THESIS

FROM REACH TO LANDSCAPE: ASSESSING BEAVER HABITAT SUITABILITY TO GUIDE WETLAND RESTORATION IN ROCKY MOUNTAIN NATIONAL PARK

Submitted by

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ABSTRACT

FROM REACH TO LANDSCAPE: ASSESSING BEAVER HABITAT SUITABILITY TO GUIDE WETLAND RESTORATION IN ROCKY MOUNTAIN NATIONAL PARK

Beavers play a critical role in shaping riparian and wetland ecosystems, enhancing water retention, increasing habitat complexity, and supporting biodiversity. This study investigated the vegetative and geomorphic factors influencing beaver occupancy and habitat suitability across the east side of Rocky Mountain National Park, with the goal of informing broader wetland restoration efforts.

Data were collected at two spatial scales: a landscape-level assessment of beaver occupancy and habitat condition, as well as a fine-scale analysis of nine focal riparian areas representing a gradient of beaver activity (active, recent, and historic). The broad-scale survey revealed that current beaver activity is considerably reduced compared to historical levels. The habitat condition assessment showed substantial variability across the landscape, with a strong negative correlation between ungulate browsing pressure and willow height.

At the fine-scale, multivariate analyses showed that active beaver occupancy is most closely linked to geomorphic characteristics—specifically, wider and deeper stream channels, broad valley bottoms, and expansive riparian zones. In contrast, vegetation metrics such as willow height and forage biomass were uniformly suitable across sites. The fine-scale analysis offered a more nuanced perspective, revealing that vegetation is not currently a limiting factor and that many suitable sites remain unoccupied.

These findings suggest that while ungulate browsing contributed to historical habitat degradation and beaver decline, it is unlikely to be the primary factor limiting beaver re-establishment today. Whereas past declines may have been driven by vegetation loss, current occupancy patterns appear to be more strongly influenced by geomorphic suitability and limited beaver dispersal.

This study highlights the importance of integrating multi-scale assessments of habitat suitability into wetland restoration planning. By identifying the key drivers and constraints of beaver occupancy, this research offers a more holistic understanding of beaver habitat dynamics and provides practical guidance for restoration site selection.

ACKNOWLEDGEMENTS

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I. Introduction

Ecological Importance of Beavers

The absence of activity by the North American beaver (*Castor canadensis)* is evident across North American watersheds, where once intricate wetland systems have now transformed into simplistic, single-threaded, and frequently incised streams (Brazier et al., 2021; Wohl, 2021). The disproportionate impact of beaver activity on hydrologic systems, habitat heterogeneity and biodiversity has led to their classification as both keystone species and ecosystem engineers (Baker & Hill, 2003). Through a combination of foraging patterns and dam and canal building processes, beavers enact large-scale modifications to the structure and function of ecosystems temporally and spatially. While the trajectory of their impact on a stream can vary, many streams evolve from a single-threaded state into a wetland complex, which over time can fill with sediment and transition into a beaver meadow (Baker & Hill, 2003; Naiman et al., 1988; Pollock et al., 2014; Polvi & Wohl, 2012; Westbrook et al., 2006, 2011; Westbrook, 2021) (Figure 1).

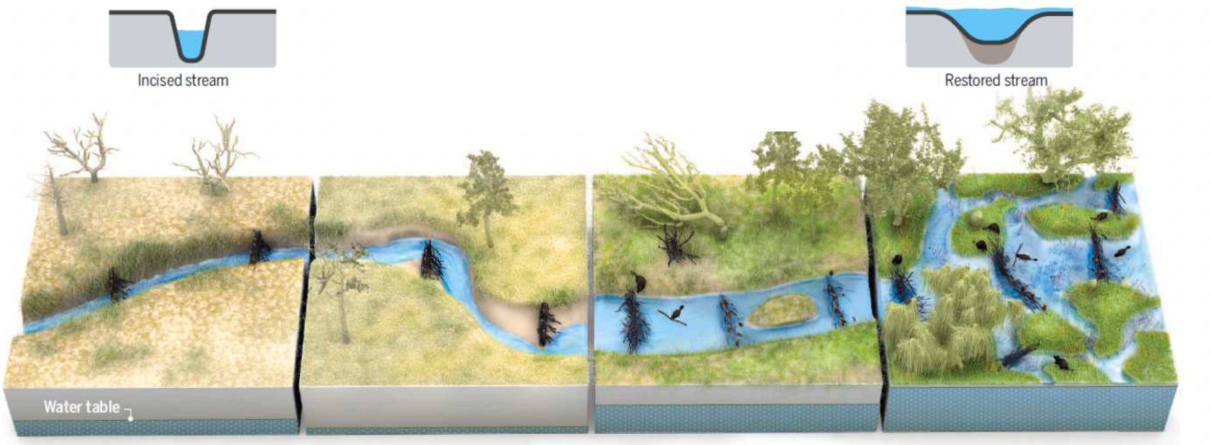

Figure 1. Shows how beaver dams transform incised streams into complex, multithreaded channels. The first section shows dams built in an incised stream during low flows. The second section shows how dams widen the channel by diverting flows and allowing for sediment accumulation. The third section shows how sediment accumulation allows for the water table to rise, additionally the lower flows from the wider channel allow beaver to build more stable damns. The final panel shows the continuation of beaver dam building and how the raised water table and overbank flooding reconnects the stream with the floodplain, promoting riparian vegetation (adapted from (Goldfarb, 2018)).

Beaver activity creates a patchwork of habitat diversity that supports species biodiversity and enhances ecosystem resilience and functioning. Beaver-influenced landscapes support a diverse array of species, including vegetation, mammals, birds, fish, invertebrates, and reptiles/amphibians (Albert & Trimble, 2000; Anderson et al., 2015; Baker & Hill, 2003; Bouwes et al., 2016; Pollock et al., 2004; Rosell et al., 2005; Westbrook et al., 2011). Ŧheir foraging behavior alters vegetation species composition, density and distribution, particularly of woody vegetation (Baker et al., 2012; Peinetti et al., 2009). When intact, these landscapes exhibit greater resilience to disturbances such as drought and wildfire, serving as a buffer against climate change (Fairfax & Whittle, 2020; Hood & Bayley, 2009). Unfortunately, the current extent of beavers is much less than it was historically.

Historical Impact of Beavers on the Landscape

Beavers have influenced streams spanning from the east to the west coast of North America for millions of years through their dam-building processes (Baker & Hill, 2003; Ruedemann & Schoonmaker, 1938; Wohl, 2021). The extent of their impact on the landscape has fluctuated over time, particularly in the last few centuries, due to drastic shifts in their populations. Prior to European settlement, an estimated 60-400 million beavers were present in North America (Seton, 1929). However, extensive hunting and trapping practices led to their local extirpation from many areas across the continent (Baker & Hill, 2003). Following protective measures, beavers rebounded, with current population estimates being 10 million (Naiman et al., 1988; Pollock et al., 2023). Despite their recovery throughout much of North America, the absence of beavers is still obvious throughout many watersheds, notably affecting the structure and function of rivers, which now lack the complexity that beaver activity creates (Brazier et al., 2021).

Beavers as a Tool for Restoration

Recognition of the ways in which beavers shape, modify, and benefit wetland systems has led to their consideration as a restoration tool (Brazier et al., 2021; Naiman et al., 1988). Current efforts to improve wetland systems using beavers as a restoration tool include riparian wetland protection or restoration, implementation of beaver mimicry structures (i.e. Beaver Dam Analogs (BDAs)), a reduction of human-beaver conflict and translocations (Pollock et al., 2023). Beavers improve both intact and marginal wetland habitat by increasing water storage, trapping sediment, reducing channel erosion and enhancing riparian vegetation (Baker & Hill, 2003; Hood & Larson, 2015). Their activity also restores incised streams by increasing lateral connectivity, reconnecting them with the floodplain (Beechie et al., 2008; Pollock et al., 2007; Westbrook et al., 2011). Mechanical restoration and revegetation efforts for degraded wetlands and incised streams are costly, labor-intensive, and exhibit varying success rates. Thus, beaver activity can be viewed as a passive form of restoration that also works proactively, as the benefits of beaver activity influence downstream functions. A 12-year case study of beaver-assisted restoration in a drained pasture found significant contributions by beavers to wetland restoration and improved vegetation heterogeneity on a scale too fine for human intervention (Law et al., 2017). However, for beavers to be effective tools for restoration, their habitat requirements must first be met.

Habitat Requirements of Beavers

A stable water source serves as the primary determinant of beaver habitat suitability. Additionally, a low stream gradient (ideally <6%) and access to sufficient woody vegetation for forage and building material constitute the next most critical requirements for beaver establishment (Baker & Hill, 2003; Pollock et al., 2023). While it is not uncommon for beaver damns to blow out, steep slopes and large flows are generally avoided for this reason (Levine & Meyer, 2019). Stream width, depth and valley confinement play a role as well, but because stream width and depth can fluctuate annually, valley width is generally thought to be a more stable variable (Macfarlane et al., 2015). Wide, unconfined valleys that are 46 meters or greater are thought to be most suitable for beaver establishment (Allen, 1983). Beaver can occupy a wide range of habitat conditions, but the magnitude and longevity over which they occupy these sites vary based on several of these factors.

Since beaver utilize woody vegetation for both forage and building material, presence of an intact riparian zone that can sustain an individual or family unit is often a limiting factor for their establishment. Beavers are known to travel around 100 meters offshore to forage and habitat models often buffer this distance to 200 meters, but their preferred range is within 30 meters because beavers are much less agile moving overland, and their risk of predation increases significantly outside the protection of the stream and their dam complexes (Allen, 1983; Anderson & Bonner, 2014).

Key vegetative variables that influence suitability include species, density, cover, and stem diameter of trees and/or shrubs (Allen, 1983; Baker & Cade, 1995; Baker & Hill, 2003; Retzer, 1956). While beaver oftentimes forage on aspen/poplar (*Populus spp.*), birch (*Betula spp.*) and alder (*Alnus spp.*), along with several herbaceous species in the summer season, willow (*Salix spp.*) is often the most utilized because of its abundance and wide range. In some areas of the intermountain West, beavers depend on willow species entirely during the winter months (Baker & Hill, 2003).

The most significant constraints to beaver establishment include habitat degradation/loss, competition with wild and domestic ungulates, and human-beaver conflict (Baker et al., 2012; Beschta & Ripple, 2009; McKinstry, Anderson, 1999; Scamardo et al., 2022). In many areas of North America, these constraints intersect, hindering beavers from reestablishing in sites within their historic range. Often, regions once suitable for beavers are no longer so due to changes in land use or competition from herbivores. A study examining the correlation between widespread declines in beaver populations and the loss of suitable habitat in Colorado revealed that while beaver populations have decreased by at least 80%, the state's capacity for beavers has only diminished by 50% (Scamardo et al., 2022). This suggests a considerable amount of suitable habitat remains available for re-establishment. Identifying suitable sites and facilitating beaver reestablishment is crucial for the large-scale restoration of wetlands across North America.

This study identified beaver occupancy and assessed habitat condition across all suitable habitat identified on the eastern slope of Rocky Mountain National Park (RMNP). A more fine-scale habitat comparison was conducted at active, recent and historic beaver-occupied sites. The baseline data collected in this study informs patterns of beaver establishment and identify limitations to their establishment, all to inform restoration efforts for degraded wetland riparian systems in RMNP. Specifically, this information allows land managers to prioritize sites for targeted restoration.

Willow are key species in these wetland riparian shrublands, which are heavily utilized by Rocky Mountain elk (*Cervus elaphus*), Shiras moose (*Alces alces shirasi*) and beaver (Zeigenfuss & Johnson, 2015) (Figure 2). Historically high populations of elk in RMNP have had long-lasting impacts on the vigor of willow populations (Zeigenfuss & Johnson, 2015). Moose impacts are less studied, but individuals are known to frequent wetland riparian shrublands with around 90% of their summer diet consisting of willow (Dungan & Wright, 2005; Zeigenfuss & Abouelezz, 2018). The combined browsing pressure of these two ungulate species on willow in RMNP has contributed greatly to the loss of local beaver activity via competition (Baker et al., 2012). Prior to high elk populations and the permanent presence of moose in RMNP, a mutualism between beavers and willow occurred (Baker et al., 2012). The forage pattern of beaver has been found to increase both productivity and structural heterogeneity of willow communities (Baker & Hill, 2003; Peinetti et al., 2009). The forage pattern of ungulates on the tips of willow stems, in severe cases, can cause individual plants to be stunted in a short stature (Baker et al., 2012; Hood & Bayley, 2009; Kaczynski, 2013).

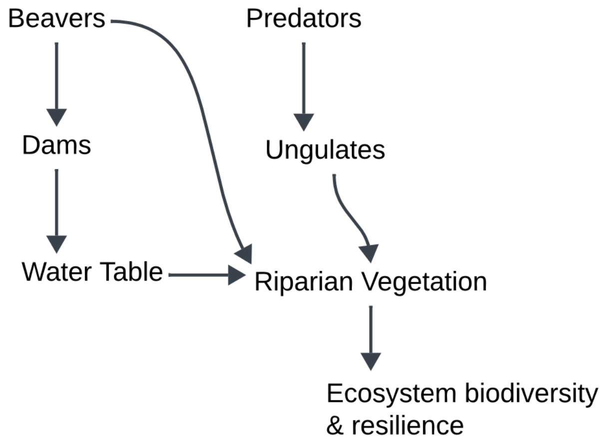

Figure 2. Systems diagram simplistically representing key biotic and abiotic factors influencing wetland riparian systems in RMNP.

Throughout RMNP, many of the willow communities are stuck in these short stature states, thereby limiting reestablishment of beavers (Baker et al., 2004). In the absence of beaver activity, altered hydrology has led to a shift to a grassland-like state, reducing willow vigor and making beaver presence unlikely. It is important to note that in RMNP, and throughout most of the western United States, these wetlands have also been impacted by historic land-use, human disturbance, water diversions, wildfire and climate change (Alstad et al., 2016; Kaczynski et al., 2014; Kaczynski & Cooper, 2015). In order to address these variables limiting willow vigor and beaver reestablishment, RMNP has already begun to implement ungulate exclosures as well as beaver mimicry structures including BDAs, Simulated Beaver Structures (SBSs) and Post-Assisted Log Systems (PALS).

This research sought to answer the following questions:

1. Does current beaver activity differ from past activity across sites identified as suitable?
    a. What percentage of suitable stream segments had active, recent or historic beaver forage sign?

    b. How does density and the core/activity ranges of beaver compare historically, recently and currently?
2. How does beaver habitat condition vary among suitable sites?
    a. Are habitat conditions (willow height, willow density, willow dieback, ungulate utilization on willow, nearest forage species to the stream's edge, and stream entrenchment rating) correlated?
    b. Does beaver sign (active, recent and historic) correlate with overall habitat condition (not suitable, low, medium and high)?
3. Do specific vegetation and stream geomorphology variables differ amongst active, recent and historic beaver sites within the eastern slope of RMNP?

II. Methods

Study Area

RMNP, located in north-central Colorado, ranges in elevation from 2200-4300-meters, spans approximately 108,000 hectares, and contains high-elevation forests, shrublands, meadows, and alpine tundra (Zeigenfuss & Johnson, 2015) (Figure 3, Maps A and C). The continental divide runs through the center of the RMNP dividing it into eastern and western slopes. Beaver-suitable habitat is found in wetland riparian shrublands in RMNP, which are systems that have experienced high levels of degradation, and now comprise only 2% of the park's landscape (Salas et al., 2005). Although riparian areas comprise a small fraction of RMNP, they harbor exceptionally high biodiversity and contribute disproportionately to ecosystem functioning and resilience (Schweiger et al., 2016).

The study area is located within the South Platte River Basin, encompassing portions of three HUC 8 subbasins: the Big Thompson, St. Vrain, and a small part of Cache La Poudre (Figure 3, Map B). Within these subbasins, the study includes HUC 10 watersheds such as Middle St. Vrain Creek, Big Thompson River, North Fork Big Thompson River, Cache La Poudre River, and South Fork Cache La Poudre River. These watersheds drain the eastern slopes of the Rocky Mountains and are critical for regional hydrology, influencing riparian habitat dynamics, beaver occupancy, and restoration potential.

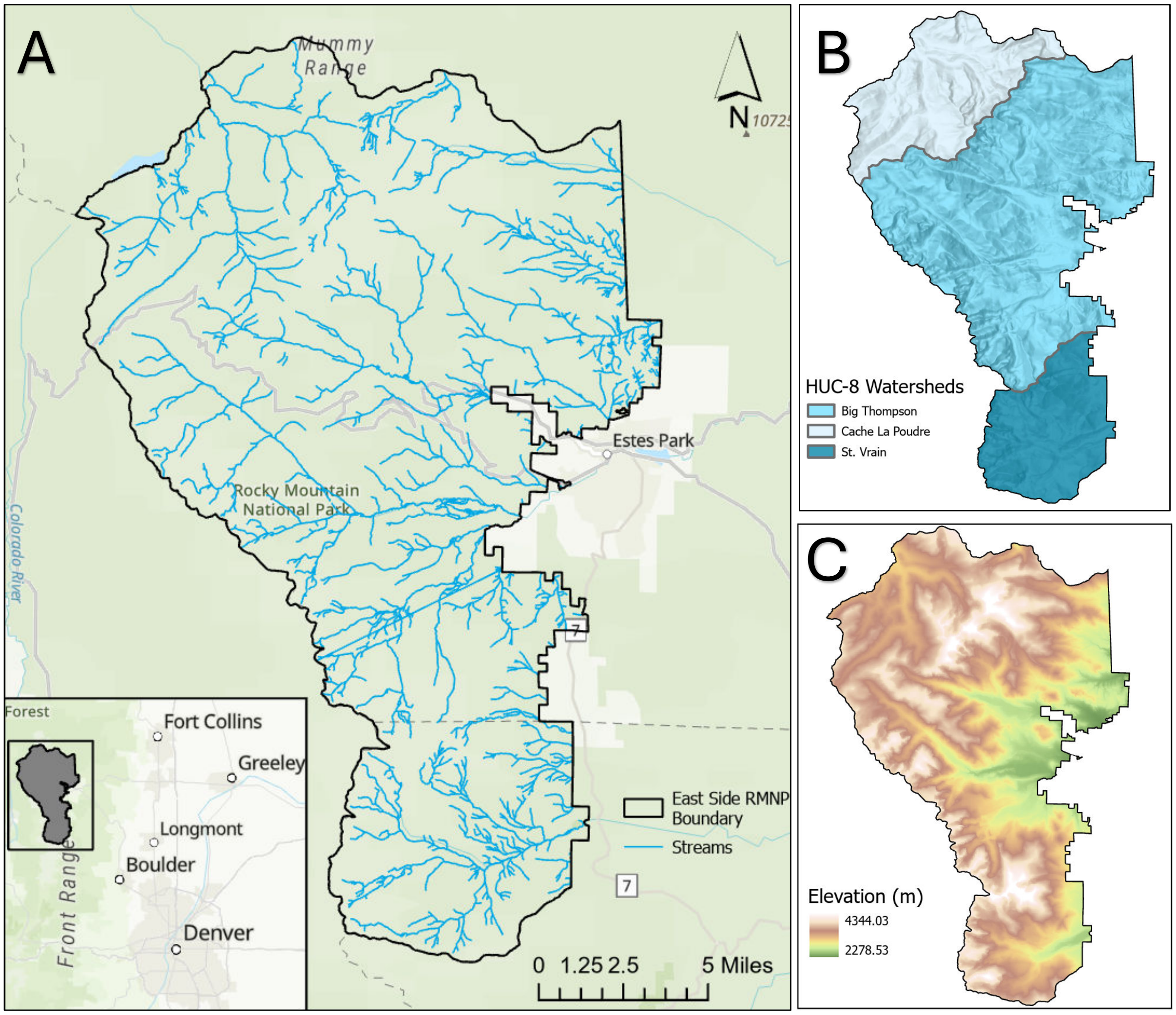

Figure 3. Map A is the study area on the east side of RMNP. Map B highlights the three HUC-8 watersheds found within the study site. Map C shows the elevation (m) gradient in the study site.

Overview of Data Collection

This study used a combination of geospatial and field-based habitat sampling. The geospatial data collected were used to either inform the field-based sampling areas or collect data on variables that were too large in scale to sample in the field.

Broadly, this study involved three separate components: (1) Primary geospatial analysis to identify suitable beaver habitat (2) Broad-scale beaver occupancy survey and habitat condition assessment across the entire east side of RMNP (3) Fine-scale field and geospatial habitat comparison of active, recent and historic sites that included both vegetation and stream geomorphology variables.

A primary geospatial analysis was first conducted to identify potential beaver habitat across the entire study area. The output of this primary geospatial analysis guided the beaver occupancy and habitat condition assessment that was performed in the field. Further, the beaver occupancy data collected in the field informed the site selection for the fine-scale habitat comparison of active, recent and historic beaver sites.

Primary Geospatial Analysis, Habitat Suitability Map

Geospatial data layers of beaver habitat requirements were combined to create a broad-scale suitability map for eastern RMNP. The original layers used, in their most recent forms, were the Digital Elevation Model (DEM) from the USGS at a 1-meter resolution, and vegetation cover from the National Land Cover Database (NLCD) at a 30-meter resolution. A vector outline of the boundaries of RMNP and the Continental Divide was used as a spatial boundary for the model. Additionally, a vector layer for streams in RMNP was obtained from the National Park Service. The vegetation (NLCD) and slope (DEM) data layers were masked to the 30-meter stream buffer, because this is the preferred forage range for beavers (Allen, 1983). Additionally, these layers were clipped to the stream because a reliable water source is the primary habitat requirement for beavers and serves as a limiting factor. Also, all areas above 3,352.8 meters (11,000 feet) in elevation were removed, since this is generally the highest elevation in which beaver are active (Baker & Hill, 2003). All layers were projected to NAD 1983 UTM Zone 13N. The suitability map was created using ArcGIS Pro version 3.1.2. (Figure 4) Details on the model parameters are found in Appendix A (Workflow A1).

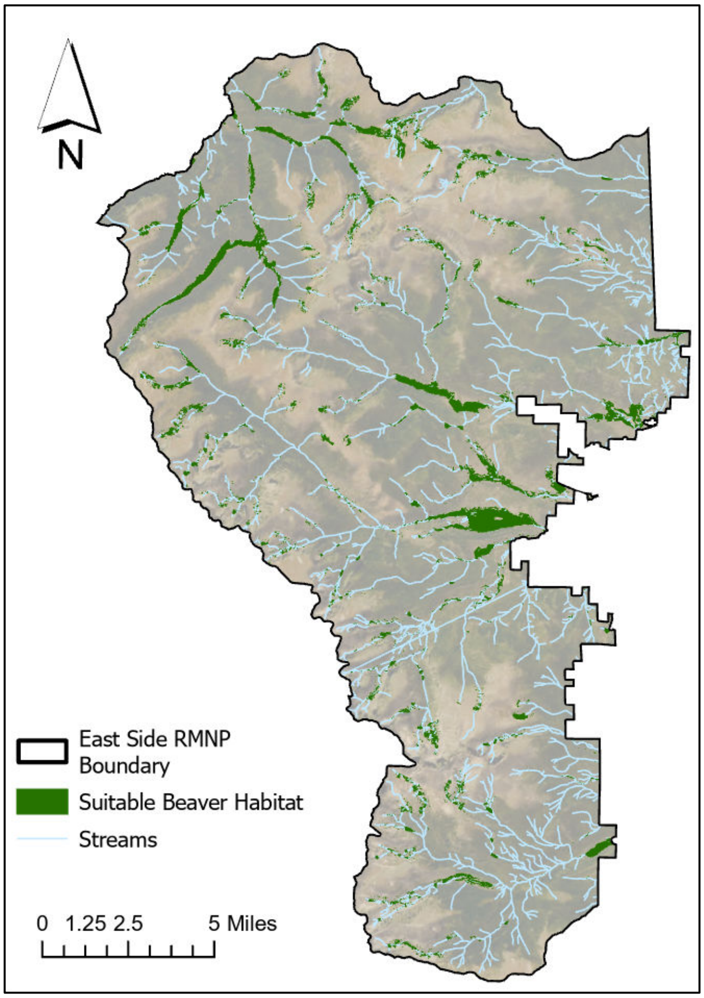

Figure 4. Suitable beaver sites identified on the east side of RMNP, output from the primary geospatial analysis.

Survey Methods

1. Broad-scale Beaver Occupancy Survey and Habitat Condition Assessment

Broad-scale surveys encompassed both a beaver occupancy survey and an assessment of habitat conditions. All accessible suitable beaver sites from the primary geospatial analysis were surveyed in the field, covering a total stream length of 139.6 kilometers (86.7 miles). The total length of streams that were inaccessible for in-field data collection was 81.3 kilometers (50.6 miles) (Figure 6.). Sites were considered inaccessible if access was unsafe (too steep) or if the site could not be reached within a day of hiking (~15 miles). All data were recorded using ArcGIS Field Maps version 24.30.

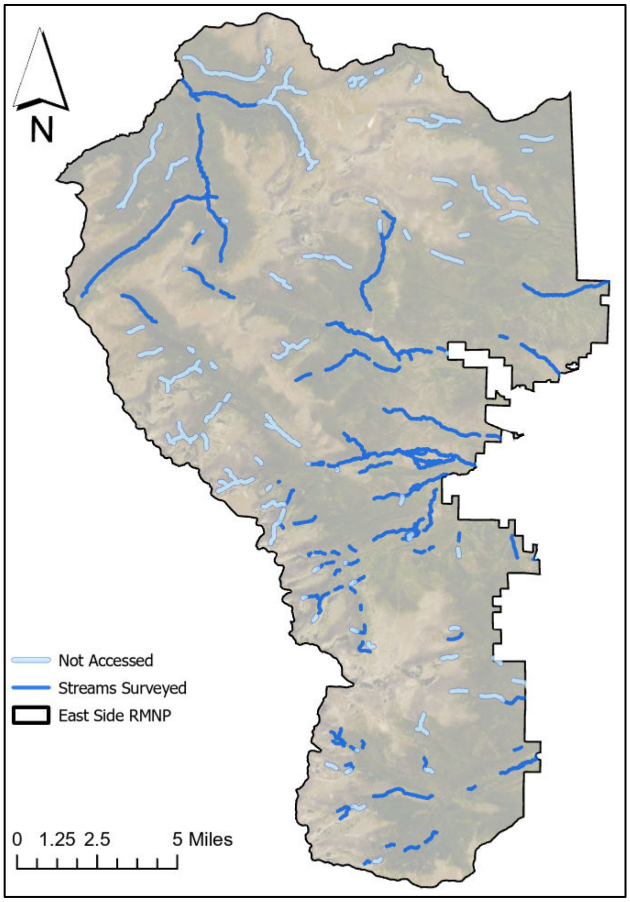

Figure 6. Map of streams accessed and not accessed for the broad-scale surveys. Habitat assessment sites were placed every 300-meters along surveyed streams.

a. Beaver Occupancy Survey

Surveyors hiked into suitable beaver areas and walked as close to the stream's edge as possible, searching for beaver sign, utilizing a standardized design adapted from Small et al. (2016) and Campbell-Palmer (2021). Beaver sign includes browse marks on woody plants (classified as historic, recent or active), dams (classified as holding water with active sign, holding water no active sign, not holding water, or dried historic), lodges, bank dens, food caches, scent mounds, or animal observations. When beaver sign was observed, a GPS point was recorded along with data on the type of sign (Figure 7).

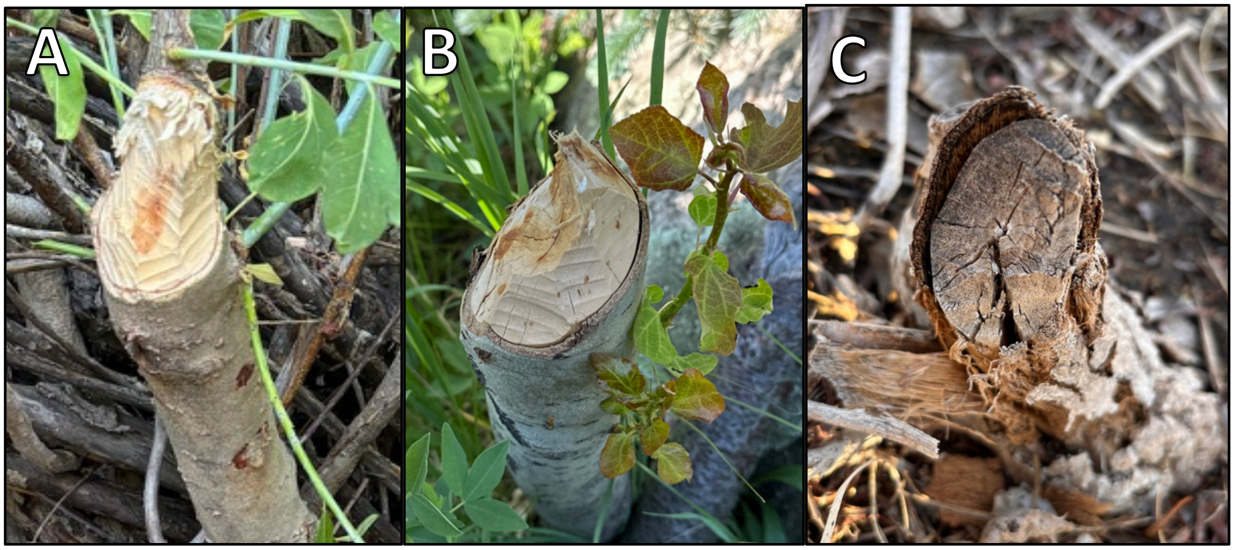

Figure 7. Beaver browse freshness rating. A represents current sign, with fresh wood apparent and no signs of decay, B represents recent sign, note signs of discoloration and aging, and C represents historic sign, where wood is gray, and splitting is commonly seen. Active sign is likely 0-1 years old, recent sign is 1-3 years old, and historic sign over 3 years old.

b. Broad-scale Habitat Condition Assessment

Broad-scale habitat condition assessment sites were spaced every 300 meters along suitable stream segments (Figure 8), with a 30-meter buffer around each point. Assessment sites were spaced every 300 meters because this was the optimal spacing that allowed surveyors to gather a significant amount of data while still moving quickly enough to meet the time constraints of this study, and encompassed an area of 30-meters squared because this is the preferred distance beavers will travel to forage from the stream (Allen, 1983; Anderson & Bonner, 2014). Surveyors walked the perimeter of the assessment area and bisected the area twice using the application, ArcGIS Field Maps, as a spatial reference. After assessing the area, technicians qualitatively and visually estimated willow height, density, dieback, and ungulate utilization, as well as stream entrenchment and proximity of the stream's edge to the nearest preferred forage species. The preferred forage species of beaver in RMNP are species of willow, alder, aspen/cottonwood, and birch.

Figure 8. Snapshot of broad-scale habitat condition assessment areas spaced every 300-meters with 30-meter buffer.

Willow height was classified into four categories: no willow present, low (<1 meter), medium (1–2 meters), high (>2-meters). Willow density was categorized based on visual estimation into four classes: no willow, low (sparse willows), medium (scattered dense clumps where the distance between plants was 3-5 meters), and high (more continuous willow coverage where the distance between plants was less than 2-meters) (adapted from the methodology of (Peinetti et al., 2002)).

Willow dieback and standing dead material were classified into four categories: no willow present, low (0–20% dieback), medium (20–60% dieback), and high (>60% dieback) (adapted from the methodology of (Peinetti et al., 2002)). Browsing severity by ungulates was classified into four levels: no willow present, low (minor browsing with healthy leader growth and no structural impacts), medium (some secondary branches impacted with visible dead wood), and high (several secondary branches impacted with over 50% dead wood and significant structural alteration) (adapted from the methodology of (Hood & Bayley, 2009)).

Stream entrenchment was classified using Rosgen's entrenchment classes as low, medium, or high, with an additional category for sites where no stream was present (Rosgen, 1996). Finally, the distance from the stream bank to the nearest preferred forage species was categorized as no forage in sight, low (<5 meters), medium (5–20 meters), or high (>20 meters).

2. Fine-scale Habitat Comparison of Active, Recent and Historic Beaver Sites

Fine-scale habitat comparisons at active, recent and historic sites were completed throughout June – August 2024. Only sites with previous beaver activity were considered to leverage the benefits of colonizing beaver for restoration efforts (Ritter et al., 2020). Sites were initially chosen based on prior knowledge of beaver activity on the east side of RMNP (from research and RMNP staff) and were modified or confirmed based on data from the broad-scale beaver occupancy survey. It is important to note that many historic beaver sites have been severely degraded by over-browsing and wildfire to the extent that beaver forage sign is no longer evident. Therefore, many sites that likely contained beavers historically were not considered for the habitat comparison.

Nine sites in total were characterized, three in each category of active, recent or historic. Only three active sites were confirmed on the east side of RMNP during the broad-scale beaver occupancy survey and thus selected as our active sites for the fine-scale comparison, including three Moraine Park Exclosures, a Horseshoe Park Exclosure and Wild Basin. Wild Basin is the oldest active colony on the east side of RMNP. Both Moraine and Horseshoe Park have been occupied by beaver more recently, approximately in the last 3-6 years. The recently active sites selected had a fair amount of both recent and historic forage sign and included: Hollowell Park, Cow Creek, and Endovalley. The three historic sites selected were Glacier Creek/Boulder Creek area, two Beaver Meadows Exclosures and Hidden Valley (Figure 9). It is important to note that in areas such as Moraine Park, Horseshoe Park and Beaver Meadows only the areas within the exclosures were sampled because beaver sign was found only within the exclosures and the ecosystem outside the exclosure was significantly different (i.e. riparian willow habitat within and grassland outside).

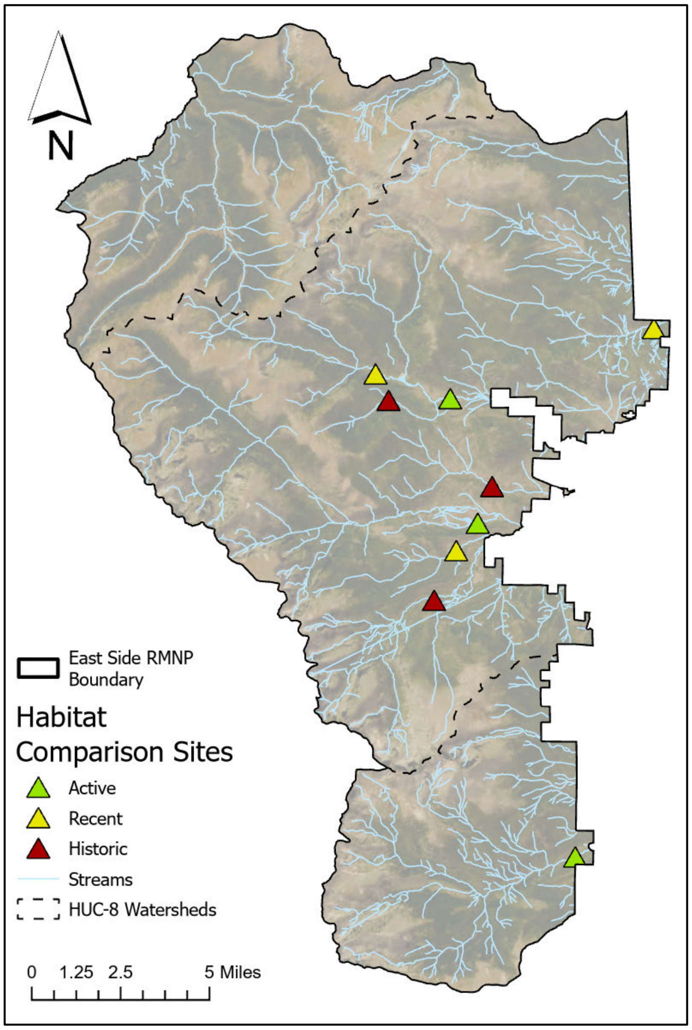

Figure 9. Map showing locations of active, recent and historic beaver sites sampled for the fine-scale habitat comparison. Dotted lines signify watershed boundaries.

The variables chosen to characterize habitat either represent general characteristics of vegetation or stream geomorphology that impact the suitability of an area for beaver establishment or limiting variables specific to RMNP (see Tables B1, B2, B3 in Appendix B). This methodology was adapted from a study by Ritter et al. (2020) unless noted otherwise in the tables.

Sites were sampled at random points generated either along the stream for the geomorphology variables or within a 30-meter buffer around the stream for the vegetation variables. For vegetation, at each random point within the 30-meter buffer, we sampled a 4x4-meter quadrat. For stream geomorphology, a transect across the stream was established at the random point. The number of quadrats sampled was relative to the area of the site, and we sampled at least 1-2% of each site. In cases of narrow riparian areas where plots fell within an upland area, vegetation plots were relocated to ensure the riparian shrubland was characterized, rather than characterizing the surrounding uplands. Surveyors used ArcGIS Field Maps version 24.30 to collect data.

Geospatial Analyses: Beaver Occupancy Survey and Habitat Condition Assessment

Total current, recent, and historic beaver activity (based on aged beaver forage sign) was calculated and visualized in several ways geospatially. The first was to calculate the density of beaver forage sign types (active, recent, historic) per 500-meter stream segment, and also calculate the percentage of beaver sign type found in all the segments surveyed (see GIS Workflow A3 in Appendix A). The second was to calculate the difference between current, recent, and historic beaver activity in order to understand a change in activity over time (Campbell-Palmer et al., 2021). In order to do this, a 30-meter (core-range) and 100-meter (activity-range) buffer was placed around each beaver forage sign type to calculate active, recent and historic beaver core and activity ranges in the survey area.

The percentages of ranked habitat condition for each variable (willow height, density, dieback and utilization and stream incision and distance to forage) were also calculated based on point data that was spaced every 300-meters. These point data were interpolated using the Inverse Distance Weighted tool in ArcGIS Pro to all stream segments surveyed for both visualizations of habitat condition across the study area, as well as to connect habitat condition to beaver sign (see GIS Workflow A2 and Figure A1 in Appendix A). The relationship of each habitat condition variable to each other variable was interpreted with the Spearman's rank correlation coefficient (Spearman's ρ), which measures the strength and direction of a consistent relationship between each habitat variable. All zeroes were removed from the habitat condition data for the Spearman's rank correlation because the relationship of zero to directionality of the categorical data varied for each variable. Additionally, zero represented either no willow, no forage or no stream – which made the area unsuitable for beaver habitat.

To analyze the association between beaver forage sign (active, recent, or historic) and habitat conditions (including willow height, willow density, willow dieback, ungulate utilization, nearest forage, and stream entrenchment), habitat data were interpolated, weighted, and spatially joined with beaver forage sign to quantify how often different forage types fell within specific habitat condition ranks (see GIS Workflow A2 in Appendix A). The weighting of habitat variables was influenced by the Spearman's rank correlation coefficient.

Statistical Analyses: Fine-scale Habitat Comparison of Active, Recent and Historic Sites

A variety of statistical approaches were employed to analyze differences in habitat characteristics across active, recent, and historic beaver sites. All statistical analyses were conducted in R (version 2024.04.2+764) using the lme4, emmeans, dplyr, glmer, glmmTMB, ordinal or tidyr packages. The nine sites in the fine-scale comparison were independent, but the quadrats within the sites were correlated. Therefore, a combination of mixed-effects models, ordinal models, beta regression and other statistical methods were used to evaluate differences in habitat characteristics across active, recent, and historic beaver sites (see example R Code in Appendix C). Model selection was based on the data structure and distribution of response variables, with transformations applied where necessary to meet model assumptions. Model assumptions (normality and equal variance) were checked using visual inspection of residual diagnostic plots. Post-hoc Tukey-adjusted pairwise comparisons were conducted when applicable to assess significant differences among site groups.

Willow height classes, ground cover type percentages and canopy cover percentages of shrub types (willow, other forage and non-forage) were best analyzed with visualizations as there was not a good fit for statistical analysis. Summary statistics were calculated for these primary responses based on expert recommendation due to the ordinal nature and multiple ordered categories of the data. This approach provided a clearer and more interpretable representation of patterns in the data. Where applicable, variables were condensed for formal statistical analysis (standing water ground cover type and canopy cover of all forage shrub species).

1. Linear Mixed-effects Models

Most continuous habitat variables—including stream width, stream depth, thalweg depth, valley floor width, riparian zone width, willow zone width, bank full depth, width: depth ratio, entrenchment rating, floodplain incision, channel complexity, stream gradient, sinuosity, shrub species richness, average willow stem diameter, average largest willow stem diameter, tallest willow leader height, Shannon Diversity Index, forage biomass index, and number of conifers—were analyzed using mixed-effects models. In these models, beaver occupancy classification (active, recent, and historic) was treated as a fixed effect, while site was included as a random effect to account for repeated measurements. Due to unequal variances, riparian zone width and willow zone width were log-transformed to better satisfy assumptions. Models were evaluated via ANOVA (F-test), and Tukey-adjusted pairwise comparisons were conducted to evaluate differences among groups.

2. Ordinal Logistic Regression

For ordinal response variables such as substrate size index, forage height classes, ungulate utilization ranks, and conifer age, ordinal logistic regression models were used. These models also incorporated site as a random effect. As with the other analyses, Tukey-adjusted pairwise comparisons were performed to determine differences among beaver occupancy groups.

3. Beta Mixed-effects Regression

Beta regression models were utilized for variables expressed as proportions or percentages, such as willow dieback, average shrub canopy cover (relative to ground cover), canopy cover of beaver forage shrub species (relative to other non-forage shrub species), and standing water (relative to other ground cover types). Mixed-effects beta regression was applied to account for site-level variability. As with the other analyses, Tukey-adjusted pairwise comparisons were performed to determine differences among beaver occupancy groups.

4. Analysis of Species Presence Data

For species presence data (aspen, conifer, and sapsucker damage), presence was recorded as a binary variable (1 = present, 0 = absent) for each plot. To assess differences among groups, contingency tables were constructed and analyzed using Chi-square tests. Complementary to this approach, generalized linear mixed-effects models with a binomial error distribution were fitted and Tukey-adjusted pairwise comparisons were performed to determine differences among beaver occupancy groups.

III. Results

Broad-scale Beaver Occupancy Survey and Habitat Condition Assessment

1. Beaver Occupancy Survey

The spatial extent of beaver activity differed among the three-forage age classes and was much greater historically than it is currently. Core ranges (30-meter buffer) derived from aged beaver forage sign totaled 57,074 m^2 for active sites, 208,894 m^2 for recent sites, and 773,879 m^2 for historic sites. Accordingly, activity ranges (100-meter buffer) displayed active sites covering 467,306 m^2, recent sites 1,348,366 m^2, and historic sites 4,628,421 m^2. Both core and activity ranges of beaver activity indicate that current occupancy is only a fraction of its historical extent, highlighting a significant contraction in spatial use over time.

Beaver occupancy was also assessed by measuring the density of forage sign per 500-meter stream segment, with active forage sign exhibiting a density of 0.09, recent forage sign a density of 0.42, and historic forage sign a density of 1.48. The low density of active forage sign resulted from the fact that active sign was only found in three sites across the entire surveyed area. In total, 4.4% of surveyed segments showed active sign, 9.7% showed recent sign, and 24.4% showed historic sign. Active beaver sign was detected in only 18% of the stream segments that were historically influenced by beaver.

2. Habitat Condition Assessment

For the habitat condition assessment, willow height varied across the landscape, with the most common category being willows less than 1 meter tall, covering 36% of the area. Willows 1-2 meters in height were present in 21% of the surveyed area, while taller willows (exceeding 2 meters) made up 20%. Sparse willow cover (low) was the most frequently observed category, accounting for 33% of the surveyed area. Areas with scattered clumps of willow (medium) covered 26%, while areas with more continuous willow cover (high) represented 18%. Utilization by ungulates was widespread, with 29% of the area experiencing moderate ungulate pressure, evidenced by visible impacts on vegetation structure and growth form. High ungulate browsing was observed in 27% of the area, while low browsing pressure was found in 22%. Moderate levels of willow dieback (impacting 20-60% of the plant impacted) were most common, occurring in 46% of the surveyed area. Low levels of dieback (0-20%) were observed in 24% of the area, while severe dieback (affecting over 60% of the plant) was present in 8% of the area. Approximately 23% of the surveyed area was devoid of willows entirely.

The majority of the surveyed area (54%) was characterized by low stream entrenchment and strong connectivity to the floodplain. Medium entrenchment was observed in 30% of the area, whereas highly entrenched streams accounted for only 5%. A small portion (11%) of the surveyed area lacked any visible stream.

The majority of forage was located close to the stream, with 77% of the surveyed area having forage within 5 meters of the channel. Moderate distances (5-20 meters) accounted for 9%, while only 4% of the area had forage located more than 20 meters from the stream. Areas lacking forage altogether comprised 10% of the total area (Figure 10).

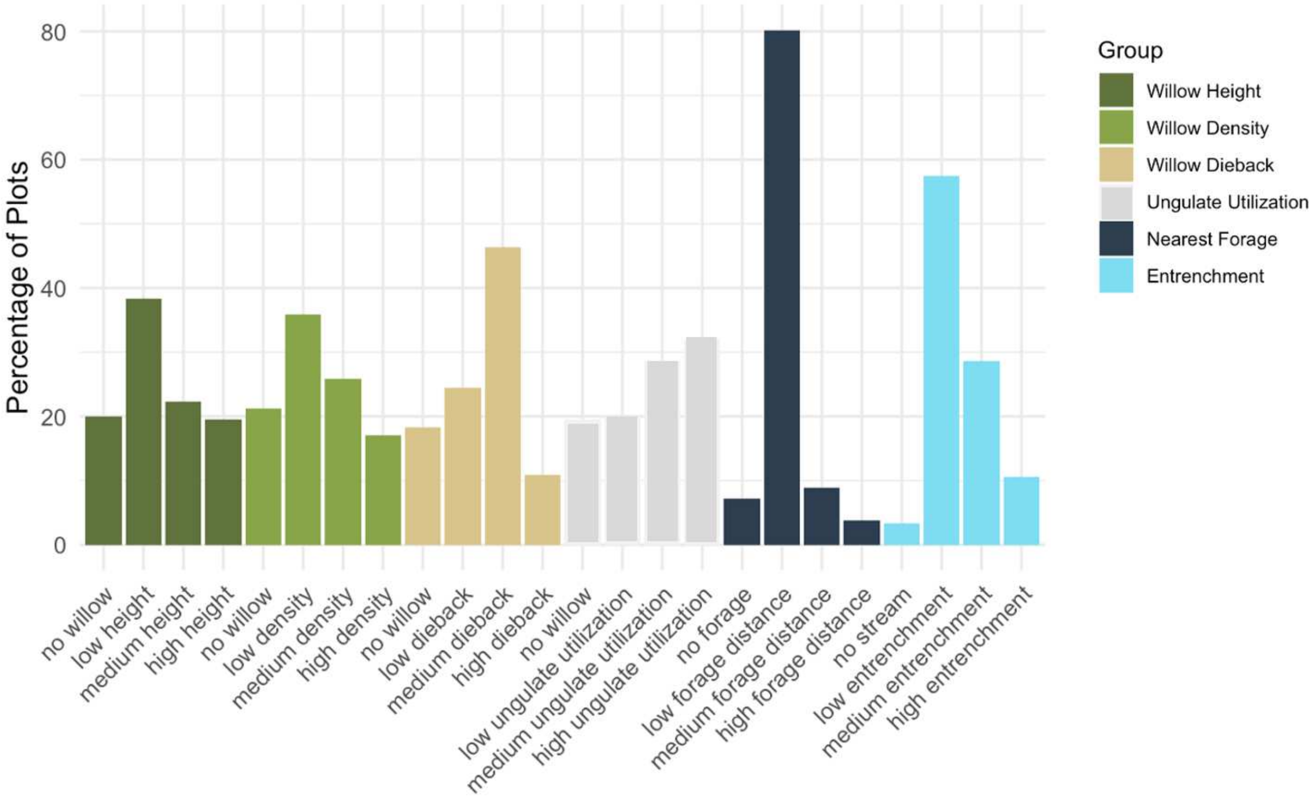

Figure 10. Bar plots showing the percentage of each habitat condition (willow height, density, dieback, ungulate utilization, nearest forage and entrenchment) found in surveyed sites across the east side of RMNP.

These results offer a landscape-scale assessment of vegetation patterns and stream conditions across the study sites. An overlay of these habitat conditions, derived from model-based estimates and field assessments, revealed that 23% of modelled beaver habitat was classified as not suitable, 36% as low-suitability, 20% as medium-suitability, and 21% as high-suitability. This distribution highlights the considerable variability in habitat quality across the east side of RMNP.

3. Correlation of Habitat Condition Variables

The correlations among habitat condition variables did not always correspond with the expected relationships. The strongest correlation was observed between willow height and ungulate utilization (Rho = -0.55), indicating that sites with the highest ungulate utilization had the lowest willow heights (Figure 11). In contrast, the weakest correlations were found between stream entrenchment ratio and both willow density (Rho = -0.01) and ungulate utilization (Rho = -0.04), suggesting negligible relationships between these variables.

The majority of relationships between variables yielded weak correlations (ρ = 0.1–0.3), with several aligning with expected patterns. For instance, willow dieback positively correlated with ungulate utilization, as anticipated. Similarly, willow height showed expected negative correlations with entrenchment ratio, ungulate utilization, and willow dieback, and a positive correlation with willow density. However, some weak relationships deviated from expectations. Willow dieback was positively correlated with willow density and negatively with both entrenchment ratio and nearest forage, contrary to expectations. Additionally, nearest forage and ungulate utilization showed an unexpected negative correlation, though these deviations were relatively minor.

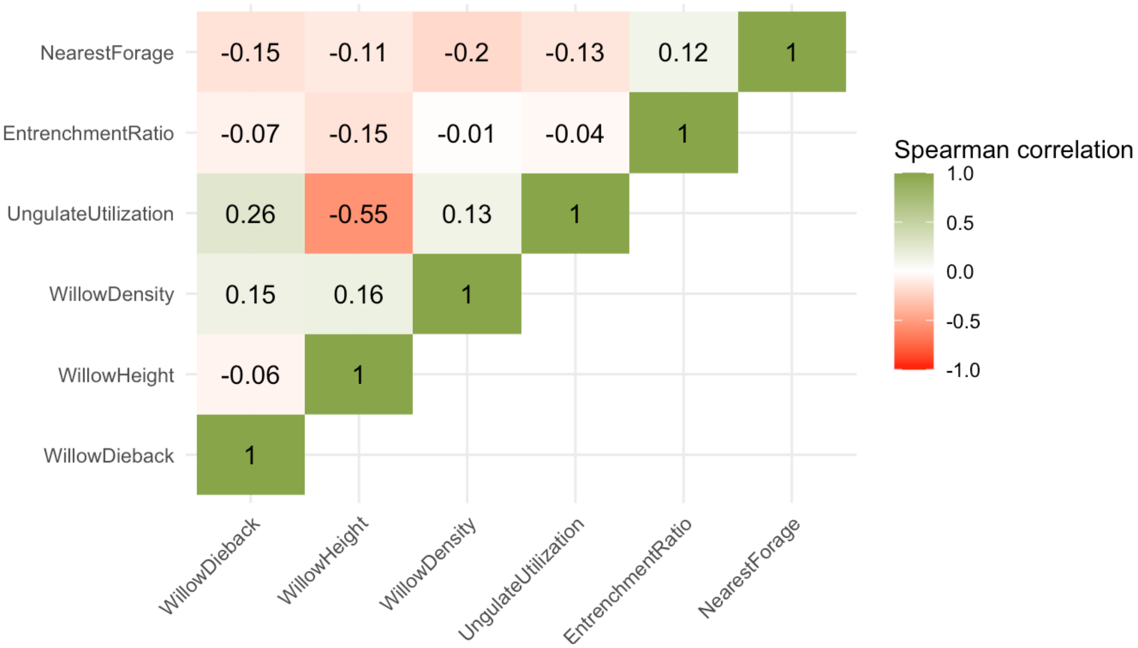

Figure 11. Spearman correlation heatmap with Rho values for all habitat condition variables from the broad-scale habitat condition assessment.

4. Beaver Sign Associated with Habitat Conditions

Analysis of beaver sign across habitat conditions revealed varying associations. Active forage was most commonly associated with high-suitability habitat (66%), while active dams were evenly distributed between medium (67%) and high-suitability habitats (33%). Recent forage was found primarily in medium-suitability (54%) and high-suitability habitats (43%), while historic forage was distributed more broadly across all habitat suitability categories (high-suitability (50%), medium-suitability (34%) and low-suitability (10%)). For all forage sign types, the majority of points occurred in medium to high suitability habitats, indicating a preference for more optimal conditions (Table D1 in Appendix D). Because of widespread habitat degradation, it is likely that several of the historic forage sign points found in low-suitability areas were actually high- or medium-suitability areas at the time the beaver were active.

Fine-scale Habitat Comparison of Active, Recent and Historic sites

Overall, the mixed model analyses demonstrate that key geomorphic variables (stream width, depth, riparian zone, and valley floor width) vary significantly among group types—particularly between active and historic sites. In contrast to these geomorphic variables, vegetation metrics exhibited no differences between group types. A complete table of means and standard error for each variable can be found in Appendix D, Table D7.

1. Geomorphology

Analyses of geomorphic characteristics revealed significant differences among active, recent, and historic groups (Figure 12). Stream width was significantly higher in active sites (9.07 ± 0.29 m) compared to both recent sites (3.90 ± 0.25 m; t = 3.099, p = 0.049) and historic sites (3.08 ± 0.39 m; t = 3.570, p = 0.027). Similarly, stream depth was significantly greater at active sites (0.73 ± 0.024 m) than at recent sites (0.41 ± 0.023 m; t = 3.961, p = 0.017) and historic sites (0.38 ± 0.018 m; t = 3.646, p = 0.027). Riparian zone width showed a similar pattern, with active sites having the widest zones (384.08 ± 18.21 m) and historic sites the narrowest (97.52 ± 7.63 m); the difference between active and historic sites was significant (t = 3.845, p = 0.020). In line with riparian width, valley floor width also differed among group types—with a significant contrast between active sites (500.14 ± 30.31 m) and historic sites (107.55 ± 8.78 m; t = 3.222, p = 0.041). Thalweg dimensions followed a comparable trend, with recent sites (0.54 ± 0.029 m) being significantly shallower than active sites (1.04 ± 0.042 m; t = 3.342, p = 0.035).

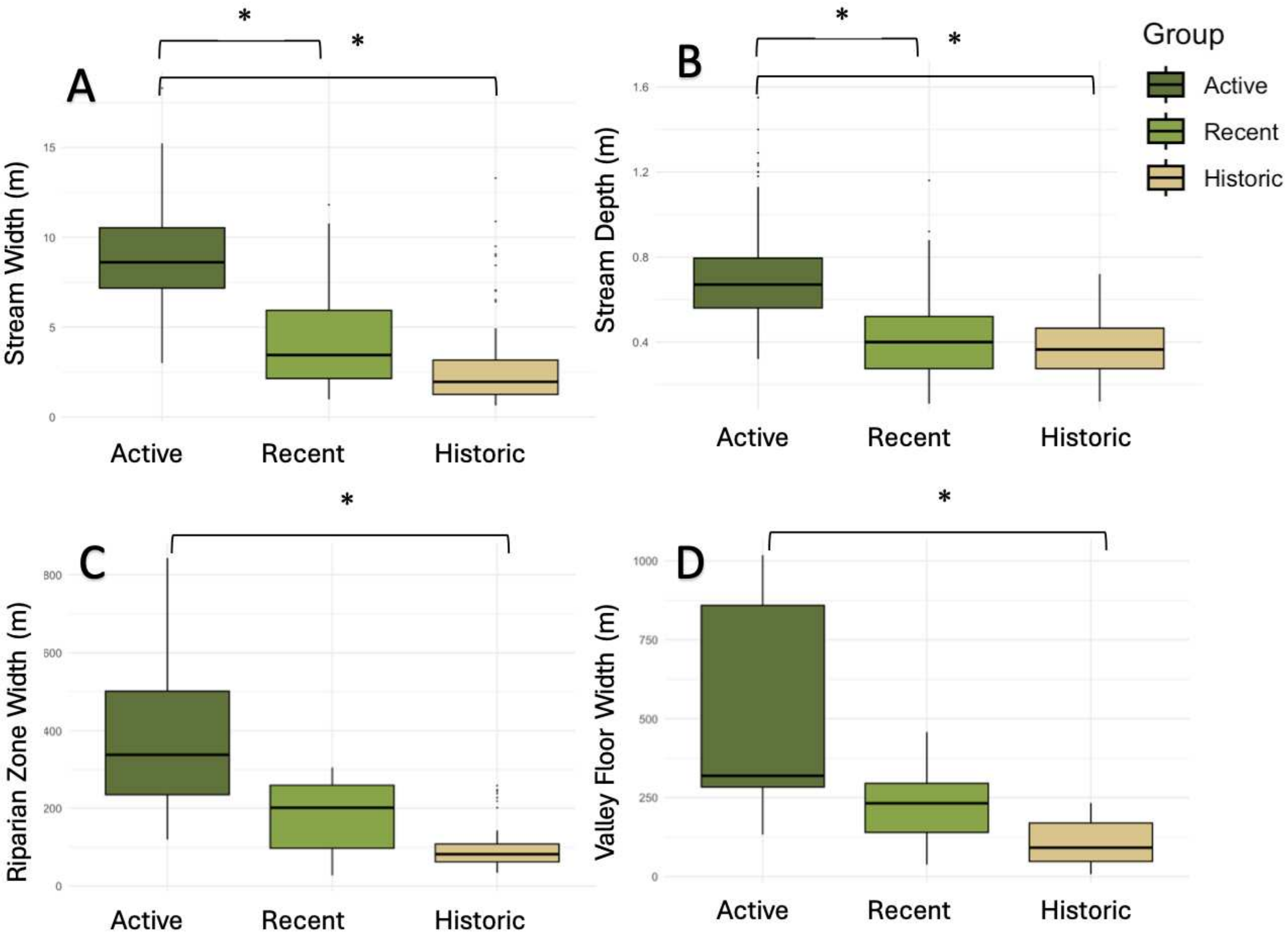

Figure 12. Comparison of geomorphic variables among active, recent and historic beaver site groups. Boxplot A compares average stream width, boxplot B compares average stream depth, boxplot C compares average riparian zone width, and boxplot D compares average valley floor width. Brackets with stars above indicate significant differences among groups.

No statistically significant differences were detected among group types for other geomorphic variables such as bank full depth (Active: 1.10 ± 0.14, Recent: 1.07 ± 0.14, Historic: 0.76 ± 0.15), floodplain incision (Active: 1.07 ± 0.66, Recent: 2.63 ± 0.66, Historic: 1.71 ± 0.67), entrenchment (Active: 1.04 ± 0.10, Recent: 1.41 ± 0.10, Historic: 1.39 ± 0.11), substrate size index (Active: 3.68 ± 0.14, Recent: 3.63 ± 0.12, Historic: 3.54 ± 0.204) and the width: depth ratio (Active: 13.51 ± 0.57, Recent: 11.38 ± 0.71, Historic: 8.87 ± 1.12). Additionally, complexity (Active: 1.87 ± 0.09, Recent: 1.33 ± 0.05, Historic: 1.20 ± 0.07), sinuosity (Active: 2.14 ± 0.007, Recent: 1.64 ± 0.04, Historic: 1.50 ± 0.07), and gradient (Active: 0.026 ± 0.002, Recent: 0.062 ± 0.005, Historic: 0.067 ± 0.006) did not differ significantly. Although these additional models did not yield significant differences, their full summary statistics are provided for reference (Table D2 in Appendix D).

2. Vegetation

Vegetation parameters exhibited less variability among group types compared to geomorphology variables (Figure 13). All mean vegetation variables were relatively consistent across groups and did not show significant differences (Table 1). For example, vegetation and habitat variables such as average willow stem diameter, tallest willow leader, forage biomass index and percent willow dieback all showed relatively minor variations. While these vegetation variables did not yield significant differences, their full summary statistics are provided for reference (Table D3, D4, D5 and D6, Appendix D).

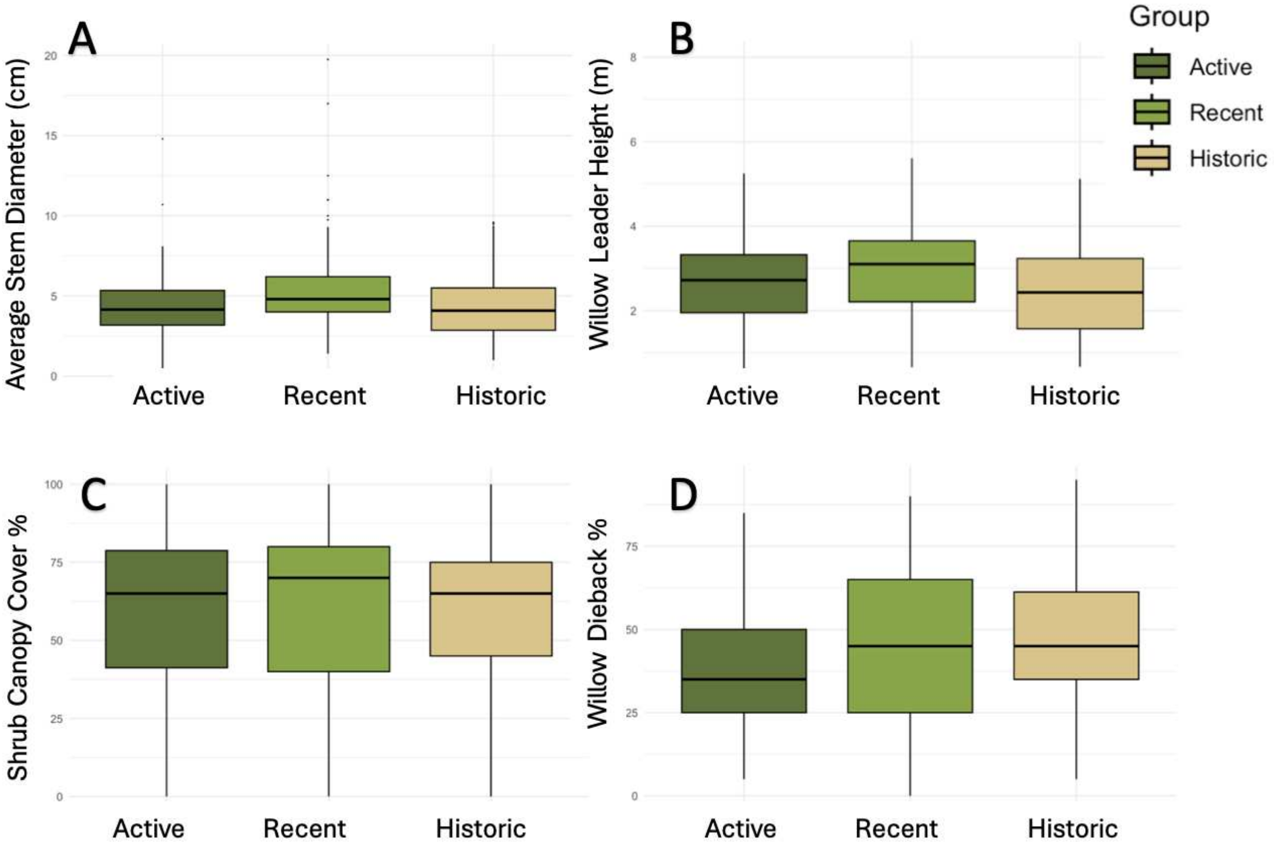

Figure 13. Comparison of vegetation variables among active, recent and historic beaver site groups. Boxplot A compares average willow stem diameter (cm), boxplot B compares average willow leader height (m), boxplot C compares average shrub canopy cover percentage, and boxplot D compares average willow dieback percentage.

Table 1. Means and standard error for each vegetation variable.

Variable	**Mean and Standard Error for each Group**		
	Active	**Recent**	**Historic**
Shrub Species Richness	2.73 (0.20)	2.32 (0.20)	1.97 (0.21)
Average Willow Stem Diameter (cm)	4.42 (0.39)	5.33 (0.39)	4.62 (0.44)
Average Largest Willow Stem Diameter (cm)	7.43 (0.69)	8.82 (0.69)	6.96 (0.77)
Tallest Willow Leader (m)	2.65 (0.15)	2.91 (0.15)	2.51 (0.17)
Shannon Diversity Index	0.60 (0.07)	0.33 (0.07)	0.48 (0.07)
Forage Biomass Index	9834.49 (736.78)	6567.76 (571.36)	2738.71 (232.05)
Number of Conifers	0.10 (0.24)	0.46 (0.25)	0.55 (0.24)
Willow Dieback %	38.73 (1.60)	45.50 (1.80)	45.99 (1.59)
Shrub Canopy Cover %	60.90 (1.77)	58.94 (2.20)	60.25 (1.64)
Forage Species %	85.12 (2.08)	80.49 (2.54)	88.66 (2.06)
Standing Water %	11.02 (1.99)	3.61 (1.08)	4.77 (1.40)
Willow Zone (m)	145.06 (8.60)	98.64 (7.22)	41.27 (2.73)
Forage Height Class	2.20 (0.07)	2.14 (0.08)	2.28 (0.07)
Ungulate Utilization Class	2.55 (0.08)	2.36 (0.09)	2.40 (0.14)
Conifer Age Class	0.14 (0.04)	0.27 (0.05)	0.27 (0.05)
Presence of Conifer	0.08 (0.02)	0.17 (0.03)	0.17 (0.03)
Presence of Sapsucker Damage	0.25 (0.03)	0.19 (0.03)	0.12 (0.03)
Presence of Aspen	0.05 (0.017)	0.01 (0.01)	0.30 (0.04)

Only summary statistics were calculated for willow height categories across active, recent, and historic sites. Overall, the mean percentages of each height category were similar across groups. For willows under 1-meter, mean values were comparable (Active: 14.33 ± 2.47, Recent: 14.63 ± 2.24, Historic: 19.28 ± 3.02), with historic sites having the greatest cover in this category. The 1–2 meter and 2–3 meter height categories also had similar mean values across groups: 1-2 meter (Active: 33.43 ± 3.09, Recent: 26.11 ± 2.71, Historic: 23.38 ± 2.99) and 2-3 meter (Active: 33.25 ± 3.13, Recent: 27.11 ± 2.71, Historic: 20.71 ± 2.87), with active sites having the highest cover in these height categories. For willows over 3 meters, mean values were again comparable (Active: 11.14 ± 2.19, Recent: 17.14 ± 2.54, Historic: 5.68 ± 1.58), with recent sites having the greatest cover. These summary statistics indicate that willow height distributions were broadly similar across site types (Figure 14).

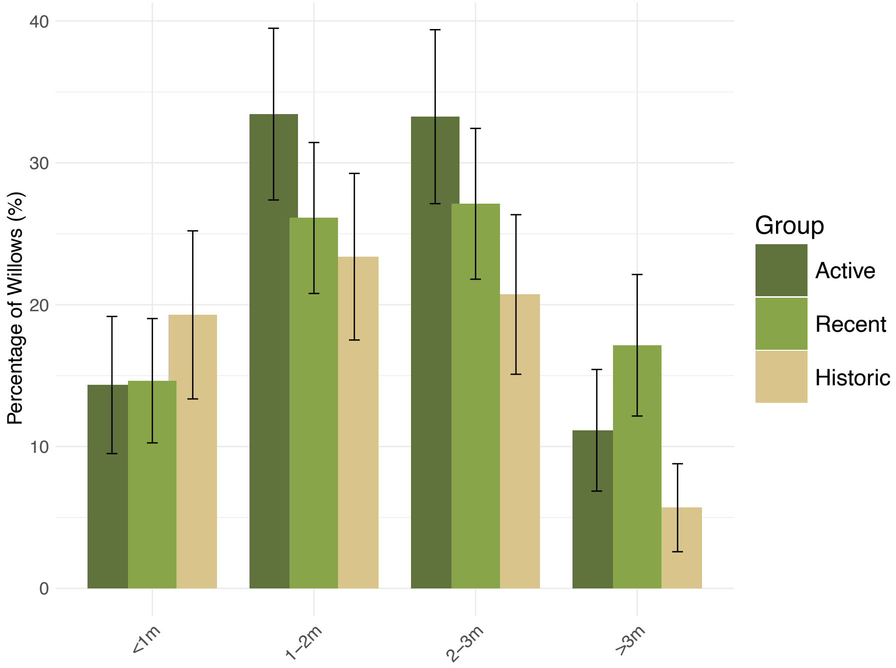

Figure 14. Mean percentage cover of different willow heights across active, recent, and historic sites. Error bars represent the 95% confidence intervals (CI) for the mean cover percentages within each group.

Only summary statistics were calculated for percent shrub canopy cover type across active, recent, and historic sites. Willow canopy cover was the dominant type for all groups, with mean values showing no substantial differences (Active: 73.86 ± 2.53, Recent: 69.81 ± 2.71, Historic: 64.96 ± 3.87). The other forage and non-forage shrub types had consistently lower cover across all groups, with similar mean values among groups: other forage (Active: 11.27 ± 1.53, Recent: 10.68 ± 1.67, Historic: 23.70 ± 3.10) and non-forage (Active: 13.07 ± 1.89, Recent: 11.17 ± 1.79, Historic: 10.04 ± 1.84). These summary statistics indicate that canopy cover distributions were generally comparable across groups, with no strong patterns of differentiation (Figure 15). More formal statistical analyses were pursued by combining cover for all shrub forage species to compare amongst groups, and no significant differences were found (see earlier Vegetation section in results).

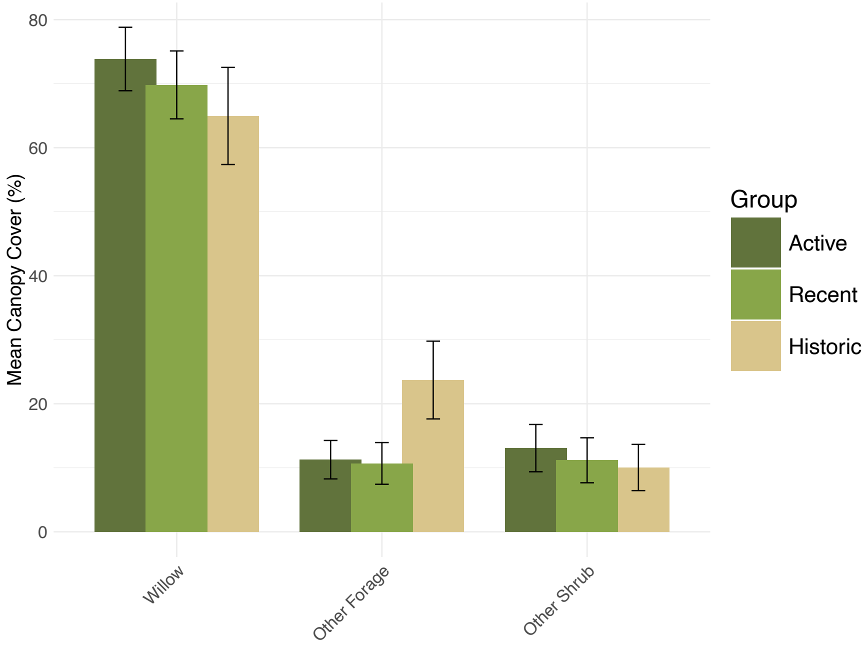

Figure 15. Mean percentage cover of different shrub canopy cover types across active, recent, and historic sites. Error bars represent the 95% confidence intervals (CI) for the mean cover percentages within each group.

Only summary statistics were calculated for ground cover types across active, recent, and historic sites. Herbaceous cover was the dominant ground cover type in all groups, with similar mean values amongst groups (Active: 62.74 ± 1.99, Recent: 66.75 ± 1.70, Historic: 76.87 ± 1.89). Comparable trends were observed for litter (Active: 20.96 ± 1.26, Recent: 24.30 ± 1.25, Historic: 17.81 ± 1.69), and bare ground (Active: 3.28 ± 0.85, Recent: 4.14 ± 0.93, Historic: 0.50 ± 0.24). The mean cover of standing water (Active: 11.02 ± 1.99, Recent: 3.61 ± 1.08, Historic: 4.75 ± 1.40) did stand out visually, so this cover type was analyzed separately with more formal statistics – no significant differences were found (see earlier Vegetation section in results). Rock/sand cover was consistently the lowest category across all groups (Active: 1.99 ± 0.79, Recent: 1.25 ± 0.45, Historic: 0.07 ± 0.07). These summary statistics indicate that ground cover distributions were generally similar across site types, with only minor variations in specific categories (Figure 16).

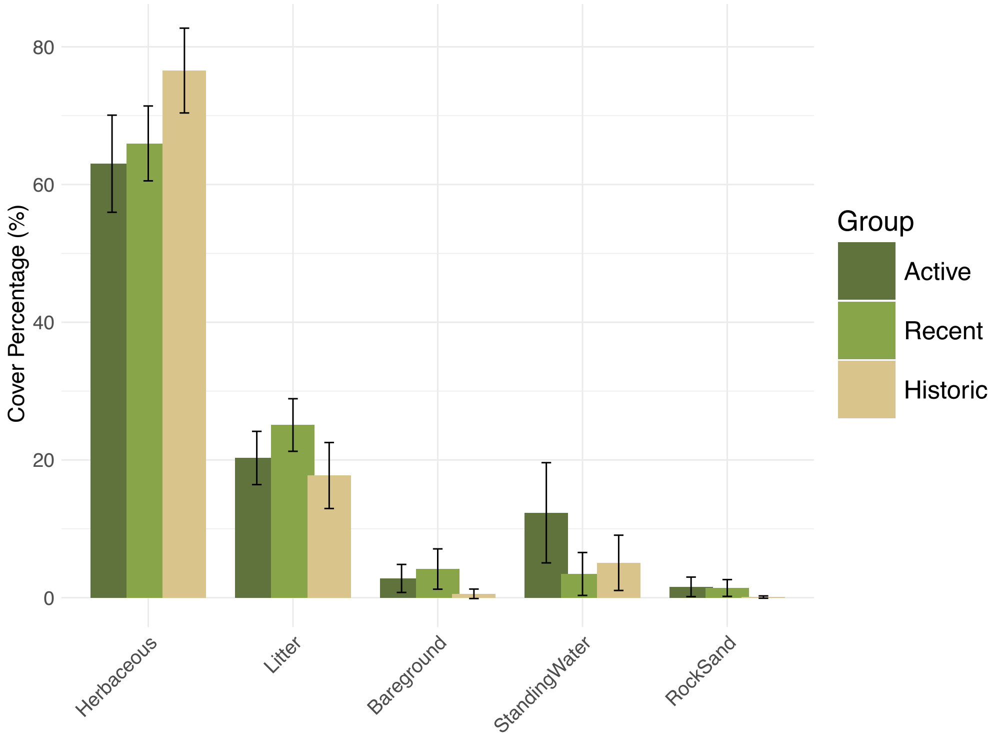

Figure 16. Mean percentage cover of different ground cover across active, recent, and historic sites. Error bars represent the 95% confidence intervals (CI) for the mean cover percentages within each group.

IV. Discussion

Key Findings

1. Overview

This study analyzed beaver habitat at two spatial scales—broad-scale surveys and fine-scale habitat comparisons—providing both a high-level overview and detailed insights into local habitat dynamics. Broad-scale analyses highlighted variability in willow condition and a strong correlation between ungulate browsing and willow height, indicating that browsing pressure greatly reduces willow condition, the key forage species for beaver at this study site. In contrast, the fine-scale analysis showed that vegetation conditions did not vary across occupancy categories, although certain stream geomorphology factors did. This suggests that geomorphic factors may be more important for beaver establishment and persistence than vegetation quality alone for areas that already have adequate forage. At first glance, these findings suggest that different drivers influence beaver establishment at different spatial and temporal scales.

2. Fine-scale Findings

A surprising finding was the lack of relationship between vegetation variables and beaver occupancy at the fine scale. Given that vegetation is typically considered a key driver in beaver habitat selection (Allen, 1983), it was expected that metrics such as willow zone width, forage biomass index, and willow stem diameter would be significantly greater at sites with currently active beavers. However, mean vegetation values across all nine sites—including the six without beavers—suggest that each site provides sufficient forage for beaver occupancy (Allen, 1983; Macfarlane et al., 2015; McComb et al., 1990)

The fine-scale habitat comparison revealed that active sites had significantly greater stream depth and width compared to recent and historic sites. These active sites also had notably broader riparian and valley zones compared to historic sites. The relationship between stream width, depth, and beaver activity is complex: while beavers can modify these characteristics through their dam-building and foraging behaviors, they also exhibit preferences for sites with inherently favorable stream conditions (Dittbrenner et al., 2018; Muller-Schwarze, 2011). Since active sites in this study exhibited naturally broader valleys and riparian zones that support wider, deeper streams, these features may be important to beaver site selection. These findings suggest that once vegetation reaches a threshold of suitability, geomorphic conditions may become the dominant driver of beaver establishment RMNP.

However, disentangling the extent to which beavers shape their environment versus respond to preexisting conditions is challenging—especially given the magnitude and longevity of their influence on the landscape (Ritter et al., 2020). This complexity makes predicting the specific site characteristics that drive beaver establishment challenging. This distinction is crucial for understanding habitat suitability and informing effective restoration strategies.

Other geomorphological factors—including width: depth ratio, floodplain incision, and substrate size—did not differ significantly among sites. However, when compared to habitat suitability metrics for beaver occupancy in the literature, all sites exhibited geomorphic conditions considered highly suitable (Macfarlane et al., 2015; McComb et al., 1990; Pollock et al., 2004; Suzuki & McComb, 1998). While no significant differences were found in stream complexity, gradient, or sinuosity, these results align with research indicating that larger valleys and wider riparian zones tend to support more complex geomorphology, enhancing habitat suitability for beavers (Dittbrenner et al., 2018; Van Appledorn et al., 2019). Lower stream gradients create favorable conditions for dam-building by reducing water velocity and erosion, leading to more stable dam construction (Baker & Hill, 2003; Rugg et al., 2023). Such environments allow beaver to more readily manipulate water flow, forming deep pools that expand wetland habitat.

For beaver restoration efforts, establishing long-term beaver complexes—consisting of multiple colonies—requires optimal stream geomorphology (e.g., wide valleys, low gradient) and sufficient forage availability. The findings suggest that when vegetation availability is relatively similar among sites, geomorphic factors may play a more influential role in beaver establishment.

Long-term source population sites provide greater potential for habitat expansion, enhanced predator protection, and a higher likelihood that offspring can establish nearby colonies without traveling long distances (Anderson, 1989; Sun et al., 2000).

3. Broad-scale Findings

Findings from the broad-scale habitat assessment reveal considerable variability in beaver habitat across the study area, with an overall trend toward lower suitability. Willows were generally short, with sparse cover being the most common category. Moderate levels of ungulate browsing and willow dieback were also prevalent. However, some conditions remained favorable for beavers, particularly low stream entrenchment and high forage proximity to the stream's edge. This suggests that, at a broad scale, these factors are not primary limitations for beaver habitat.

Among habitat variables, the strongest correlation was between willow height and ungulate utilization, reinforcing concerns that elk and moose browsing are degrading riparian shrublands in RMNP. Other correlations were weak or negligible. For example, while increased ungulate browsing was expected to correspond with greater willow dieback (Kaczynski, 2013), the strength of this relationship was weaker than anticipated. Some unexpected trends also emerged, such as a weak positive relationship between willow dieback and willow density. These weak correlations suggest either that true relationships among these variables are minimal or that additional factors (e.g., species composition, elevation, past disturbances) influence habitat conditions. Further research is needed to better understand these dynamics.

The strong correlation between willow height and ungulate browsing underscores the historical impact of herbivory on willow condition, an effect that may be underrepresented in the data, as many areas in the study area that currently lack willow cover likely supported it in the past but were degraded by prolonged browsing pressure. The impact this has had on the beaver population is likely significant, as analysis of beaver sign suggests that beavers are selecting the most suitable sites. While they may forage in lower-quality habitats, active sign was concentrated in areas with optimal willow condition, stream entrenchment and forage proximity, whereas historic sign was more evenly distributed across habitat qualities. This pattern indicates that habitat degradation—primarily due to ungulate over-browsing and, to a lesser extent, wildfire—has reduced willow cover and height in present day conditions, constraining the extent of current beaver activity compared to historic distributions.

Synthesizing findings from both scales reveals a dual narrative: fine-scale assessments indicate that habitat in select locations remains suitable but unoccupied, while broad-scale data highlight forage limitations and degradation due to browsing. These results suggest that while ungulate browsing contributed to historical habitat degradation and beaver decline, it is unlikely to be the sole factor preventing re-establishment today. Past declines in beaver populations may have been driven by vegetation quality, whereas geomorphological factors appear to dictate where beavers can persist or reestablish today.

4. Beaver Population Size as a Limiting Factor

This study aimed to assess whether vegetation or geomorphology limits beaver re-establishment. The findings suggest that neither is a constraint, as suitable habitat exists but remains unoccupied. Instead, limited source populations and long-term habitat dynamics may be the primary limiting factors rather than immediate habitat quality. This raises the possibility that other influences, such as beaver population dynamics, are restricting re-establishment (Fryxell, 2001). Rather than habitat limitations, a shortage of dispersing individuals may be preventing beaver populations from expanding into all suitable areas.

This idea of beaver populations being the main limiting factor in RMNP is further supported by results from the beaver occupancy survey, which indicate that historically, beaver activity was much more widespread than it is today. Current beaver activity covers a much smaller spatial extent than historical activity, with historic ranges being 10-14 times larger than active ones. Only 4% of suitable stream segments surveyed showed active sign in RMNP. In contrast, 25% of surveyed stream segments contained historic beaver sign, and this is likely an under-representation due to sign degradation over time. Natural disturbances such as wildfires, floods, and over browsing by ungulates likely contribute to the accelerated disappearance of historic beaver sign. Moreover, the historic-sign density estimate is likely underrepresented, as in this study challenges were encountered in recording all historic forage sign points in areas of exceptionally high density. The beaver occupancy survey at RMNP, aligned with statewide projections, shows a significant decline in both beaver populations and available habitat (Scamardo et al., 2022).

Overall, both the fine-scale and broad-scale beaver occupancy results point toward a lack of dispersing individuals being a major limiting factor to beaver occupancy. Because the presence of nearby source populations is a critical consideration. Habitat improvements alone may not lead to beaver establishment if no individuals are available to establish in the area. In cases where natural dispersal is limited by geographic barriers, translocating beavers from established populations to suitable but unoccupied habitat may be a viable strategy for increasing connectivity and establishment (Boyle & Owens, 2007). However, successful translocation requires careful site selection, disease screening, and post-release monitoring to ensure long-term viability (McKinstry & Anderson, 2002).

A study in Sweden found that despite the availability of suitable habitat, the spread of reintroduced beaver was influenced by dispersal limitations (Hartman, 1995). Beavers often have to travel far distances to find suitable habitat or a mate. Dispersal barriers, such as steep topography and fragmented riparian corridors, can limit re-establishment, making connectivity improvements a priority in some landscapes (Dittbrenner et al., 2018; McKinstry & Anderson, 2002). Adequate cover of riparian vegetation is not only important for beaver forage, but also cover from predators, especially when young beavers are leaving their parent colony to migrate to other sites (Sun et al., 2000). Future research should explore strategies to enhance movement corridors and evaluate how restoration efforts influence population expansion.

Ecological and Restoration Implications

The unexpected lack of relationship between vegetation and beaver occupancy at the fine scale may reflect regional variations in the importance of geomorphic versus vegetation-based habitat predictors. While broad-scale predictors such as access to perennial water, a stream gradient below 15%, and sufficient forage remain essential, the degree to which these factors influence beaver occupancy varies by region due to differences in hydrology, vegetation composition and historical land-use (Baker & Hill, 2003; Dittbrenner et al., 2018).

Some beaver habitat suitability models, such as one for the Snohomish River Basin, found geomorphic variables to be more predictive of beaver occupancy than vegetation data (Dittbrenner et al., 2018). This aligns with findings from the fine-scale assessment in this study. Interestingly, a habitat suitability model created to predict beaver occupancy in the Rocky Mountains selected stream gradient, bank steepness, and vegetation density as the major variables (Retzer, 1956), yet these variables did not differ amongst activity groups in this study. If these variables had been compared across a broader gradient of habitat suitability, differences might have emerged.

This raises the issue of scale. Broad-scale models, like beaver habitat suitability models, are invaluable for guiding site selection in beaver restoration projects. However, broad-scale findings may not always apply at the local, fine-scale. In one case, a widely used beaver habitat selection model (McComb et al., 1990) failed to predict occupancy accurately, underscoring the need for local validation before broad application (Barnes & Mallik, 1997). While understanding broad-scale drivers is essential, targeted restoration plans may require a more localized perspective. Site-specific knowledge and context is important to consider as these broad-scale models may not capture localized beaver preferences, predator pressure, mortality from human conflict or habitat connectivity, or competition for forage with ungulates (Baldwin, 2013; Barnes & Mallik, 1997; EcoMetrics, 2022; Stoll & Westbrook, 2020).

Even in this study, which modeled broad-scale habitat conditions to assess beaver habitat on the east side of RMNP, discrepancies between localized conditions and the broad-scale model emerged. While the broad-scale analysis categorized most fine-scale sites as highly suitable, some portions were ranked as medium, low, or unsuitable. For example, in Beaver Meadows, where aspen predominates over willow, the broad-scale analysis deemed the area unsuitable. In contrast, the fine-scale analysis, which considered forage species beyond just willow, found that forage height, biomass, and cover were not only adequate but highly suitable for beaver establishment. This contrast highlights how fine-scale analysis can provide a more nuanced and accurate understanding of habitat suitability than broader-scale assessments.

V. Conclusion

This study underscores the importance of tailoring restoration efforts to site-specific conditions, as the findings highlight the need to assess beaver habitat suitability across multiple spatial scales—emphasizing the value of ground-truthing predictive models used for restoration site selection. The finding that fine-scale data revealed a more detailed and nuanced story is not unique, but it reinforces the limitations of predictive models and the enduring importance of field-based insight. In the case of RMNP, this study provides targeted guidance for prioritizing restoration at sites with optimal geomorphology to address key ecological drivers and constraints. Without this understanding, broad-scale vegetation enhancement alone may not have supported successful beaver establishment.

In restoration and conservation, we often hear the phrase, “build it and they will come.” In this case, I propose a revision: “build it right, and perhaps they will build it better”—capturing the essence of beaver-based restoration as a low-tech, cost-effective, nature-based solution that works with our understanding of ecosystem processes. Looking ahead, continued monitoring of beaver restoration projects is essential to identify knowledge gaps, especially as implementation increasingly outpaces research. In such a context, the principles of adaptive management become vital for long-term success.

While management decisions must be informed by local context, broader goals—such as restoring hydrologic processes, supporting resilient vegetation communities, and maintaining landscape connectivity—offer a strong foundation. Restoring riparian shrublands and supporting beaver activity can create cascading ecological benefits, as these systems harbor high biodiversity and contribute disproportionately to ecosystem functioning and resilience in our changing world (Schweiger et al., 2016).

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Appendix A: GIS Workflows

Workflow A1. Primary GIS Beaver Habitat Suitability Analysis

1. Data Acquisition:
   - A vector outline of Rocky Mountain National Park (RMNP) and the Continental Divide was used as the spatial boundary.
   - A vector layer of RMNP streams was obtained from the National Park Service (preferred over NHD flowlines due to higher accuracy).
   - A 1-meter resolution Digital Elevation Model (DEM) was downloaded from the USGS and processed as follows:
     - Projected to match the RMNP boundary.
     - Clipped to the RMNP boundary.
     - Slope analysis performed and reclassified to include only slopes under 15%.
     - Further clipped to a 30-meter stream buffer.
   - The National Land Cover Database (NLCD) vegetation cover data (30-meter resolution) was processed as follows:
     - Clipped to the RMNP boundary.
     - Reclassified into vegetation types: woody wetlands, open water, shrub/scrub, and emergent herbaceous wetlands.
     - Clipped to a 30-meter stream buffer.
2. Habitat Suitability Model:
   - The slope and vegetation layers were overlaid.
   - Areas above 11,000 feet in elevation were removed.
   - All layers were projected to NAD 1983 UTM Zone 13N to ensure spatial consistency.

Workflow A2. Interpolating Habitat Data & Connecting Beaver Sign to Habitat Data

1. Data Processing:
    - Buffered streams to 60 meters and dissolved boundaries.
    - Performed Inverse Distance Weighting (IDW) interpolation on habitat variables:
        - Dieback (ranked 0-5, adjusted symbology to 0-4 due to no observations of 5).
    - IDW outputs clipped to a 30-meter stream buffer for visualization.
2. Standardizing Habitat Suitability Rankings:
    - Reclassified IDW habitat layers to a 0-3 scale, with Density (DN), Height (HT), and Utilization (UT) grouped into the highest category.
    - Weighted overlay applied with the following importance:
        - Density (0-4): 25%
        - Height (0-4): 35%
        - Utilization (0-4): 0%
        - Dieback (0-4, adjusted to 0-3): 5%
        - Nearest Forage (0-3): 5%
        - Entrenchment Ratio (0-3): 30%
    - Reclassified again to adjust tool limitations (values 0-3 converted to 1-4).
    - Adjusted value scaling for better differentiation:
        - 1 → 1, 2 → 10, 3 → 50, 4 → 100
    - Converted raster to polygon format:
        - Created multipart features (without simplifying polygons).
        - Applied symbology to display ranked suitability classes.
    - Clipped final suitability map to a 30-meter stream buffer.

3. Connecting Beaver Sign to Habitat Suitability:
    - Buffered streams to 60 meters to capture all beaver sign points.
    - Re-clipped weighted habitat polygons to the 60-meter buffer.
    - Performed a spatial join between the weighted polygon (60m clip) and beaver sign points.
    - Used the summarize tool to count beaver sign types per habitat rank.

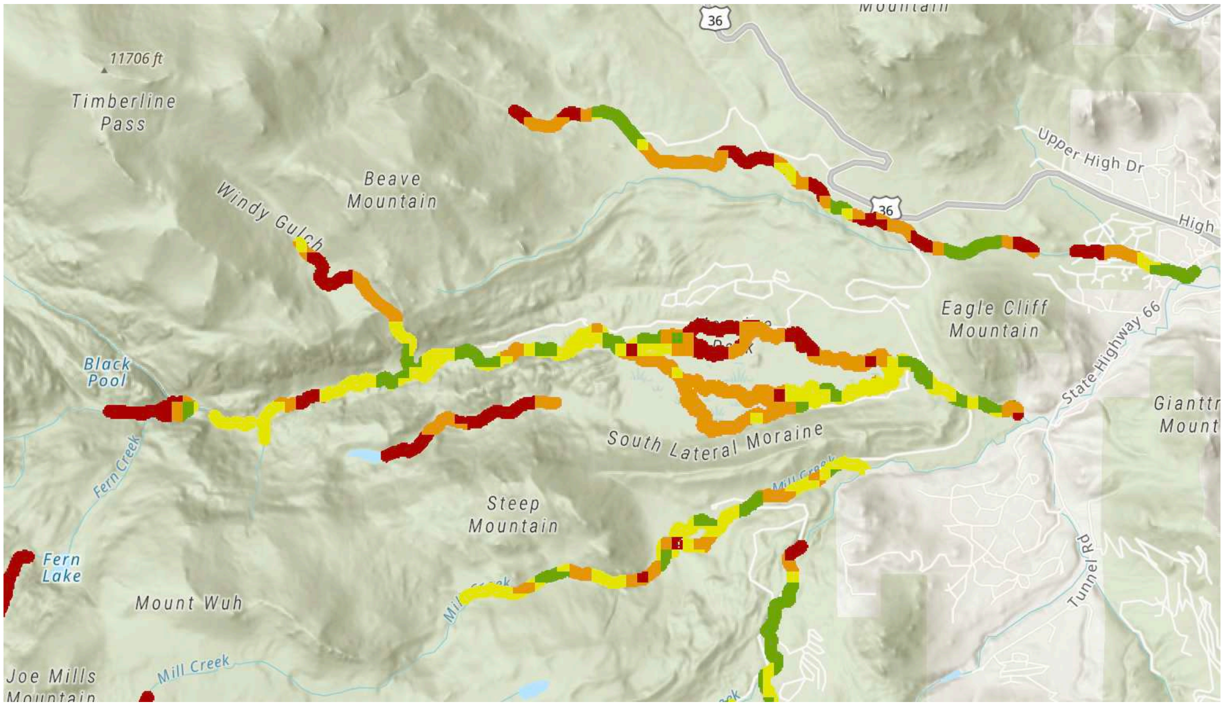

Figure A1. Snapshot of modeled beaver habitat suitability – Inverse Distance Weighted (IDW) output for overlayed habitat conditions.

Workflow A3. Beaver Sign Density per 500m of Stream

1. Stream Segmentation:
    - Manually split stream segments into ~400-600m sections.
    - Buffered segments to 30 meters (flat ends, no dissolve).
2. Spatial Join for Active Beaver Sign:

  - Target Features: 500m stream segments with a 30m buffer.
  - Join Features: Active beaver forage sign points (A, R, or H).
  - Join Operation: One-to-One.
  - Match Option: Intersect (search radius: 15m).

3. Beaver Sign Density Calculation:
   - Added a new field for stream length in the spatial join table.
   - Used the Join Field tool to populate stream length using a common identifier.
   - Calculated beaver sign density per 500m:
     - Density_500m = (Join Count / Stream Length) * 500
   - Averaged density counts to determine Active, Recent, and Historic Beaver Forage Sign per 500m.
4. Visualization Strategy, layer ordering for clear interpretation:
   - Active Signs: Green (all other layers transparent).
   - Recent Signs: Yellow (all other layers transparent).
   - Historic Signs: Red (non-sign areas gray for contrast).

Appendix B: Methods Variables

Table B1. Field-based vegetation variables used to investigate differences between active, recent and historic beaver sites on the east side of RMNP, CO, USA.

Variable	Unit	Method	Description
Ground cover types	%	Estimated for herbaceous, litter, rock/sand, bare ground, standing water, summing to 100%.	Absolute ground cover percentages estimated for different categories (Small et al., 2016).
Shrub species identification	Species code	All shrubs identified to species level.	More species potentially indicate higher biodiversity and better habitat quality.
Shrub canopy cover	%	Estimated for each shrub species (absolute, species evenness).	Species evenness and canopy cover percentage for each species.
Total number of shrub species, richness	Number	Count of total shrub species in the plot.	Species richness, indicating higher biodiversity and potentially better forage availability.
Total shrub canopy cover	%	Estimated relative to ground cover.	More shrub canopy cover can indicate better habitat quality for beavers.
Shannon Diversity Index (shrub species)	-	$H' = -\sum (p_i \cdot \ln(p_i))$	Higher Shannon Diversity Index means more diverse forage and construction resources.
Willow height class	%	Estimate the percentage of willows in height classes: <1m, 1-2m, 2-3m, >3m – summing to 100%	Higher willow height classes may indicate better forage and cover for beavers.
Tallest willow leader	m	Identified tallest willow leader in each plot to measure.	Taller leaders may indicate better forage resources (Peinetti et al., 2002).
Forage height class	Categorical	Average classification: 0: no forage, 1: short <1m, 2: medium 1-2m, 3: tall >2m. Forage: aspen, birch, alder, willow, cottonwood.	Taller forage species means greater forage availability.
Forage biomass index	-	Riparian width × (Canopy cover of forage species + Forage species height).	More biomass means better forage and construction resources for beavers.

Willow stem diameter	cm	Measured 5-10 willow stems at the base of the plant and averaged.	Larger stems can indicate older, more mature willows with more resources.
Largest willow stem diameter	cm	Measured 3-5 of the largest stems in the plot.	Larger stems can indicate older, more mature willows with more resources.
Willow dieback	%	Percentage of willow dieback/standing dead in the plot, 0-100%	More dieback may indicate lower habitat quality for beavers (Peinetti et al., 2002).
Willow utilization by ungulates	Categorical	0: no willow, 1: no evidence of browsing, 2: “low” some evidence but healthy leader growth and no dead wood/structure and growth form no impacted, 3: “medium” some secondary branches and some dead wood/visible impacts to structure and growth form, 4: “high” several secondary branches and over 50% dead wood/significant impact on structure and growth form.	Higher browse severity indicates more browsing pressure from ungulates (Hood & Bayley, 2009).
Conifer presence	Presence/ Absence	Presence or absence of conifers, number of conifers, and if adult age conifers are present (>12.5 cm DBH).	Conifer encroachment often signals riparian degradation (Macfarlane et al., 2017).
Aspen presence	Presence/ Absence	Presence or absence of aspen, or nearest distance to aspen stands.	Aspen is a preferred forage species, though rare in RMNP beaver habitat (Baker & Hill, 2003).
Presence of sapsucker damage on willow	Presence/ Absence	Presence or absence of sapsucker damage (*Cytospora* canker) on willow.	Damage by sapsuckers can impact willow health, influencing beaver forage availability (Kaczynski et al., 2014).

Table B2. Field-based stream geomorphology variables used to investigate differences between active, recent and historic beaver sites on the east side of RMNP, CO, USA.

Variable	Unit	Method	Description
Stream width	m	Width of stream channel measured from the high-water mark indicators. Indicators included break in slope, change in vegetation or soil/substrate, and/or debris lines.	Wider streams mean more water availability and cover, although too wide can preclude dam building. Although, flow rate also needs to be low enough for dam construction.
Stream depth	m	Depth at ¼ stream width from each bank and ½ across stream measured to the high-water mark indicators. All measurements averaged.	Higher depth is more suitable because it offers more cover and requires less dam building. Although, flow rate also needs to be low enough for dam construction.
Width: depth Ratio	-	Calculated as average stream width / average depth.	Stream channels that are too wide and shallow or too narrow and deep are hard to dam. Preferred ratio is between 10:1 and 20:1.
Thalweg depth	m	Deepest part of stream bed to the high-water mark indicators.	Localized deep spots provide refuge and are important for initial lodge/den construction.
Bank full height	m	Measured from thalweg to indicator mark of bank full stage.	Higher bank full height may indicate incision and reduce stream's access to floodplains.
Substrate type	Categorical	Visual assessment: dominant substrate type assigned a score (1 = mud/silt, <0.06mm, 2 = sand, 0.06-2mm, 3 = gravel, 2-4mm, 4 = pebble, 4-64mm, 5 = cobble, 64-256mm, 6 = boulders, >256mm)	Finer sediments may facilitate damming, while coarser substrates may be less suitable for dam anchoring.
Floodplain incision – floodplain connectivity	-	Bank full Height / Thalweg Depth	Measures the depth of channel incision relative to the thalweg. Higher values indicate a more incised channel, while lower values suggest better floodplain connectivity (Harrelson et al., 1994)

Entrenchment rating – floodplain accessibility	-	Lowest Bank Height / Bank full Height	Evaluates floodplain disconnection by comparing the lowest bank height to the bank full height. <1 → Frequent overbank flooding (less incised). >1 → Restricted floodplain access (more incised) (Harrelson et al., 1994).

Table B3. GIS-based stream geomorphology variables used to investigate differences between active, recent and historic beaver sites on the east side of RMNP, CO, USA.

Variable	Unit	Method	Description
Willow zone width	m	Measured at same geomorphology field-based points using aerial imagery.	Wider willow zone means increased riparian forage, and cover protection from predators.
Riparian zone width (Floodplain)	m	Measured at same geomorphology field-based points using aerial imagery.	Wider riparian zone/floodplain means a larger wetted area for dams to flood and habitat to expand.
Valley floor width	m	Measured at same geomorphology field-based points using aerial imagery.	Larger valley floor means more area for foraging and dam construction.
Total sinuosity	-	Stream distance / straight line distance between endpoints.	Higher sinuosity benefits riparian forage and slows flow for dam stability.
Channel complexity	Number	Count of channels along transect.	More secondary channels allow for more cover, foraging area, and more stable dams.
Stream gradient	% rise	Difference in elevation between start and end points divided by stream distance of sampling segment.	Lower gradients are more suitable as dams are more stable.

Appendix C: R Code

This appendix provides examples of the R code used for statistical analyses conducted in this study.

General Mixed Model

```
library(lme4)
# Mixed-effects model for log-transformed Floodplain Zone Width
Model <- lmer(log(Floodplain.Zone.Width) ~ Group + (1|Site), data = combined_data)

# ANOVA F-test for fixed effects
anova(Model)

#Tukey adjusted pairwise comparisons
emmeans(Model, pairwise ~ Group)

# Residuals vs. Fitted Plot
plot(Model)
```

Ordinal Regression Model

```
library(ordinal)
# Cumulative link mixed model (CLMM) for Substrate Type
ModelSubstrate <- clmm(Substrate_Type ~ Group + (1 | Site), data = combined_data)

# Model summary
summary(ModelSubstrate)

# Post-hoc pairwise comparisons with Tukey adjustment
library(emmeans)
emmeans(ModelSubstrate, pairwise ~ Group, adjust = "tukey")

# Plot estimated marginal means
plot(emmeans(ModelSubstrate, ~ Group), type = "response")
```

Beta Regression with Mixed Effects Model

```
library(glmmTMB)
# Beta mixed-effects model for Adjusted Willow Dieback
Model_Dieback_Mixed <- glmmTMB(
  Adjusted_Dieback ~ Group + (1 | Site),
  family = beta_family(),
  data = combined_data_veg)

# Model summary
summary(Model_Dieback_Mixed)

# Pairwise comparisons
pairwise_comparisons_mixed <- emmeans(Model_Dieback_Mixed, pairwise ~ Group)
summary(pairwise_comparisons_mixed)
```

Chi-Square Test

```
library(dplyr)
# Create binary presence column for Aspen
combined_data_veg <- combined_data_veg %>%
  mutate(Aspen_Presence_Binary = ifelse(Aspen_Presence > 0, 1, 0))

# Create contingency table for Aspen presence
aspen_counts <- table(combined_data_veg$Group, combined_data_veg$Aspen_Presence_Binary)

# Chi-square test
chi_square_aspen <- chisq.test(aspen_counts)
print(chi_square_aspen)
```

Appendix D: Results Tables and Figures

Table D1. Associations between beaver sign types and habitat suitability classifications.

Beaver Sign Type Points	Habitat Condition Categories			
	Not Suitable	Low Suitability	Medium Suitability	High Suitability
Active Forage	0.0%	0.0%	34.6%	65.4%
Active Dam	0.0%	0.0%	66.7%	33.3%
Recent Forage	0.0%	3.0%	54.0%	43.0%
Dam Holding Water	3.3%	3.3%	44.3%	49.2%
Historic Forage	6.3%	10.3%	33.5%	49.8%
Dam not Holding Water	8.3%	8.3%	41.7%	41.7%
Historic Dried Dam	0.0%	20.0%	40.0%	40.0%
Lodge	0.0%	5.6%	38.9%	55.6%
Food cache	0.0%	12.5%	50.0%	37.5%
Bank Den	0.0%	0.0%	0.0%	100.0%

Table D2. Summary of statistical results for Geomorphological variables analyzed with Linear Mixed-Effects Models. Group Comparison column codes: A-R (Active vs. Recent), A-H (Active vs. Historic), R-H (Recent vs. Historic). Green highlighted values represent significant differences amongst groups.

Variable	Group Comparison	p-value	Test Statistic
Width (m)	A-R	0.049	3.099
Width (m)	A-H	0.027	3.570
Width (m)	R-H	0.878	0.491
Depth (m)	A-R	0.027	3.646
Depth (m)	A-H	0.017	3.961
Depth (m)	R-H	0.921	0.389
Riparian Zone (m)	A-R	0.102	2.506
Riparian Zone (m)	A-H	0.020	3.845
Riparian Zone (m)	R-H	0.421	1.350
Thalweg (m)	A-R	0.057	2.982
Thalweg (m)	A-H	0.035	3.342
Thalweg (m)	R-H	0.919	0.393
Valley Floor Width (m)	A-R	0.324	1.579
Valley Floor Width (m)	A-H	0.041	3.222

Valley Floor Width (m)	R-H	0.299	1.646
Willow Zone (m)	A-R	0.6075	0.993
Willow Zone (m)	A-H	0.1904	2.009
Willow Zone (m)	R-H	0.5926	1.019
Bankfull Depth (m)	A-R	0.988	0.148
Bankfull Depth (m)	A-H	0.2951	1.651
Bankfull Depth (m)	R-H	0.3503	1.509
W:D Ratio	A-R	0.8164	0.618
W:D Ratio	A-H	0.4286	1.333
W:D Ratio	R-H	0.7592	0.724
Entrenchment Rating	A-R	0.0948	-2.594
Entrenchment Rating	A-H	0.1168	-2.376
Entrenchment Rating	R-H	0.987	0.154
Floodplain Incision	A-R	0.2923	-1.669
Floodplain Incision	A-H	0.7843	-0.678
Floodplain Incision	R-H	0.6161	0.977
Complexity Rating	A-R	0.5548	1.089
Complexity Rating	A-H	0.364	1.478
Complexity Rating	R-H	0.9181	0.397
Stream Gradient	A-R	0.183	-2.054
Stream Gradient	A-H	0.209	-1.931
Stream Gradient	R-H	0.995	0.098
Sinuosity	A-R	0.157	2.179
Sinuosity	A-H	0.096	2.534
Sinuosity	R-H	0.92	0.391

Table D3. Summary of statistical results for Vegetation variables analyzed with Linear Mixed-Effects Models. Group Comparison column codes: A-R (Active vs. Recent), A-H (Active vs. Historic), R-H (Recent vs. Historic).

Variable	Group Comparison	p-value	Test Statistic
Shrub Species Richness	A-R	0.3846	1.435
Shrub Species Richness	A-H	0.0843	2.637
Shrub Species Richness	R-H	0.4811	1.228
Average Stem Diameter (cm)	A-R	0.3093	-1.641
Average Stem Diameter (cm)	A-H	0.9397	-0.338
Average Stem Diameter (cm)	R-H	0.4902	1.209
Average Largest Stem Diameter (cm)	A-R	0.3936	-1.427
Average Largest Stem Diameter (cm)	A-H	0.8924	0.459
Average Largest Stem Diameter (cm)	R-H	0.2467	1.801

Tallest Willow Leader (m)	A-R	0.4837	-1.237
Tallest Willow Leader (m)	A-H	0.802	0.645
Tallest Willow Leader (m)	R-H	0.2524	1.787
Shannon Diversity Index	A-R	0.0709	2.772
Shannon Diversity Index	A-H	0.4877	1.217
Shannon Diversity Index	R-H	0.3236	-1.580
Forage Biomass Index	A-R	0.6227	0.966
Forage Biomass Index	A-H	0.2238	1.880
Forage Biomass Index	R-H	0.6491	0.919
Number of Conifers	A-R	0.5954	-1.013
Number of Conifers	A-H	0.4453	-1.305
Number of Conifers	R-H	0.9617	-0.267

Table D4. Summary of statistical results for variables analyzed with Beta Mixed-Effects Regression. Group Comparison column codes: A-R (Active vs. Recent), A-H (Active vs. Historic), R-H (Recent vs. Historic). All variables were collected as percentage data up to 100%.

Variable	Group Comparison	p-value	Z-Score
Willow Dieback %	A-R	0.9972	-0.071
Willow Dieback %	A-H	0.8357	-0.571
Willow Dieback %	R-H	0.8699	-0.503
Shrub Canopy Cover %	A-R	0.5663	-1.017
Shrub Canopy Cover %	A-H	0.9155	0.400
Shrub Canopy Cover %	R-H	0.3431	1.396
Forage Species %	A-R	0.9389	-0.338
Forage Species %	A-H	0.8900	-0.460
Forage Species %	R-H	0.9916	-0.123
Standing Water %	A-R	0.778	0.675
Standing Water %	A-H	0.5988	0.965
Standing Water %	R-H	0.9586	0.277

Table D5. Summary of statistical results for variables analyzed with Ordinal Logistic Regression. Group Comparison column codes: A-R (Active vs. Recent), A-H (Active vs. Historic), R-H (Recent vs. Historic). Means and standard errors are given in their original categorical form with corresponding meaning in the Notes column.

Variable	Group Comparison	p-value	Z-Score
Substrate Size Index	A-R	0.9961	0.084
Substrate Size Index	A-H	0.9609	0.269
Substrate Size Index	R-H	0.9812	0.186
Forage Height Class	A-R	0.9993	0.036

Forage Height Class	A-H	0.9355	-0.348
Forage Height Class	R-H	0.9221	-0.384
Utilization Class	A-R	0.9823	0.180
Ungulate Utilization Class	A-H	0.987	-0.154
Ungulate Utilization Class	R-H	0.9405	-0.334
Conifer Age Class	A-R	0.2867	-1.509
Conifer Age Class	A-H	0.2386	-1.616
Conifer Age Class	R-H	0.9919	-0.121

Table D6. Summary of statistical results for variables analyzed with Chi Square and Generalized Linear Mixed Models. Group Comparison column codes: A-R (Active vs. Recent), A-H (Active vs. Historic), R-H (Recent vs. Historic).

Variable	Group Comparison	p-value	Z-Score
Presence of Conifer	A-R	0.2135	-1.678
Presence of Conifer	A-H	0.2637	-1.559
Presence of Conifer	R-H	0.9907	0.130
Presence of Sapsucker Damage	A-R	0.7852	0.663
Presence of Sapsucker Damage	A-H	0.4748	1.164
Presence of Sapsucker Damage	R-H	0.8624	0.518
Presence of Aspen	A-R	0.709	0.790
Presence of Aspen	A-H	0.5452	-1.050
Presence of Aspen	R-H	0.1744	-1.786

Table D7. Mean and standard error for all variables of the fine-scale habitat comparison analyzed with statistical models. For substrate type, 3= gravel (2-4mm), 4= pebble (4-64mm). For forage height, 0= no forage, 1= >1m, 2= 1-2m and 3=<3m. For ungulate utilization, 0= no browse, 1= low browse, 2= medium and 3= high browse. For conifer age class, 0=sapling and 1=adult.

Variable	Mean and SE		
	Active	Recent	Historic
Width (m)	9.07 (0.29)	3.90 (0.25)	3.08 (0.39)
Depth (m)	0.73 (0.02)	0.41 (0.02)	0.38 (0.02)
Riparian Zone (m)	384.08 (18.21)	180.87 (8.17)	97.52 (7.63)
Thalweg (m)	1.04 (0.04)	0.54 (0.03)	0.48 (0.03)
Stream Gradient	0.0268 (0.002)	0.0626 (0.005)	0.0671 (0.006)
Sinuosity	2.14 (0.0788)	1.64 (0.04)	1.50 (0.07)
Valley Floor Width (m)	500.14 (30.31)	231.51 (10.86)	107.55 (8.78)
Bankfull Depth (m)	1.10 (0.14)	1.07 (0.14)	0.76 (0.15)
W:D Ratio	13.51 (0.57)	11.38 (0.71)	8.87 (1.12)
Entrenchment Rating	1.04 (0.10)	1.41 (0.10)	1.39 (0.11)
Floodplain Incision	1.07 (0.66)	2.63 (0.66)	1.71 (0.67)

Complexity Rating	1.87 (0.09)	1.33 (0.05)	1.20 (0.07)
Willow Zone (m)	145.06 (8.60)	98.64 (7.22)	41.27 (2.73)
Number of Shrub Species	2.73 (0.20)	2.32 (0.20)	1.97 (0.21)
Average Willow Stem Diameter (cm)	4.42 (0.39)	5.33 (0.39)	4.62 (0.44)
Average Largest Stem Diameter (cm)	7.43 (0.69)	8.82 (0.69)	6.96 (0.77)
Tallest Willow Leader (m)	2.65 (0.15)	2.91 (0.15)	2.51 (0.17)
Shannon Diversity Index	0.60 (0.07)	0.33 (0.07)	0.48 (0.07)
Forage Biomass Index	9834.49 (736.78)	6567.76 (571.36)	2738.71 (232.05)
Number of Conifers	0.10 (0.24)	0.46 (0.25)	0.55 (0.24)
Willow Dieback %	38.73 (1.60)	45.50 (1.80)	45.99 (1.59)
Shrub Canopy Cover %	60.90 (1.77)	58.94 (2.20)	60.25 (1.64)
Forage Species %	85.12 (2.08)	80.49 (2.54)	88.66 (2.06)
Standing Water %	11.02 (1.99)	3.61 (1.08)	4.77 (1.40)
Substrate Size Index	3.68 (0.14)	3.63 (0.12)	3.54 (0.20)
Forage Height Class	2.20 (0.07)	2.14 (0.08)	2.28 (0.07)
Ungulate Utilization Class	2.55 (0.08)	2.36 (0.09)	2.40 (0.14)
Conifer Age Class	0.14 (0.04)	0.27 (0.05)	0.27 (0.05)
Presence of Conifer	0.08 (0.02)	0.17 (0.03)	0.17 (0.03)
Presence of Sapsucker Damage	0.25 (0.03)	0.19 (0.03)	0.12 (0.03)
Presence of Aspen	0.05 (0.017)	0.01 (0.01)	0.30 (0.04)