1	40.375072	-105.859883	268
	4	40.375224	-105.85985	
	7	40.375432	-105.859847	
HBDL_9	1	40.425805	-105.850843	268
	4	40.425606	-105.850863	
	7	40.425411	-105.850861	
HBDL_10	1	40.458434	-105.87469	194
	4	40.458411	-105.874469	
	7	40.458315	-105.874211	
HBDL_11	1	40.458495	-105.873739	14
	4	40.458414	-105.873994	
	7	40.458481	-105.874297	
HBDL_13	1	40.392194	-105.84719	268
	4	40.392394	-105.847183	
	7	40.392595	-105.847176	
HBDL_14	1	40.389884	-105.848473	268
	4	40.390051	-105.848497	
	7	40.390273	-105.848502	
HBDL_15	1	40.398078	-105.850367	268
	4	40.398253	-105.850343	
	7	40.398405	-105.850334	
HBDL_16	1	40.391217	-105.848039	268
	4	40.391366	-105.847997	
	7	40.391586	-105.848001	
HBDL_17	1	40.350415	-105.86967	88
	4	40.350217	-105.869701	
	7	40.350027	-105.869715	

Historic Dam ID	Plot Number	Latitude	Longitude	Bearing (°)
HBDL_18	1	40.37575	-105.853842	268
	4	40.375881	-105.853818	
	7	40.376083	-105.85382	
HBDL_19	1	40.385441	-105.84841	268
	4	40.38561	-105.84841	
	7	40.385781	-105.848396	

Table D2. Coordinates and transect bearings for control transects included in the study. Each coordinate listed is the first plot of the transect, there are three plots per transect. Those marked with an asterisk (*) only have the first two plots out of the three.

Control Transect ID	Latitude	Longitude	Bearing (°)
KVC_2	40.370731	-105.858875	268
KVC_3	40.357336	-105.858746	268
KVC_4	40.358645	-105.859076	268
KVC_5	40.370006	-105.857612	88
KVC_8	40.444366	-105.848783	268
KVC_9	40.426068	-105.852084	88
KVC_10	40.365377	-105.855798	88
KVC_11	40.407125	-105.850301	268
KVC_12	40.3465	-105.859329	88
KVC_13	40.342624	-105.859421	268
KVC_14	40.336609	-105.8574	88
KVC_15	40.33416	-105.856648	88
KVC_16	40.330878	-105.857533	88
KVC_17	40.329237	-105.855825	88
KVC_18	40.322607	-105.855431	268
KVC_19	40.32135	-105.854327	268
KVC_25	40.326227	-105.861535	268
KVC_26	40.348031	-105.866643	268
KVC_27	40.345601	-105.869329	268 *
KVC_28	40.34039	-105.86845	268
KVC_29	40.339417	-105.867716	88
KVC_30	40.330932	-105.862595	88

Table D3. Coordinates and transect bearings for river-associated transects included in the study. Each coordinate listed is the first plot of the transect, there are three plots per transect. Those marked with an asterisk (*) only have the first two plots out of the three.

Feeding Line	Plot ID	Latitude	Longitude	Bearing (°)
KVFL_1	1	40.369787	-105.857809	268
	4	40.369362	-105.858055	268
KVFL_3	1	40.377435	-105.857362	88
	4	40.376321	-105.858048	88
	7	40.37564	-105.858015	88
	10	40.374623	-105.857541	88
	13	40.373986	-105.85862	268
	16	40.373383	-105.857749	268
	19	40.372755	-105.857662	268
	22	40.372262	-105.858471	268
	25	40.37176	-105.858974	268
KVFL_4	1	40.378795	-105.854404	88
	4	40.378222	-105.85503	88
	7	40.378782	-105.855924	88 *
	10	40.377868	-105.856108	88
	13	40.377759	-105.857372	268
KVFL_5	1	40.395449	-105.845961	268
	4	40.395442	-105.846985	268
	7	40.394652	-105.847279	268
	10	40.395006	-105.848161	88
	13	40.394845	-105.849135	268
	16	40.394026	-105.850258	88
KVFL_6	1	40.393926	-105.850553	268 *
	4	40.393202	-105.850182	88
	7	40.392718	-105.849741	88
	10	40.391982	-105.850113	88
	13	40.391499	-105.851081	88 *
	16	40.390608	-105.851159	88
	19	40.389951	-105.851394	88
	22	40.389303	-105.850641	88
	25	40.388612	-105.850674	88
	28	40.38772	-105.850479	88
	31	40.386975	-105.850075	88
	34	40.386609	-105.851678	88
	37	40.385891	-105.851587	88
	40	40.38511	-105.851551	88
	43	40.384511	-105.850919	88
46	40.383624	-105.849735	88	
KVFL_7	1	40.35738	-105.857514	268
	4	40.355879	-105.857926	268
	7	40.355208	-105.858392	268
KVFL_8	1	40.371367	-105.858876	88

Feeding Line	Plot ID	Latitude	Longitude	Bearing (°)
	4	40.370627	-105.858635	88
KVFL_9	1	40.369569	-105.857846	88
	4	40.36894	-105.857417	88
	7	40.368619	-105.85655	268
	10	40.368036	-105.855796	88
	13	40.367575	-105.855325	88
	16	40.366835	-105.855318	88
	19	40.366749	-105.856162	88
	22	40.366018	-105.856425	88
KVFL_10	1	40.364061	-105.858221	88
	4	40.363363	-105.857552	88
	7	40.362811	-105.85792	88
	10	40.362122	-105.857395	88
	13	40.361625	-105.856771	88
	16	40.360961	-105.857259	88
	19	40.360407	-105.856641	88
	22	40.359727	-105.856927	88
	25	40.358828	-105.857619	88
	28	40.35894	-105.858578	88 *
	31	40.358252	-105.858002	88
	34	40.357621	-105.858484	88
	37	40.357589	-105.85756	88
	40	40.35692	-105.857249	88
	43	40.356393	-105.857857	88
	46	40.355709	-105.857774	88
	49	40.354983	-105.85821	88
	52	40.354286	-105.858435	88
	55	40.353548	-105.858536	88
	58	40.353463	-105.85947	88
	61	40.352909	-105.858752	88
	64	40.352375	-105.858122	88 *
	67	40.350647	-105.859026	88 *
	70	40.35028	-105.86013	88
73	40.349525	-105.860045	88	
76	40.348785	-105.86019	88	
79	40.348234	-105.859517	88	
82	40.347401	-105.859904	88	
KVFL_11	1	40.418727	-105.851499	88 *
	4	40.417906	-105.851547	268
	7	40.41783	-105.85056	268
	10	40.417103	-105.850454	268
KVFL_12	1	40.400483	-105.849951	88
	4	40.399697	-105.849929	88 *
	7	40.398048	-105.849882	88
	10	40.397362	-105.850067	88 *
	13	40.396949	-105.850848	88

Feeding Line	Plot ID	Latitude	Longitude	Bearing (°)
	16	40.396218	-105.851021	88
	19	40.395434	-105.851019	88
	22	40.39477	-105.850725	88
KVFL_13	1	40.357751	-105.858546	268
KVFL_14	1	40.335801	-105.857071	88
	4	40.335201	-105.857043	88
KVFL_15	1	40.332453	-105.856877	88
	4	40.331394	-105.857278	88
KVFL_16	1	40.329747	-105.856649	88
KVFL_17	1	40.322065	-105.854445	268 *
KVFL_21	1	40.352269	-105.868112	268
	4	40.35163	-105.867615	268
	7	40.351056	-105.868227	268
	10	40.350376	-105.868088	268
	13	40.350099	-105.867198	88
	16	40.349318	-105.867188	268
	19	40.348905	-105.866577	268
KVFL_22	1	40.346634	-105.86795	268
	4	40.346584	-105.869009	268
KVFL_23	1	40.344905	-105.868533	268
	4	40.344177	-105.868324	268
	7	40.343516	-105.868412	268
	10	40.342766	-105.867808	268
	13	40.341786	-105.867864	268
	16	40.340971	-105.867911	268
KVFL_24	1	40.340125	-105.868453	88
KVFL_25	1	40.337423	-105.866441	88
	4	40.337307	-105.865595	268
	7	40.336526	-105.865147	88 *
	10	40.335867	-105.865479	88
	13	40.335048	-105.865834	88
	16	40.334261	-105.865925	88
	19	40.333651	-105.865496	88
	22	40.333127	-105.864914	88
	25	40.332365	-105.8646	88
	28	40.33185	-105.863367	88
KVFL_26	1	40.329627	-105.862121	88
	4	40.3294	-105.86098	268
	7	40.328812	-105.861053	268
KVFL_28	1	40.345394	-105.859546	88
	4	40.344287	-105.859132	268
	7	40.343536	-105.85912	268
KVFL_31	1	40.328007	-105.86105	268