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Methods, Tools, and Technologies

Estimating widespread beaver dam loss: Habitat decline and surface storage loss at a regional scale

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Abstract

The loss of beaver populations has commonly been accompanied by the failure of beaver dams, leading to stream incision, water table lowering, and the eventual transition from a beaver meadow to a drier riparian corridor. Widespread decline in North American beaver populations (*Castor canadensis*) has been documented from pre-European settlement to the current day, representing an estimated 80% to 98% loss of historical populations. While individual case studies have investigated the ecosystem impacts of local beaver population loss, few studies have quantified large-scale changes associated with widespread population decline. Here, we use the Beaver Restoration Assessment Tool to model landscape-scale habitat suitability and beaver dam capacity in Colorado, USA, in order to determine whether a widespread loss in beaver population corresponds to a similar scale decline in the capacity to sustain beaver on the landscape and declines in physical benefits associated with beaver, such as surface water and sediment storage. Currently, the statewide stream network (298,119 stream kilometers) can support approximately 1.36 million beaver dams, compared with 2.39 million dams historically. All regions of Colorado have seen a decline in beaver dam capacity from historical conditions, likely due to agriculture, urbanization, and loss of vegetation necessary to beaver. Beaver dam capacity loss is accompanied by an approximate 40% decline in beaver-mediated surface water and sediment storage potential across the state. Regions with high percent loss in storage potentials also had a high percentage of drainage network that had experienced beaver dam capacity losses of 15 or more dams per kilometer, which highlights the disproportionate impacts of losing high dam density reaches (i.e., beaver meadows). Extreme dam density declines were rare, and instead, most reaches have undergone a shift from high to moderate capacity. Statewide shifts in beaver dam capacity highlight the opportunity for using beaver-related restoration in Colorado and across the American West.

KEYWORDS
beaver, *Castor canadensis*, Colorado, habitat loss, pond sedimentation, stream restoration, water storage, wetland

INTRODUCTION

Unsustainable trapping and land use changes led to substantial population declines and local extinction of Eurasian beaver (*Castor fiber*) by the 16th century (Nolet & Rosell, 1998). The commercial fur trade then focused on North American beaver (*Castor canadensis*), leading to the near extirpation of this species across its historical range by the 19th century (Baker & Hill, 2003; Rutherford, 1964). The decline in population density and associated changes to river corridors are better documented for North American beaver because of the more recent history of human effects. Prior to European settlement, beaver populations in North America were estimated to be around 60 to 400 million individuals (Seton, 1929), compared with just 9–12 million beaver today (Naiman et al., 1988; Pollock et al., 2015). The estimated historical population level, however, is extrapolated from populations in a small number of regions in North America and thus includes substantial uncertainty. What is clear is that declines in beaver populations can be accompanied by the loss of habitat and ecosystem services, but regional-scale impacts of beaver loss have not been previously investigated.

The presence or absence of beaver in a watershed can have a significant impact on the function of the river corridor (including the channel, floodplain, and hyporheic zone [Harvey & Gooseff, 2015]). Beaver are ecosystem engineers and a keystone species that have a disproportionately large ecologic, geomorphic, and hydrologic effect on their environment compared with their abundance (Baker & Hill, 2003; Rosell et al., 2005). Beaver primarily alter streams by constructing channel-spanning dams, which reduce surface flow velocity and pond water upstream, and enhance the magnitude and duration of overbank flow and groundwater recharge (Burchsted et al., 2010; Westbrook et al., 2006). Dams cause significant storage of fine-grained sediment in upstream ponds and in floodplains inundated by overbank flow (Butler & Malanson, 1995; Naiman et al., 1986), which can aggrade the channel bed and reconnect incised streams with their floodplains (Pollock et al., 2014). Additionally, river corridors dammed by beaver can store high concentrations of terrestrial carbon (Johnston, 2014; Wohl, 2013) and attenuate downstream fluxes of nutrients and solutes (Naiman & Melillo, 1984; Wegener et al., 2017). The magnitude of downstream attenuation of solutes, water, sediment, and organic carbon depends on factors such as size, complexity, and number of dams built by beaver. A single dam and pond may create limited attenuation during peak flow (Burns & McDonnell, 1998), but numerous dams in a beaver wetland can effectively attenuate even the largest peak flows and serve as a sink for nitrates and organic carbon (Wegener et al., 2017). Beaver wetlands also provide diverse habitat for vegetation (Westbrook et al., 2011), fish (Pollock et al., 2003), aquatic insects and their riparian predators (Fuller & Peckarsky, 2011; McCaffery & Eby, 2016; McDowell & Naiman, 1986), frogs and other amphibians (Anderson et al., 2015; Arkle & Pilliod, 2015), and other semiaquatic mammals such as mink and otter (Rosell et al., 2005). Ponded water and high riparian water tables associated with beaver dams can also reduce the effects of climatic extremes such as drought (Hood & Bayley, 2008) and make the river corridor more resistant to wildfire (Fairfax & Whittle, 2020). Generally, beaver meadows increase the resilience of the river corridor to perturbation (Naiman et al., 1986).

The loss of beaver in an ecosystem can therefore lead to physical and ecological degradation. Following the loss of beaver, river corridors can transform from wet, multithreaded channel–wetland systems housing a diversity of plants and animals to a dry, single-threaded, incised channel representative of a drier steady state known as an elk grassland (e.g., Laurel & Wohl, 2019; Polvi & Wohl, 2013; Wolf et al., 2007) or a mesic meadow (Decker et al., 2020). Failure of abandoned beaver dams can cause stream incision, riparian water table decline, and the loss of suitable beaver-foraging material (Butler & Malanson, 2005). Streams that have transitioned into a drier steady-state post-beaver loss may no longer be suitable for beaver (Pollock et al., 2014). Given the magnitude of beaver population loss, have the habitats suitable for beaver dam building, along with associated water and sediment storage potential, declined at a similar scale?

Suitable beaver habitat requires a reliable water source and beaver foraging material. Beaver prefer to build dams on smaller streams where dam building is possible at typical low flow (i.e., baseflow), but dams will not break during typical high flows (i.e., 2-year flood). Small to medium (<20 m wide) streams with low gradients (<3%) are ideal dam-building habitat, but beaver can also build dams on steeper channels, on floodplains and side channels of wider rivers, and on hillside springs and seeps (Albert & Trimble, 2000; Olson & Hubert, 1994; Pollock et al., 2015; Townsend & Butler, 1996). Beaver will build dams on both perennial and intermittent streams as long as a woody riparian corridor is present (Gibson & Olden, 2014). Beaver diets are seasonal and diverse. In the summer, beaver prefer high nutrient, herbaceous vegetation such as sedges (*Carex* spp.) and rushes (*Juncus* spp.), as well as leaves from deciduous trees. In the winter, beaver rely on the inner bark (cambium) of trees, preferably trees of the family Salicaceae, specifically of the genus *Populus* (aspens and cottonwoods) and *Salix* (willows) (Allen, 1983; Kimball & Perry, 2008). The maximum distance beaver will travel to harvest vegetation is approximately 100 m, although beaver prefer to forage within 30 m of the stream (Allen, 1983).

Based on habitat needs, modeling potential and existing beaver habitat suitability has been ongoing for decades (Allen, 1983; Slough & Sadleir, 1977; Suzuki & McComb, 1998). Models have ranged from empirical regressions to predict dam densities to habitat suitability indices ranking habitat preferences. Recently, MacFarlane et al. (2017) developed the Beaver Restoration Assessment Tool (BRAT) to model the carrying capacity of beaver dams on stream reaches in the state of Utah, USA. BRAT uses nationally available spatial datasets for hydrology, vegetation, and topography to estimate beaver dam capacity on a stream network using fuzzy inference systems. The BRAT incorporates maximum foraging distance, preferred foraging and building material, low and high flow requirements, and other known beaver habitat preferences when estimating the capacity of a channel reach to sustain beaver dams.

Given known declines in beaver populations across the American West, we investigate whether these declines are concomitant with a decline in the ability to host beaver on the landscape and discuss the implications of regional-scale dam capacity decreases. Specifically, we use BRAT to model historical and current beaver capacity across the state of Colorado, USA, in order to understand broad patterns and magnitudes of capacity changes. Beaver were historically prevalent across all physiographic regions of Colorado (Fremont, 1845; Retzer et al., 1956), but unsustainable fur trapping in the 19th century led to a rapid decline in populations (Baker & Hill, 2003; Rutherford, 1964). In this context, Colorado represents much of the US Intermountain West, a region with arid to semiarid climate, high elevation mountain ranges and intervening alluvial basins, and rapidly expanding human population. We use these analyses to discuss how streams and beaver-suitable habitat have changed across the study region, how such changes influence potential water and sediment storage at a large scale, and how statewide suitability modeling can inform watershed management and stream restoration, including the current opportunities for and barriers to beaver-related restoration across the region. The methods used in this example from Colorado can be applied to other regions to provide insight into historical changes in river networks.

METHODS

Site description

Colorado is diverse in climate, terrain, and land use. Three major physiographic provinces trend north–south (Fenneman, 1931). Eastern Colorado lies within the Great Plains, which are characterized by low relief, limited precipitation, shallow river valleys, shortgrass steppe, agricultural land use, and, at the western edge, extensive urbanization. Most of central Colorado is within the Southern Rocky Mountains, which consist of high relief mountain ranges, intermountain valleys, and coniferous upland forests and mixed coniferous–deciduous riparian forests (Veblen & Donnegan, 2006). Urban areas, although relatively small, are concentrated in river valleys. Western Colorado is part of the Colorado Plateau, which is dominated by high elevation terrain cut by steep, rugged canyons, semiarid climate, and limited urbanization. In general, variations in elevation across Colorado result in substantially different annual precipitation (Capesius & Stephens, 2009; Kohn et al., 2016), which is significant to the streamflow and function of streams modeled in this study.

Watersheds across Colorado represent major headwaters of the Rio Grande, Arkansas, North and South Platte, and Colorado Rivers. We defined six hydrologic regions in Colorado based on climatic variations and major watershed boundaries: Plains, Foothills, Mountains, Rio Grande, Northwest, and Southwest (Figure 1). Hydrologic regions follow definitions in Capesius and Stephens (2009) and Kohn et al. (2016).

Watershed boundaries from the U.S. Geological Survey (USGS) Watershed Boundary Dataset (WBD) were used to define the study extent. The WBD contains a continuous network of nested watersheds of varied sizes, where watersheds with a low Hydrologic Unit Code (HUC) represent a large area, and watersheds with a high HUC represent a small area (Seaber et al., 1987). For this analysis, HUC-8 watersheds were used to reduce computation times associated with smaller watersheds but avoid skewing regional hydrologic regressions by using larger watersheds. Watersheds were selected for modeling based on (1) having a geographic centroid within the state of

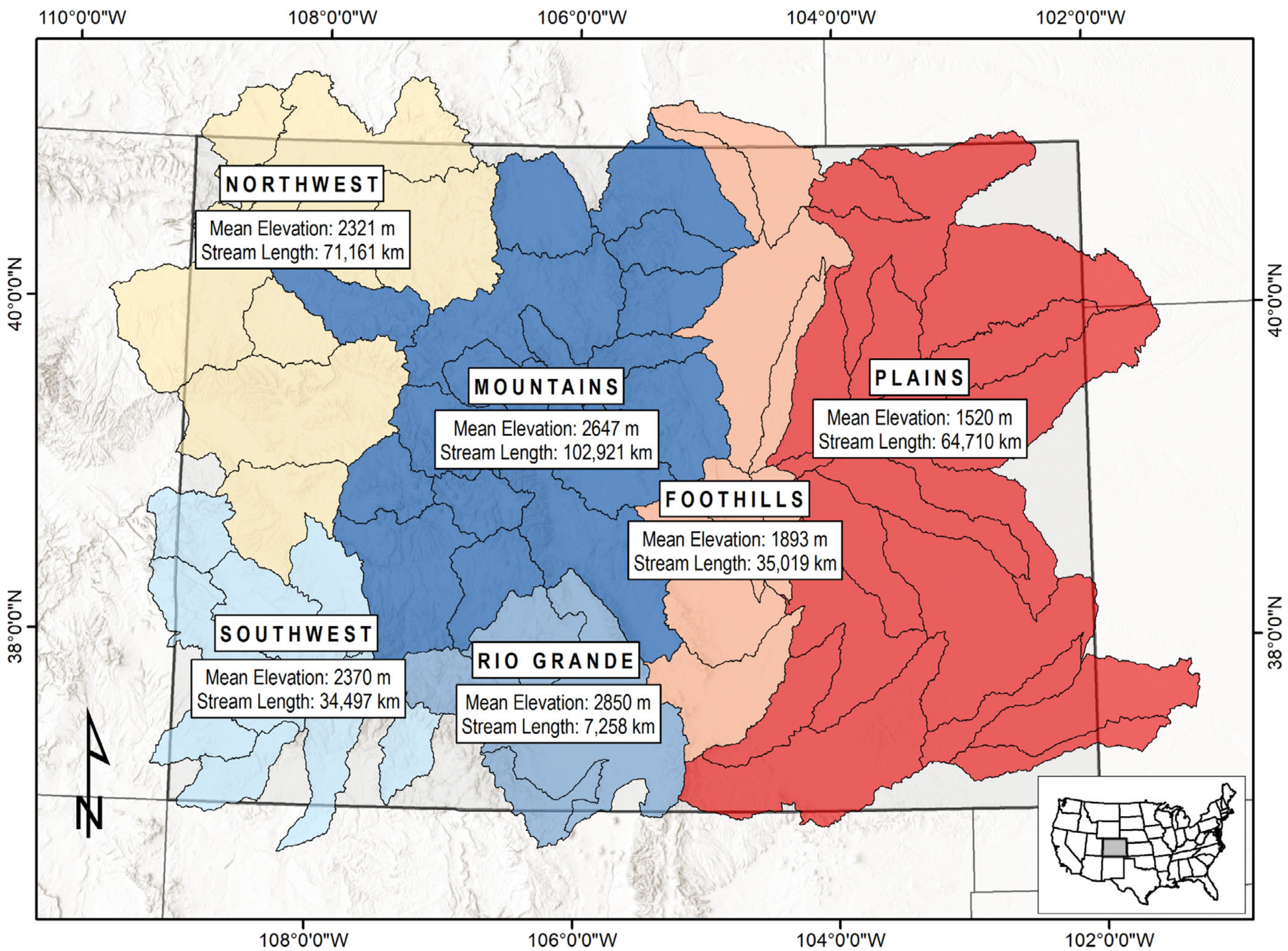

FIGURE 1 Watersheds (Hydrologic Unit Code 8) where Beaver Restoration Assessment Tool (BRAT) was used to model current and historic beaver dam capacity in Colorado ($n = 63$). Watersheds are color-coded by hydrologic region, which are differentiated by both climate and drainage divides following Capesius and Stephens (2009) and Kohn et al. (2016). Mean elevation of all watersheds and the total stream length modeled is given for each region

Colorado boundaries or (2) being tributary to downstream watersheds centered in Colorado. In total, current and historical beaver dam capacity was modeled in 63 watersheds based on these selection criteria (Figure 1).

All watersheds modeled in this study were assigned a hydrologic region for the purpose of assigning regional regressions for model streamflow and for the purpose of analyzing regional variations in model output (Figure 1). Total stream network length in each region ranges from approximately 7200 to 103,000 km, which reflects differences in area and drainage density.

BRAT modeling

BRAT was used to estimate current and historical beaver dam capacity for the study area (MacFarlane et al., 2017). BRAT calculates the capacity of dams for each stream based on four main variables: hydrology, topography, vegetation, and land use. Most spatial layers representing elements in the model were downloaded from nationally available datasets and combined into pyBRAT 3.0.18 using ArcGIS 10.4.1.

Hydrology inputs to BRAT include both the stream network and discharge. Stream networks were downloaded from the USGS National Hydrography Dataset (NHD, https://www.usgs.gov/core-science-systems/ngp/national-hydrography). Streams coded as ephemeral in the NHD were excluded because they lack discharge necessary to support beaver colonies. Perennial and intermittent streams were preprocessed according to BRAT standards and then divided into 300-m segments (Scamardo, 2019). Discharge was represented by regional regressions for the 2-year flood (Q_2) and baseflow (Q_{low}) for each of the six hydrologic regions in Colorado (Capesius & Stephens, 2009; Kohn et al., 2016). For four of the six regions, baseflow equations were given as regressions for the minimum 7-day, 2-year flow ($_7Q_{10}^{MIN}$). Baseflow regressions were not available for the Foothills and Plains regions, likely due to the variability of flow in small, ungauged streams on the Great Plains. To estimate baseflow for the Foothills and Plains, the Q_2 discharge value was divided by 500, based on the ratio of Q_2 to baseflow in other regions. Basin-averaged inputs to the baseflow equations—such as mean slope, mean elevation, and precipitation—were calculated using USGS StreamStats (Ries III et al., 2017). In watersheds where StreamStats is not available—including watersheds with outlets in Nebraska and Wyoming—basin-averaged characteristics needed to calculate regional regressions, such as outlet elevation, mean basin slope, percent clay, and precipitation intensity, were gathered from nearby USGS stream gauges, Natural Resources Conservation Service soil surveys, and local digital elevation models (DEMs).

A 1/3 arc-second (approximately 10-m) DEM for Colorado was downloaded from the USGS National Elevation Dataset and used to calculate stream gradient, drainage area, and valley bottom width in BRAT.

Current and historical dam capacities can be modeled in BRAT using current and historical vegetation layers as inputs. LANDFIRE (LF) vegetation rasters were used to represent both current and historical vegetation within all 63 watersheds (www.landfire.gov). Current vegetation was represented using the LF Existing Vegetation Type layer, and historical vegetation was represented using the LF Biophysical Settings layer. LF rasters were edited to include a vegetation suitability code category. Vegetation codes were assigned by hand to individual vegetation types included in each raster and largely followed guidelines provided in MacFarlane et al. (2017). Generally, riparian vegetation such as willows, cottonwoods, and aspen was assigned high vegetation codes for being most suitable, while barren land, agricultural fields, and urbanized settings were assigned low vegetation codes for being unsuitable.

Analysis of beaver dam capacity

Analysis of current and historical dam capacity

All post-model analyses were performed in R using the Tidyverse suite of packages (Wickham et al., 2019). Summary statistics such as median dam capacity and average change between current and historic capacities were calculated for each hydrological region. The magnitude and direction of differences between median dam capacity and change between regions is used to provide insight into variations in suitability across the climate. Because output on the entire population of streams in Colorado is presented, traditional statistical tests do not provide meaningful insight. All statistical tests would be significant, given the very large dataset ($n = 25{,}600$–$383{,}200$ per region) and a traditional alpha value of $\alpha = 0.05$. Instead, due to the completeness of the dataset, the magnitude and direction of differences in summary statistics can be interpreted independent of statistical tests. For convention, p-values of two-sample t tests are given when describing differences between two populations (e.g., output from two regions).

To further analyze the change in beaver capacity post-European settlement, we identified areas of extreme change in beaver capacity. Specifically, we identified stream reaches where historical capacity was in the highest category (pervasive, 15+ dams/km) and current dam capacity was less than 1 dam/km. The sum of the length of reaches experiencing extreme change was divided by the total length of stream network in each region to calculate the percentage of the stream network that had undergone extreme change.

Analysis of factors limiting beaver dam capacity

A simple analysis was performed to investigate potential factors limiting current beaver dam capacity, in order to identify potential barriers to beaver populations or restoration. First, physical and hydrological constraints of slope and discharge were considered; reaches with a slope greater than 17% (0.17 m/m) were considered slope-limited, reaches with a baseflow discharge stream power greater than 190 W/m were considered to have baseflows too high to construct dams (baseflow limited), and reaches with a Q_2 discharge stream power greater than 2400 W/m were considered to have peak flows high enough to consistently blowout dams (high flow limited) (MacFarlane et al., 2017). Drainage area influences were then considered such that reaches with drainage areas greater than the predefined threshold were considered drainage area-limited. Drainage area-limited streams represent reaches where stream geometry is such that beaver are more likely to build bank dens than beaver dams. Vegetation controls were then considered. Reaches where the vegetation capacity was less than or equal to the carrying capacity were considered vegetation-limited. All other reaches not limited by slope, drainage area, hydrology, or vegetation were placed in an "Other" category, which indicates that carrying capacity is either not limited (maximum capacity) or are limited by another factor such as valley bottom width. The percentage of the stream network limited by each category was calculated for each region.

Quantifying water and sediment storage

Estimates of potential surface water and sediment storage volumes behind beaver dams were calculated based on historical and current beaver dam capacities. Regional-scale approximations of sediment and water storage are dependent on assuming the shape of a beaver pond upstream of each dam. Pond dimensions were assumed to approximate a right triangular prism (Figure 2). Pond width was assumed to be channel width (i.e., no additional overbank flow), which was calculated based on regional hydraulic geometry relationships developed by Wohl and Merritt (2008) for the Mountains region and Wilkerson et al. (2014) for all other regions. Inputs of discharge (Q_2) and drainage area previously calculated using BRAT were used as inputs for the regional regression equations (Figure 2). Pond length was estimated by taking the tangent of channel gradient (*S*). At low gradients, the tangent of channel gradient is assumed to be approximately equal to the gradient itself, simplifying the trigonometric relationship to a function of slope and dam height. For all calculations, dam height was assumed to be 1 m, which is assumed to be a reasonable average height. Beaver dam heights can exceed multiple meters in the study region, but dam heights of 0.5–1.5 m are much more common (e.g., Hafen et al., 2020). At high beaver dam densities or in areas of low stream gradient, beaver ponds can extend to the upstream dam. Therefore, a maximum pond length equal to the reach length divided by the dam count for that reach was calculated for areas with successive beaver ponds. If the calculated length exceeded the maximum possible length of ponds in a given stream reach, the maximum length was used for volume calculations.

Surface water storage was estimated by calculating the volume of a right rectangular prism (volume = 0.5 $W{\cdot}H{\cdot}L$),

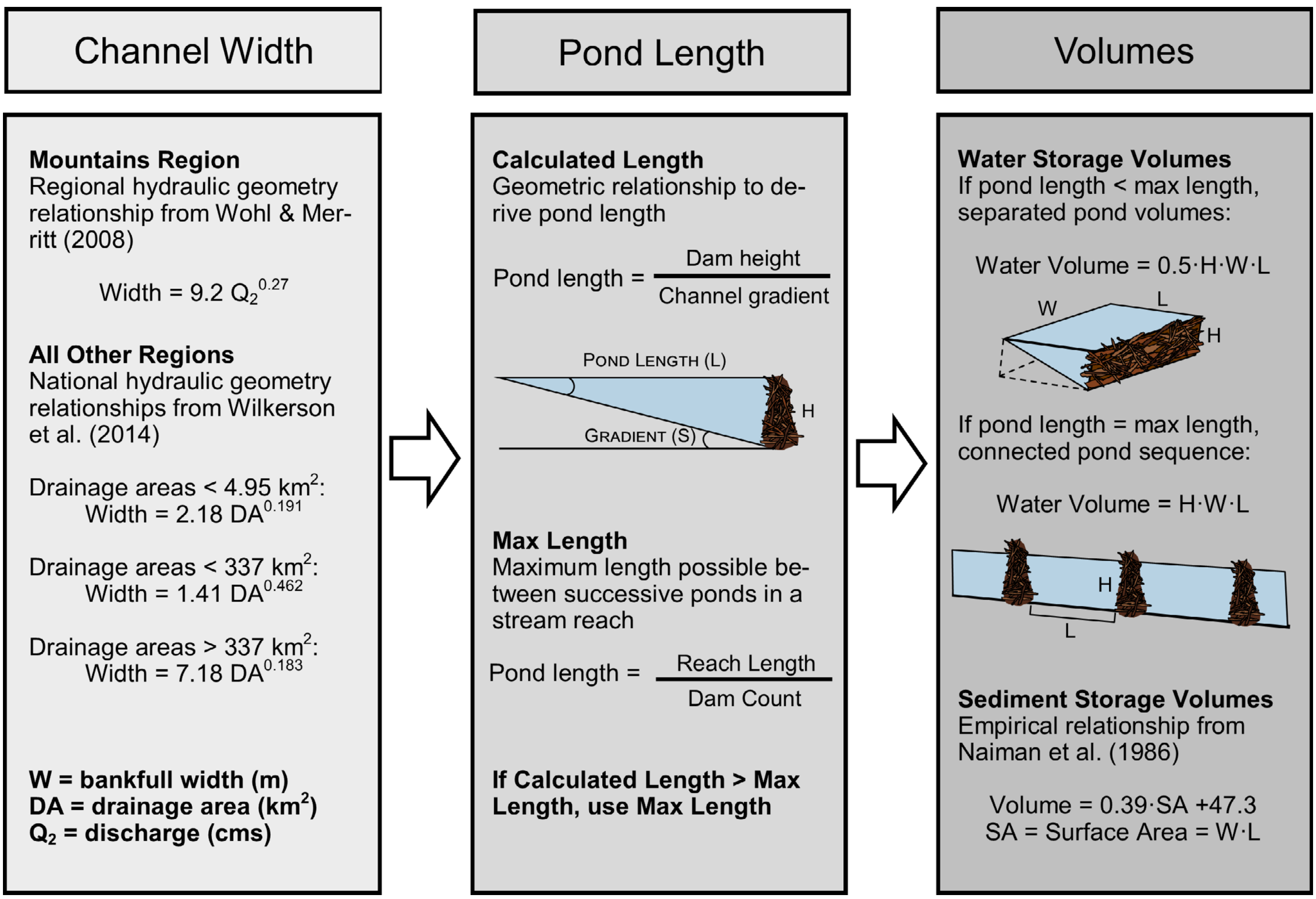

FIGURE 2 Summary of calculations needed to estimate water storage volumes and sediment storage volumes for historic and current beaver dam capacities. Estimates of channel width were made using regional and national hydraulic geometry relationships. Pond length was estimated by assuming pond shapes roughly approximate a triangular prism. In reaches with high dam capacities, beaver ponds may extend to the upstream dam. The maximum pond length was therefore calculated using stream reach length and dam count output. Water storage volumes were estimated based on simple geometric relationships, and sediment storage volumes were estimated using an empirical equation for beaver dam sedimentation proposed by Naiman et al. (1986)

based on stream width and pond length for dams within a given reach. The calculated volume was then multiplied by the number of dams the reach could sustain historically and currently, as determined by BRAT. In reaches with successive ponds, pond volumes were assumed to approximate more of a rectangular prism, and volumes were calculated accordingly (Figure 2). Sediment storage volumes are more difficult to predict for beaver dams, as they can be dependent on variables that are difficult to measure such as suspended sediment concentration and time since dam establishment. Technically, the maximum sediment storage for each beaver pond would be equal to the total volume of the pond, assuming complete filling (Pollock et al., 2003). However, complete filling of all dams across the region is unlikely. Instead, sediment storage volumes were estimated based on an empirical equation developed by Naiman et al. (1986):

$$\text{Volume} = 0.39 \times (\text{surface area}) + 47.3.$$

Pond surface area was assumed to approximate a rectangle (area = channel width × pond length). Sediment volumes were calculated for individual ponds in a reach and then multiplied by the historical and current dam capacity for each reach. Sediment and water storage volumes were calculated assuming single-threaded channels, similar to the manner in which BRAT only estimates dam capacity for NHD channels. However, in-channel estimates do not capture the entirety of potential surface water and sediment storage in historically high capacity reaches. Beaver dams can widen streams and cause overbank sediment deposition and water storage (Westbrook et al., 2011), which often causes high beaver dam density reaches (also known as beaver meadows) to become multithreaded. Beaver-mediated sediment storage in high-density reaches can also include valley aggradation over longer timescales in the Rocky Mountains (e.g., Polvi & Wohl, 2012). Estimates of sediment storage on the floodplain and secondary channels are beyond the scope of this paper, and estimated volumes should be viewed as a conservative, first-order approximation at a regional scale.

RESULTS

Current and historic beaver dam capacity in Colorado

A total of 298,119 km (1.15 million reaches) of streams were modeled using BRAT across the 63 study watersheds (Figure 3). The total modeled stream network has the capacity to support approximately 1.36 million dams currently compared with 2.39 million dams historically. The distribution of dam capacity varies by hydrologic region. Generally, dam densities are highest on first- through third-order headwater streams (Figure 3). Median dam densities in the Mountains, Rio Grande, and Southwest regions are approximately two to six times the median dam densities in the Plains, Foothills, and Northwest regions both currently and historically (Table 1). While current and historical dam densities in all regions are statistically significantly different ($p < 0.0001$ for all comparisons), median dam capacity and patterns of dam capacity are similar between the Mountains, Rio Grande, and Southwest regions, as well as the Plains, Foothills, and Northwest regions (Figure 4).

Patterns in dam capacity vary markedly between these two groups. Currently, most of the stream network in the Plains, Foothills, and Northwest regions can support rare (0–1 dam/km) dam densities (Figure 4a). In contrast, the majority (>50%) of the stream network in the Mountains, Rio Grande, and Southwest regions can support occasional (1–5 dams/km) to frequent (5–15 dams/km) dam densities. Historical dam densities follow a similar pattern, but a higher percentage of the total stream network for all regions was suitable for frequent to pervasive dam densities. Overall, the percentage of the stream network suitable for dam densities greater than 5 dams/km has decreased (Figure 4c).

Stream reaches that had undergone extreme change, defined as dropping from a capacity of 15+ dams/km to a capacity less than 1 dam/km, only represented a small proportion of the stream network in each region (Table 1). The Southwest, Mountains, and Northwest regions experienced the greatest extreme change as a percentage of the total network, but these changes still only represented less than 5% of the total stream length in each region.

Validation of the BRAT dataset in Colorado was conducted by Scamardo (2019) and showed that BRAT estimates were more likely to underpredict current dam capacities than to overpredict. Therefore, reported beaver dam capacities should be taken as a conservative estimate. Additional research has shown that locally developed vegetation layers can be used to improve BRAT output at finer scales (Kornse & Wohl, 2020); however, this resolution of vegetation mapping is currently unavailable at the level of individual US states.

Limitations on current capacity

The majority of stream reaches in all regions were limited by vegetation availability (Table 2), except for the Mountains region where vegetation only limited in 44.5% of the stream reaches. The “Other” limitation category represents the next highest percentage of the stream network in most regions, with the exception being the Plains. However, the "Other" limitation category could also represent streams that are not limited (streams with pervasive carrying capacity).

Regional loss of surface water and sediment storage

Following trends with decreasing dam capacity, surface water, and sediment storage potential have decreased compared with historical conditions (Tables 3 and 4). Beaver-associated surface water and sediment storage capacities have decreased by approximately 40%. Percent loss in sediment and surface storage varied by region, with the greatest percentage loss being experienced in the Southwest, Mountains, and Northwest regions (Tables 3 and 4).

DISCUSSION

Spatial patterns in beaver dam capacity loss and potential drivers

All hydrologic regions in Colorado have experienced a loss of in-channel beaver dam capacity (Figure 4 and Table 1). The historical and current BRAT models only differ by a vegetation layer, which indicates that modeled declines in beaver dam capacity are directly related to declines in vegetation suitability from pre-European settlement (Figure 5). Changes in beaver dam capacity across the region likely also depend on changes in streamflow; however, data on historical streamflow are largely absent, meaning that all estimates of streamflow across Colorado are based on current conditions, even for the historical model. Modern temperature increases and

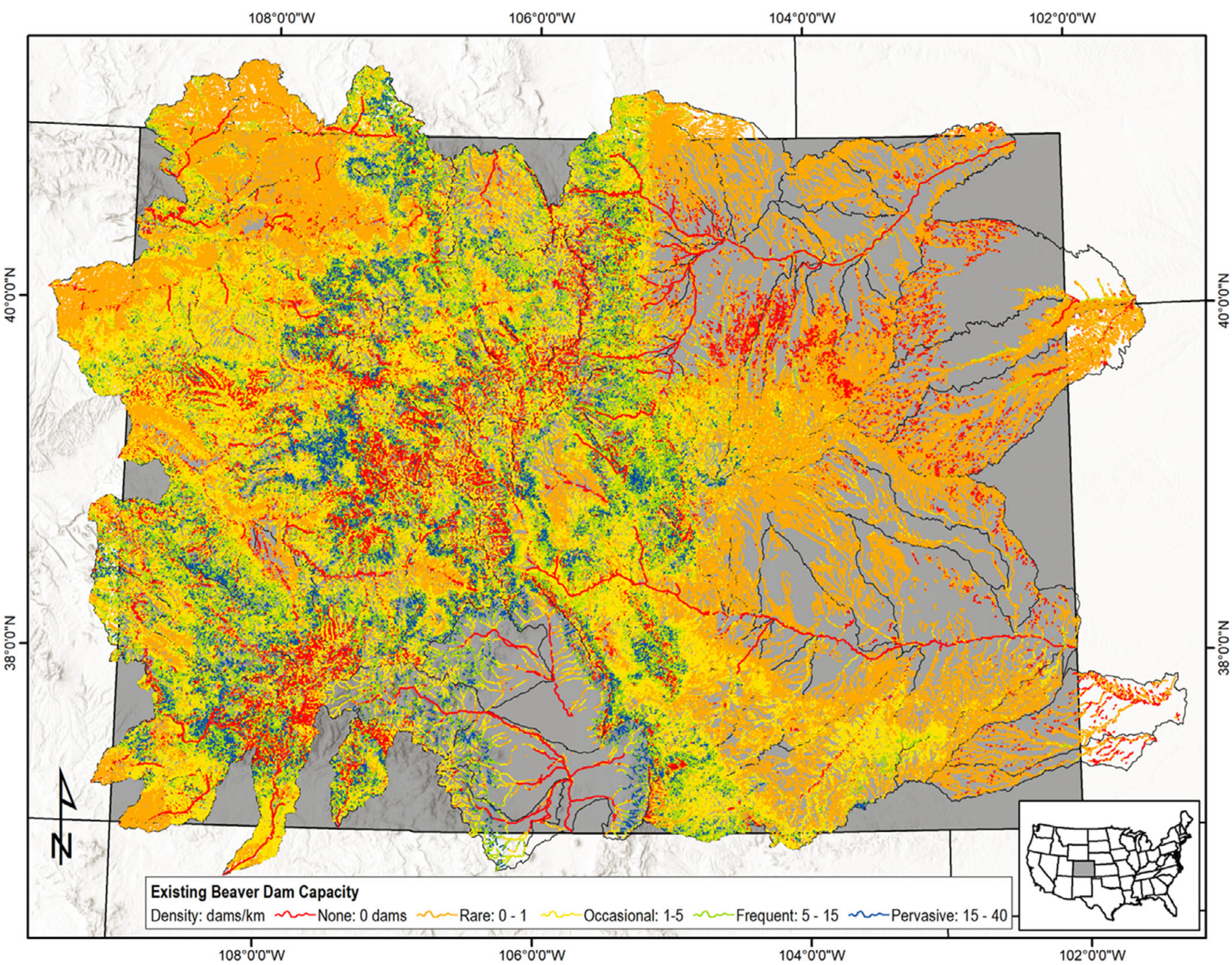

FIGURE 3 Existing beaver dam capacity on perennial and intermittent streams included in the study ($n = 63$ watersheds). Color indicates the range of beaver dam capacity (dams/km) on each 300-m stream reach. Red indicates reaches that cannot support beaver dams, while blue represents reaches where pervasive beaver activity is expected (15+ dams/km)

declining snowpacks have been driving declines in streamflow in the Colorado (Southwest and Northwest Regions) and Rio Grande (Rio Grande Region) watersheds (Lehner et al., 2017; Milly & Dunne, 2020; Woodhouse et al., 2016). Modern changes in streamflow may be reflected in riparian vegetation changes, but historically, streams that are hydrologically limited may have had sufficient streamflow in the past. Therefore, historical beaver dam capacity could have been higher, leading to even larger capacity declines than modeled here.

Median capacity in the Southwest, Northwest, Rio Grande, and Mountains regions has decreased to approximately a third of historical beaver dam capacity, based on the modeled estimates (Table 1). In the Plains region, median capacity remained unchanged despite a loss of higher capacity reaches and a gain of lower capacity reaches, which highlights the general dominance of rare beaver habitat in the Plains historically and currently. Capacity in the Foothills region has decreased to a fifth of the historical beaver dam capacity, which represents a greater proportional loss compared with other regions. Reasons for capacity loss likely vary by region based on specific land use and land cover changes and documented shifts in forest structure across Colorado and the Rocky Mountains.

Previous research has documented a decline in quaking aspen (*Populus tremuloides*), a preferred beaver foraging material, across Colorado and the Mountain West (Bartos, 2001; Bartos & Campbell, 1998; Rehfeldt et al., 2009; Worrall et al., 2008). While aspen dieback varies spatially and temporally across the Mountain West (Kulakowski et al., 2013), previous studies in Colorado have documented a major decline in aspen forests at elevations below 2900 m at low slopes (generally, <19%, Worrall et al., 2008), such as mountain valleys where beaver populations are generally found. Aspen dieback has also been accompanied by conifer establishment, which provides less suitable beaver foraging material (Busher, 1996). Specifically, aspen decline has been well documented in the Southwest and Northwest regions of Colorado (Worrall et al., 2008; Worrall et al., 2010), which could account for the loss of suitable foraging

TABLE 1 Current and historic median dam densities (as estimated by the Beaver Restoration Assessment Tool) for each hydrologic region

Region	Current median dam density (dams/km)	Historic median dam density (dams/km)	Percent of network experiencing extreme change (%)
Plains	0.6	0.6	0.8
Foothills	0.7	3.4	0.02
Mountains	4.0	11.4	1.7
Rio Grande	3.6	11.3	0.9
Northwest	1.6	3.6	3.2
Southwest	3.6	10.9	1.5

Note: All regions have experienced stability or declines in median density, but extreme changes (loss of 15+ dams/km) have occurred across less than 5% of the drainage network in each region.

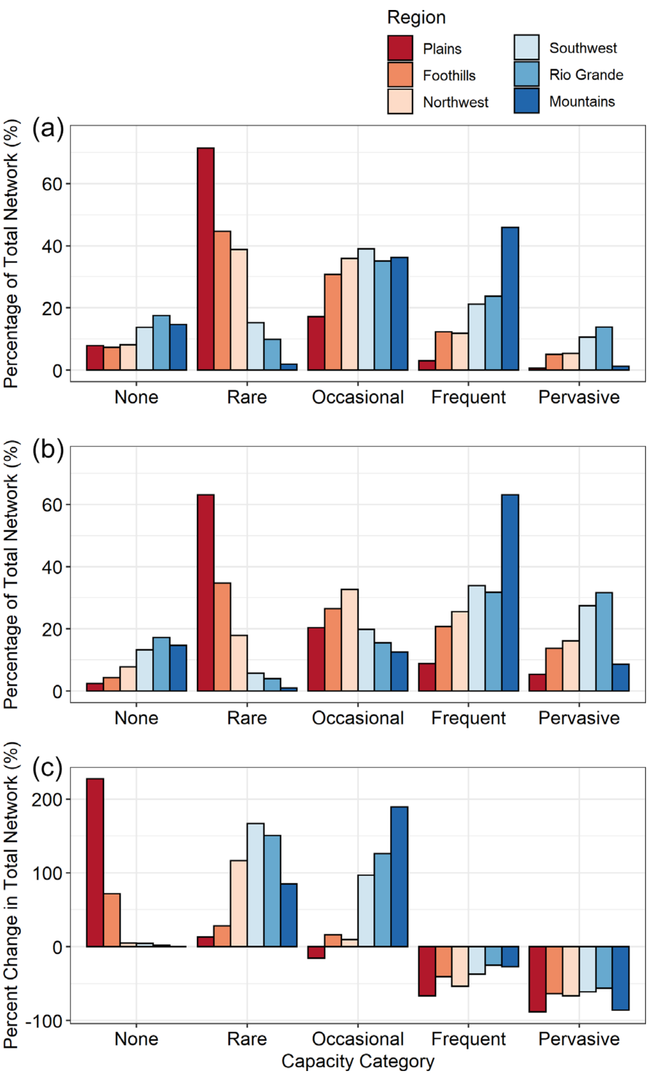

FIGURE 4 Distribution of beaver dam capacity in the six hydrologic regions of Colorado. Bar color indicates hydrologic region. (a) Percentage of the total stream network (in length) that falls within each capacity category currently. (b) Percentage of the total stream network (in length) that falls within each capacity category historically (pre-European settlement). (c) Percent change in stream network length in each capacity category from pre-European settlement to now. Negative percent change indicates a loss of stream length that falls within a given capacity class, while positive percent change indicates a gain of stream length in a capacity class

TABLE 2 Percentage of the stream network, by hydrologic region, where beaver dam capacity is limited by current vegetation, baseflow discharge, high flow (Q_2) discharge, drainage area, or other factors

Region	Vegetation limited	Baseflow limited	High flow limited	Slope limited	Drainage area limited	Other
Plains	86.1	<0.01	2.2	3.0	5.3	3.4
Foothills	79.5	<0.01	3.7	5.5	2.7	8.6
Mountains	44.5	0.05	2.45	18.3	1.4	33.3
Rio Grande	60.9	0.05	1.5	10.4	7.6	19.55
Northwest	78.3	0.05	1.4	8.45	2.0	9.8
Southwest	62.1	0.03	4.3	15.8	1.6	16.2

TABLE 3 Estimates of potential surface water storage volumes (in cubic kilometers) based on historical and current beaver dam capacities across the hydrologic regions of Colorado, as well as percent change (decline) in volumes

Region	Historic capacity (km^3)	Current capacity (km^3)	Difference (%)
Plains	0.143	0.098	−31.3
Foothills	0.055	0.034	−37.8
Mountains	0.113	0.055	−51.4
Rio Grande	0.023	0.013	−43.5
Northwest	0.083	0.039	−53.5
Southwest	0.045	0.024	−45.7
Total	0.461	0.263	−42.9

TABLE 4 Estimates of potential sediment storage volumes (in cubic kilometers) based on historical and current beaver dam capacities across the hydrologic regions of Colorado, as well as percent change (decline) in volumes

Region	Historic capacity (km^3)	Current capacity (km^3)	Difference (%)
Plains	0.0819	0.0567	−30.8
Foothills	0.0396	0.0253	−36
Mountains	0.105	0.0579	−44.8
Rio Grande	0.0151	0.0097	−35.7
Northwest	0.0702	0.0361	−48.5
Southwest	0.0419	0.0243	−41.8
Total	0.353	0.21	−40.5

material and beaver dam capacity in parts of the montane zone largely unaffected by population growth or agriculture (Figure 5).

Land use change to agriculture, primarily to planted fields or orchards but not excluding grazed land, has likely also led to a decline in suitable beaver foraging material and beaver dam capacity across multiple regions of Colorado. Established agriculture across the Plains, in the San Luis Valley along the Rio Grande, in the Grand Valley outside of Grand Junction, and in north central Colorado along the North Platte River (MacDonnell, 1999; Steinel, 1926)—corresponding to the Plains, Rio Grande, Northwest, and Mountains regions, respectively—correlates to areas of decreased vegetation suitability (Figure 5). Proximal to these areas are dispersed regions of increased vegetation suitability, which could be due to irrigation-influenced return flows that may be supporting an increase in suitable vegetation. However, these minor and dispersed vegetation increases do not balance out the overall decline in suitable beaver foraging material across Colorado. Depending on historical vegetation, the shift from natural vegetation to agricultural land could represent a major change in beaver suitability, such as in areas that historically had highly suitable forest or riparian areas, or a minor shift, such as in the Plains where historical shortgrass prairie only represented minor to moderate beaver suitability. Beyond suitability shifts due to planted crops, foraging competition by livestock could limit the viability of beaver populations on working ranches and grazed public lands (e.g., Small et al., 2016).

Population growth in Colorado also cannot be ignored when discussing changes in beaver suitability across the state. Increases in population, particularly along the Front Range corridor running north–south through Denver, Colorado, have resulted in increased urbanization in the Foothills region. Urbanization is commonly accompanied by the loss of riparian vegetation corridors and changes to the sediment and flow regime of urban streams, thus resulting in a loss of beaver habitat and foraging material. Anthropogenic changes can benefit beaver populations under certain circumstances.

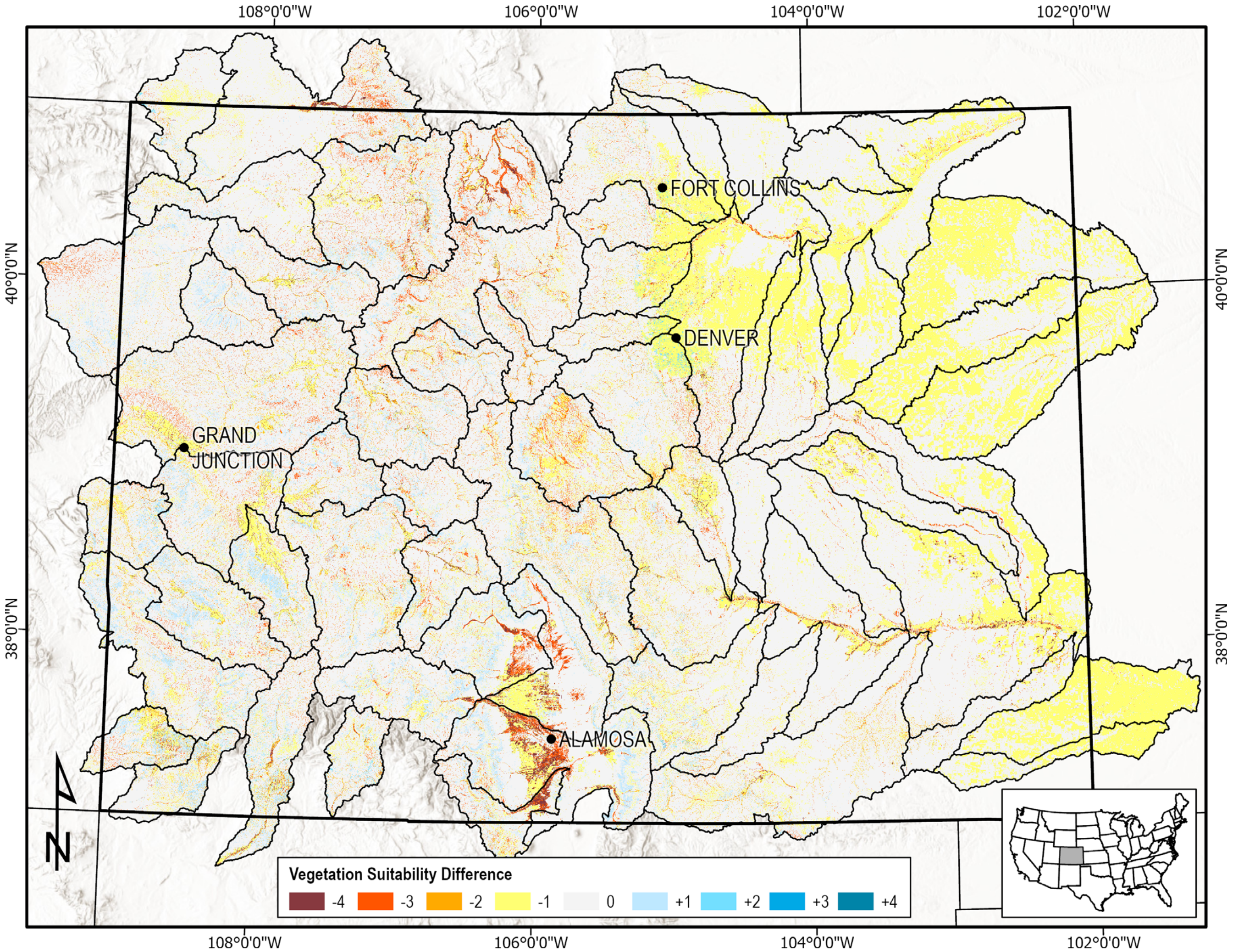

FIGURE 5 Comparison of beaver foraging suitability of current vegetation and historic vegetation. Color represents the change in suitability from pre-European settlement to current day. Warm colors represent a decrease, and cool colors represent an increase in beaver foraging suitability

Artificially increased summer baseflows through the Denver metropolitan area (Fillo et al., 2021), for example, have allowed for the establishment of high densities of beaver dams within an urban setting. However, traditional beaver-suitable habitat has largely declined, and population increases in the Front Range could be driving the proportionally greater decrease from historical beaver dam capacities in the Foothills region compared with other regions.

As beaver suitability declines at the reach scale, reaches still suitable for beaver colonization become fragmented and disconnected, which could potentially limit future beaver recruitment to the area. Beyond ecological and anthropogenic stressors, local beaver population declines alone can cause a loss of suitable beaver habitat because of the ability of beaver to create self-enhancing feedback loops that sustain riparian willow carrs (e.g., Wolf et al., 2007).

Ecological and physical feedbacks from widespread beaver loss

The historical loss of beaver populations due to unsustainable trapping and ecological competition across the western United States, including Colorado, is well documented (Baker et al., 2005; Jenkins & Busher, 1979; Naiman et al., 1988; Ringelman, 1991). Previous estimates of historical and contemporary beaver populations (Naiman et al., 1988; Pollock et al., 2015; Seton, 1929) represent an 80%–98% loss in beaver populations post-European settlement. Mirroring this loss of population, current dam capacity has significantly decreased from historical capacities in Colorado. At the statewide level, beaver dam capacity has decreased by approximately 1.02 million dams, representing a loss of 42.7% compared with historical capacities. By comparison, Utah has experienced an estimated 29% loss in beaver dam capacity compared with present, from a total of 320,658 modeled historical dams (MacFarlane et al., 2014). In Colorado, the greatest loss in carrying capacity was on streams where capacity was historically the highest (Figure 4c). Median dam densities in the mountainous, high elevation regions of Colorado—the Mountains, Rio Grande, and Southwest regions—decreased to approximately a third of historical median dam densities (Table 1).

Accompanying the near extirpation of beaver populations in many valleys once housing thriving populations was a documented shift to drier steady states (Baker et al., 2005; Laurel & Wohl, 2019; Neff, 1957; Wolf et al., 2007). Beaver colony abandonment is typically accompanied by eventual failure of beaver dams, loss of surface water storage and ponding, and the concentration of surface flow into a single-threaded channel that is more likely to incise (Butler & Malanson, 2005; Wohl, 2021). Results show that the current potential for surface water and sediment storage has decreased significantly compared with historical potential (Tables 3 and 4). The loss of water and sediment storage in beaver ponds can cause streams to incise and water tables to lower, abandoning riparian vegetation and causing the floodplain to shift from a wet meadow or shrubland to a mesic meadow (e.g., Wolf et al., 2007). Loss of vegetation, in particular, can inhibit natural beaver recolonization or managed beaver reintroduction on a stream reach, causing a positive feedback that maintains the reach in a drier stable state. Given decreased pond potential, the loss of suitable foraging material, and a high percentage of vegetation-limited reaches statewide, results highlight the potential transition to a drier steady state on a large scale. Factors such as urbanization and agriculture have likely exacerbated the loss of ecosystem services and suitable habitat associated with a beaver-impoverished drier steady state.

However, despite significant loss in beaver dam capacity (Table 1, Figure 4), changes in capacity have not kept pace with predicted changes in beaver populations. While beaver populations have declined by an estimated minimum of 80%, capacity for beaver has only declined by approximately 50%, leaving potentially significant opportunity for reoccupation and reintroduction on streams once housing beaver. Additionally, less than 5% of streams across the state (and less than 1% of streams reaches in many regions) have undergone extreme capacity loss, defined as decreasing from a capacity of 15+ dams/km historically to less than 1 dam/km currently (Table 1). This minimal extreme change suggests beaver habitat and subsequent carrying capacity has decreased on most reaches but has not been eliminated. However, the regions with the highest percentage of reaches with extreme capacity loss (Mountains, Southwest, and Northwest regions) have seen the greatest proportional declines in potential surface water and sediment storage (Tables 3 and 4). The Mountains and Southwest regions saw an order of magnitude decline in median dam densities from pre-European settlement to current day, which could additionally explain the loss of potential water and sediment storage. The Northwest region did not see a similar decrease in median dam density yet has the highest proportional decrease in potential pond storage. This suggests that the loss of a few high-density reaches (likely beaver meadows or valley bottoms heavily altered by beaver) can have a more significant impact on potential water and sediment storage than the loss of an individual dam. Although this result is intuitive, it highlights the outsized importance of beaver meadows and emphasizes the potentially disproportional impact of restoring streams using multiple permeable dams versus single structures.

Implications for watershed management and stream restoration

Considering the substantial alterations that beaver modifications create in small- to moderate-sized river corridors, the dramatic loss of beaver populations across the Northern Hemisphere during the past few centuries likely completely transformed the upper portions of river networks (Wohl, 2021). The net effect of these transformations was to make river corridors less retentive of water, solutes, sediment, and particulate organic matter (Kramer et al., 2012; Wegener et al., 2017; Westbrook et al., 2011); less resilient to droughts, wildfire, and floods (Fairfax & Small, 2018; Fairfax & Whittle, 2020); and less able to support abundant and diverse populations of other species (Rosell et al., 2005). Small, intermittent to perennial channels highly suitable to and occupied by beaver would have essentially been a chain of ponds, with the backwater from one beaver dam reaching nearly upstream to the base of another beaver dam (Butler & Malanson, 1995). Floodplain environments occupied by beaver on larger rivers would have included numerous ponds in various stages of infilling by sediment. These ponds created a patchy environment that attenuated downstream fluxes and provided habitat diversity. The removal of beaver caused multithread channels surrounded by floodplain wetlands—beaver meadows (Polvi & Wohl, 2012)—to metamorphose into more incised, single-thread channels that are less hydrologically connected to the adjacent floodplain (Westbrook et al., 2006). Restoring beaver populations and beaver modifications of river corridors has the potential to enhance river resilience to disturbances (Fairfax &

Whittle, 2020; Hood & Bayley, 2008; Puttock et al., 2021; Westbrook et al., 2020), carbon storage in floodplain soils (Johnston, 2014; Laurel & Wohl, 2019), and habitat and biodiversity in river corridors (Brazier et al., 2021; Law et al., 2016; Rosell et al., 2005). Enhancing resilience and river corridor water storage is particularly important in the Intermountain West, in which climate change is creating warmer, drier conditions even as population growth continues to increase the consumptive demand for water resources.

Model results emphasize the expected loss of beaver habitat and potential dam building across the study area. Specifically, beaver dam capacity has been reduced to 42.7% of historical capacity, with some regions of Colorado reduced to as little as a fifth of historical beaver dam capacity. Despite a widespread loss of capacity, most regions in Colorado have not experienced a large increase in stream reaches with no capacity to support beaver (Figure 4c). This suggests that beaver restoration could be a useful tool in many stream reaches, although reaches likely cannot be restored to pre-European conditions initially. Generally, capacity has been reduced but not lost on most stream reaches across the state. Changes in beaver dam capacity across the region highlight options and opportunities for watershed management and stream restoration across the historic beaver range. Where frequent to pervasive beaver dam capacity is still predicted, such as many reaches in the Mountains region, beaver reintroduction could push river corridors into a self-sustaining, wet steady state (Figure 6). Where rare to

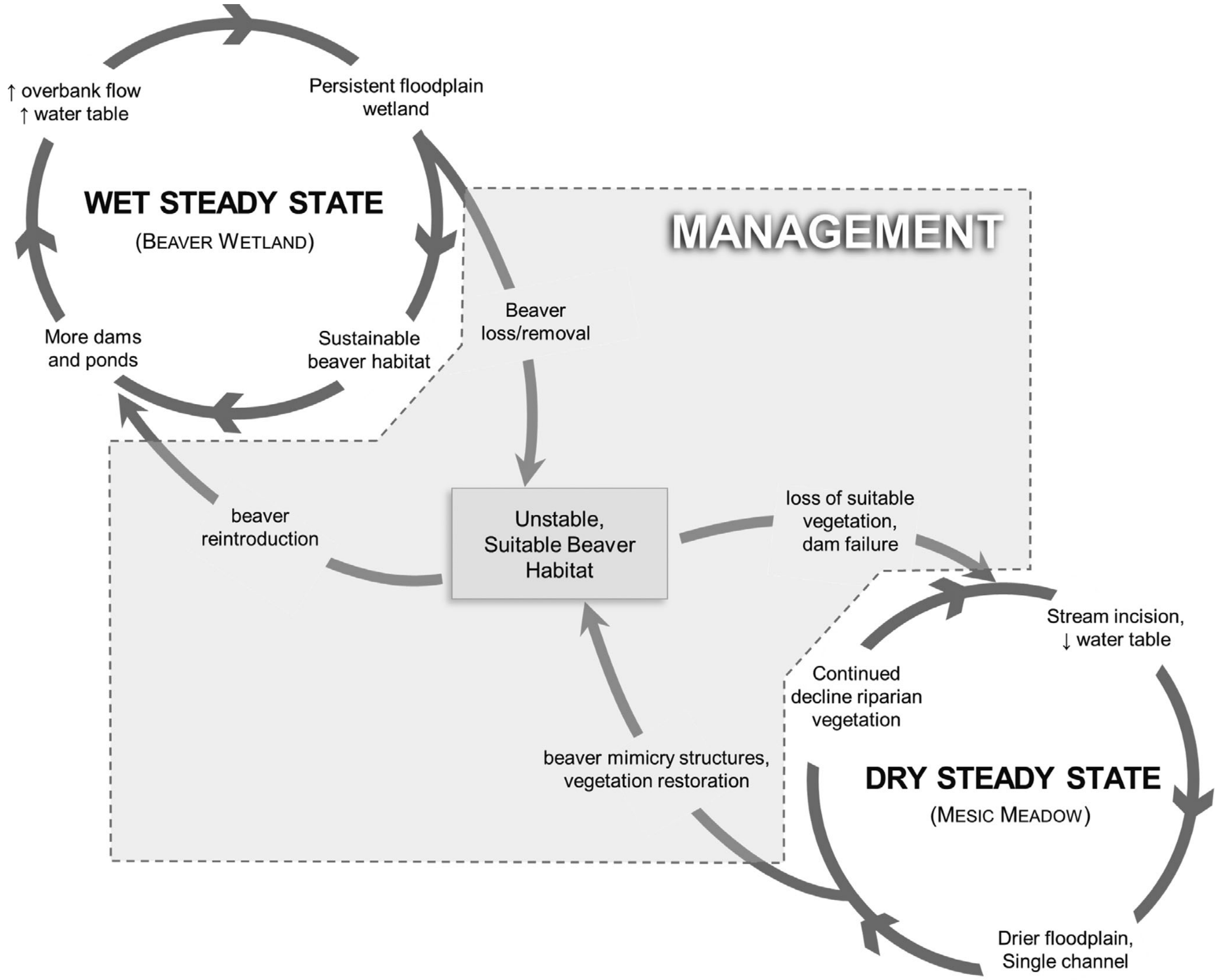

FIGURE 6 Conceptual model outlining the shift from a beaver-driven wet steady state to a non-beaver dry steady state (adapted from Laurel & Wohl, 2019). After beaver loss, stream reaches may still maintain or carry suitable vegetation for beaver foraging, thus allowing the reintroduction of beaver. Once streams fall into a dry steady state and lose suitable beaver vegetation, beaver mimicry structures or vegetation restoration can be used to regain suitable habitat prior to reintroduction. As enthusiasm for beaver-related restoration increases, opportunities for restoration and management lie between the two steady states

occasional beaver dam capacity is predicted or where beaver dam capacity has been significantly decreased from historic estimates, streams are likely to have shifted or started to shift to a drier steady state. Therefore, vegetation restoration or beaver mimicry structures could be deployed to shift streams to a more suitable state prior to beaver reintroduction (e.g., Munir & Westbrook, 2021; Scamardo & Wohl, 2020) (Figure 6).

The space between two self-sustained steady states—a beaver-mediated wet steady state and an alternative dry steady state—represents an opportunity for stream restoration and management (Figure 6). Results for Colorado suggest that many sites historically suitable to beaver exist between these two states and these patterns may be present in other portions of the American West.

CONCLUSIONS

Unsustainable trapping and land use shifts have resulted in widespread loss of beaver across North America. This study highlights how beaver population loss has been met with significant loss of beaver habitat and dam capacity in Colorado. All regions in Colorado have experienced a decrease in median beaver dam capacity in the stream network. The highest relative population loss occurred in the Foothills region, where a decrease in capacity to a fifth of historic capacities may be driven by significant urbanization. Loss of suitable vegetation is driving loss of beaver dam capacity, and vegetation suitability is the dominant limiting factor to beaver dam capacity in all regions of Colorado.

Widespread declines in beaver suitability and the capacity for riverscapes to support dam building coincide with a significant loss in sediment and surface water storage potential. Regions where higher percentages of streams experienced extreme loss of beaver dam capacity also experienced the highest proportional loss of potential water and sediment storage, which emphasizes disproportional ecosystem services provided by high dam density reaches (i.e., beaver meadows). The loss of beaver dam capacity and potential water and sediment storage could be indicative of positive feedback shifting systems toward a drier steady state less suitable to beaver.

However, while dam capacities have declined regionally, few stream reaches that could historically support beaver have completely lost the ability to sustain dam building. Beaver reintroductions could be used to sustain moderately suitable stream reaches and to restore reaches to wet meadows. In reaches where vegetation loss and dam capacity declines suggest a shift to a drier steady state, restoration techniques such as vegetation planting and beaver dam analogues could be used to rehabilitate the stream to a more suitable habitat capable of sustaining natural dams. Restoring stream reaches to historically wetter conditions once created by beaver can help maintain functional valley bottoms that retain solutes and pollutants and are resilient to disturbances such as floods and wildfires.

Results from statewide modeling can be used to guide management decisions, along with careful field surveys and knowledge of the regional history. This case study from Colorado also illustrates how BRAT or other beaver habitat modeling can be used to identify spatial and temporal trends in not only beaver habitat suitability within a region but also inferred changes in the resilience of river networks to disturbance. In the context of restoration in Colorado and the American West, results highlight the opportunity to restore incised, disconnected stream networks using beaver-related techniques, as habitat loss has not kept pace with beaver population decline.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Colorado Natural Heritage Program at https://csurams.maps.arcgis.com/apps/webappviewer/index.html?id=1051266316f0449f8d657ac3bf9a53ed. Shapefiles can be downloaded by hydrologic region or for the state from the Colorado BRAT repository, which can be accessed using the "Download Data" button at the top of the map viewer.

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