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RESEARCH ARTICLE

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Assessing restoration potential for beaver (*Castor canadensis*) in the semiarid foothills of the Southern Rockies, USA

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Abstract

We used the Beaver Restoration Assessment Tool (BRAT) developed at Utah State University to develop spatially explicit estimates of maximum beaver-carrying capacity in a 160 km^2 watershed in the foothills of the Southern Rockies. The watershed does not currently have beaver but has extensive evidence of past beaver occupation. BRAT uses input data on stream flow, topography, and vegetation. We compared BRAT results using three different types of vegetation inputs: the default LANDFIRE data at 30-m spatial resolution and pixel-based and object-based image analysis (OBIA) with 1-m resolution National Agriculture Imagery Program imagery. OBIA produced the most accurate results relative to ground-based vegetation mapping. Changes in vegetation input data resulted in substantial changes in BRAT estimates of beaver-carrying capacity. Using historic LANDFIRE vegetation data and field evidence of past beaver activity, contemporary beaver-carrying capacity is much lower than historical capacity throughout the watershed. These changes are especially pronounced in low-order stream segments, suggesting that beaver reintroduction in this watershed could be facilitated by measures to restore riparian vegetation along low-order streams. This case study demonstrates the value of using BRAT as a tool prior to beaver reintroduction and stream restoration.

KEYWORDS
beaver, BRAT, river restoration, Southern Rockies

1 | INTRODUCTION

Beaver can substantially influence form and process in river corridors. Abundant evidence indicates that historic population densities of beaver (*Castor canadensis* in North America, *C. fiber* in Eurasia) along forested rivers corridors in the northern hemisphere engineered ecosystems via herbivory and construction of dams and canals (Naiman, Melillo, & Hobbie, 1986; Rosell, Bozser, Collen, & Parker, 2005). Beaver-modified river corridors have greater spatial heterogeneity (Laurel & Wohl, 2019). Beaver dams reduce longitudinal connectivity but enhance lateral and vertical connectivity between the channel, floodplain, and hyporheic zone (Burchsted, Daniels, Thorson, & Vokoun, 2010; Hood & Larson, 2015; Polvi & Wohl, 2012). These changes in connectivity attenuate downstream fluxes of water, solutes, sediment, organic matter, and large wood (Wegener, Covino, & Wohl, 2017) and result in greater organic carbon stock in river corridors (Johnston, 2014; Wohl, Dwire, Sutfin, Polvi, & Bazan, 2012). Beaver-modified river corridors have greater habitat abundance and diversity, as well as enhanced biodiversity (Naiman et al., 1986). The higher riparian water tables and greater abundance of open water and wetlands, as well as high connectivity to densely vegetated floodplains, promote greater resilience to natural and human disturbances (Hood & Bayley, 2008; Naiman et al., 1986; Pollock et al., 1995).

These enhancements of ecosystem services have been significantly reduced as beaver populations have declined in the northern hemisphere during the past few centuries because of commercial fur trapping and habitat loss. Contemporary estimates are 6–12 million beaver in North America, compared to estimates of 60–400 million beaver prior to European settlement of the continent (Naiman, Johnston, & Kelley, 1988). Loss of beaver has contributed significantly to the concomitant loss of an estimated 195,000–260,000 km^2 of wetlands in the United States (Shaw & Fredine, 1971; Vileisis, 1997).

Commercial fur trapping in the Southern Rockies ended by the 1840s, by which time beaver populations had been nearly eliminated (Wohl, 2001). Although beaver subsequently partly recovered (e.g., Mills, 1913; Packard, 1947), intensive land uses such as cattle grazing in riparian zones limited the recovery of beaver on some areas of private land. We have no records of the history of fluctuations in beaver population in the study watershed.

As concern grows over cumulative degradation of natural physical and ecological functions in river corridors, an increasing number of stream restoration projects are employing beaver reintroduction or construction of simulated beaver dams (Pollock et al., 2014; Pollock, Lewallen, Woodruff, Jordan, & Castro, 2017; Stringer & Gaywood, 2016; Weber et al., 2017). Beaver reintroduction is not always successful because of conditions such as unsuitable habitat or insufficient food supply that limit the animals' ability to survive (Pollock et al., 2017). Habitat suitability assessment prior to reintroduction has the potential to increase the success of reintroduction and investigators at Utah State University have developed the Beaver Restoration Assessment Tool (BRAT) for this purpose (Macfarlane et al., 2017; http://brat.riverscapes.xyz/).

BRAT is a planning tool that uses freely available national datasets to quantitatively estimate the upper limit of beaver-dam density for individual stream reaches throughout a drainage network. As part of a landowner-initiated stream restoration initiative, we used BRAT to assess beaver-carrying capacity within a 380 km^2 watershed on the border of the US states of Wyoming and Colorado. The watershed had no active beaver colony at the time this study began but contained abundant evidence of past beaver activity. Our primary objectives were to (i) compare BRAT estimates of carrying capacity for historical and contemporary conditions to ground-based observations of past beaver-dam density in order to identify portions of the watershed that might be prioritized for beaver reintroduction or other stream restoration efforts, and (ii) assess BRAT-estimated carrying capacity using different types of vegetation data as inputs to the model. We suspected that the default vegetation data used in BRAT would not accurately characterize riparian vegetation along smaller streams in the study area that have supported beaver in the past, so we tested this assumption by comparing field-mapped past beaver activity to vegetation data with varying spatial resolution. We used our assessments to make recommendations for using BRAT in stream restoration planning.

2 | STUDY AREA

The Dale Creek watershed is almost entirely on privately owned land that straddles the state boundary between Wyoming and Colorado (Figure 1). Dale Creek is tributary to the North Fork of the Cache la Poudre River. The creek as a whole drains 380 km^2, but the downstream-most portion

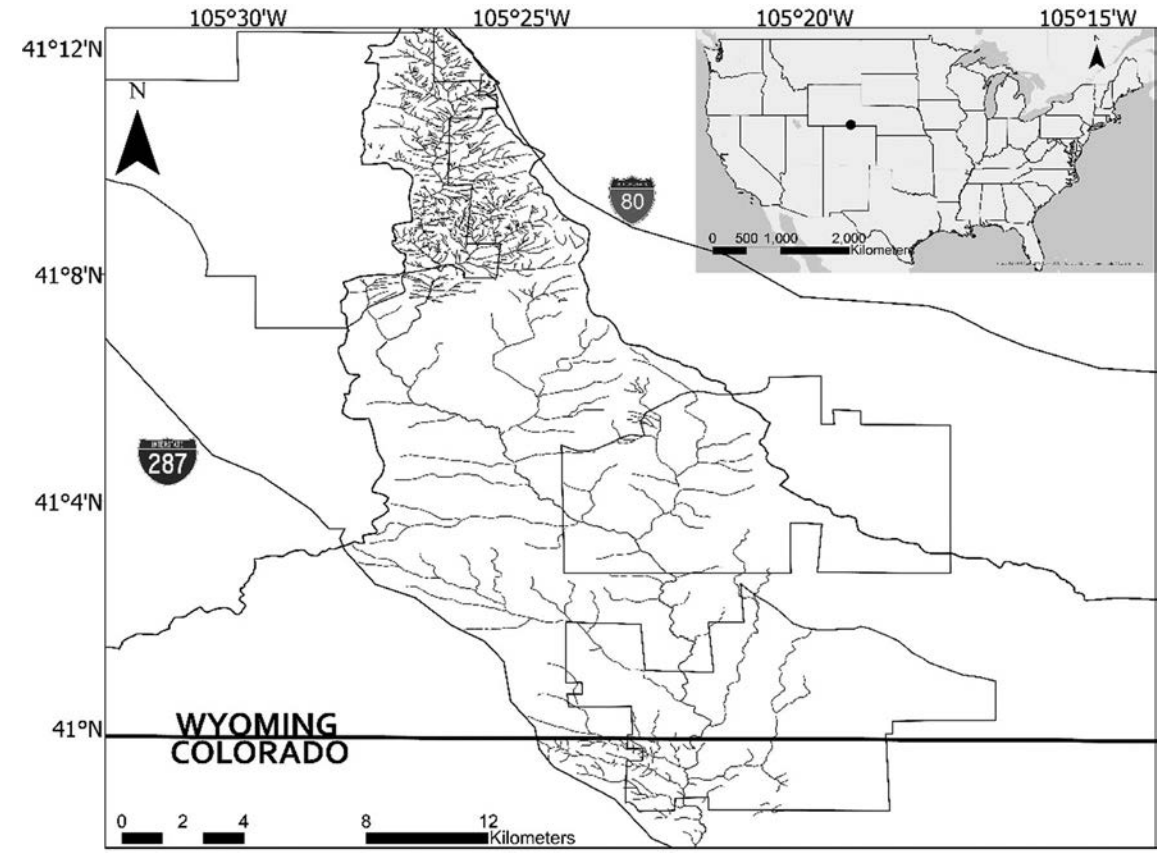

FIGURE 1 Map of the Dale Creek drainage. Inset map indicates location within the continental United States

of the study area represents a drainage area of 160 km^2. The mean elevation of the watershed is ~2,400 m and the vegetation is primarily semiarid, short-grass prairie with open conifer (*Pinus* spp., *Juniperus* spp.) woodland on the higher hills and willows (*Salix* spp.), aspen (*Populus tremuloides*), and cottonwood (*Populus* spp.) in the riparian zones. Precambrian-age Sherman Granite outcrops locally throughout the watershed (Ver Ploeg & McLaughlin, 2010) and particularly affects the topography of the stream corridor in two zones where Dale Creek flows for about a kilometer through a bedrock canyon with a 30–40 m wide valley bottom. Within the watershed, primary upland soil types are loams to very gravelly loamy sand over about 85% of the watershed (Soil Survey Staff, 2020). The stream corridor is mapped as gravelly substratum loams, although field observations reveal the presence of histosols indicative of saturated conditions along portions of the stream corridor.

Although the watershed receives localized convective rainfall during summer thunderstorms, stream flow is dominated by an annual snowmelt peak flow during June. Using regional regressions developed by the US Geological Survey (Capesius & Stephens, 2009), estimated 2-year peak flow at the downstream end of the study area is 3.2 m^3/s (base flow is ~0.01 m^3/s). First-order channels can be shallow, marshy, and poorly defined. Larger channels are commonly pool-riffle (or step-pool in the canyon reaches), with coarse gravel, cobble, and small boulder substrate. Channels are either meandering or straight and width/depth ratio is mostly 2–3. Within the study area, channels go up to fourth order (Strahler, 1952). We also defined zero-order channels where broad, shallow wetland swales consistently have surface, but poorly channelized, flow.

3 | METHODS

3.1 | Field mapping

We used field observations during the summers of 2018 and 2019 to assess the location and spatial extent of past beaver ecosystem engineering in the study area. At the start of field work, no active beaver colonies existed in the watershed. Beaver were reintroduced to three locations during our field work, but the evidence of past beaver activity is widespread.

We subsampled the stream network based on a random sampling design stratified by stream order. We examined 135 stream reaches for evidence of past beaver activity based on four primary indicators: vegetated berms, beaver-chewed wood, abrupt bends around vegetated berms, and histosols. Vegetated berms that are former beaver dams commonly have multi-stemmed willows on the berm, with *Calamagrostis* spp., sedges, and rushes growing in the former pond area (typically now filled with sediment) (Figure 2(a)). Beaver-chewed wood pieces protruding from the berm, exposed in cutbanks, or present in living or dead willows along the channel and valley bottom exhibit distinctive tapering points, sometimes with teeth marks still visible. Otherwise straight or gently meandering channel segments that make an abrupt, tight bend around a vegetated berm transverse to flow direction can also indicate former beaver dams (Figure 2(b)). Histosols form in organic soil materials in saturated, reducing areas (Stephens, Allen, & Chen, 1984). Soil is generally classified as a histosol if ≥50% of the upper 80 cm of the unit is organic material (Soil Survey Staff, 2020). Haplosaprists, a subset of histosols, are predominantly found in association with seeps, springs, ponded water, or overbank flows caused by beaver activities (Johnston, 2014). We distinguished histosols associated with seeps or springs, which are present in the study area, from histosols associated with the past presence of beaver based on (i) thickness (greater thickness in beaver-modified areas) and (ii) the presence of vegetated berms or chewed wood. Abandoned and active beaver dams were mapped using handheld Garmin eTrex GPS units (± 3 m horizontal resolution).

Geomorphic characteristics noted at each sample reach include valley bottom width, geology, width/depth ratio of the bankfull channel, and categorical assessments of channel planform (straight, meandering, anastomosing, and braided); bedforms (step-pool, plane-

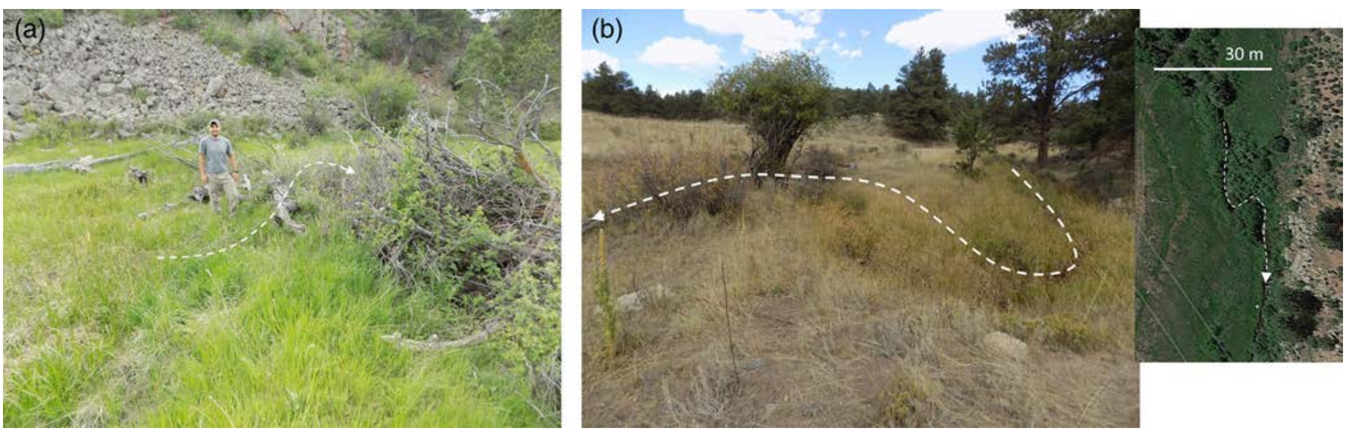

FIGURE 2 Examples of field evidence of past beaver occupation. (a) Man is standing at the base of a long-abandoned beaver dam. Because the vegetated berm that represents the former dam is difficult to see, the dashed white arrow indicates both the surface topography and flow direction. Note the remnants of shrubby willows in the right foreground growing on the berm. (b) Ground photo at left of a beaver dam berm (foreground centre) around which the contemporary channel takes an abrupt bend, as indicated by the dashed line and arrow. Aerial view of another abandoned berm forming an abrupt meander in the channel [Color figure can be viewed at wileyonlinelibrary.com]

bed, pool-riffle, and dune-ripple); substrate grain-size (large boulder, small boulder, cobble, pebble, sand, and silt-clay); bank angle, exposure, and grain size; and flow regime (ephemeral, intermittent, and perennial). At each sample reach, we also noted the characteristics of riparian vegetation. Riparian vegetation was categorized as herbaceous (including grasses, sedges, and rushes), willow, other deciduous (aspen, cottonwood), and conifer types, and we noted the condition as being browsed, stressed, or healthy. We noted the GPS coordinates of the upstream and downstream extent of each type of vegetation within the sample reach, as well as the average width along each side of the channel. These data were used to assess the accuracy of different sources of vegetation input data for BRAT modelling.

Sampled reaches were 130 m long on zero-order streams and 125, 70, 50, and 50 m long on first-, second-, third-, and fourth-order streams, respectively. We chose sample numbers and lengths to ensure that we sampled at least 5% of the total length of zero-order streams and 10% of the total length of all other stream orders.

3.2 | BRAT modelling

BRAT is a numeric model developed at Utah State University that can be used to estimate maximum beaver-carrying capacity at the reach scale. Although beaver are extremely adaptable and occupy diverse fluvial environments, they prefer low gradient (< 6%) alluvial channels, without boulder or bedrock substrates, perennial or at least intermittent flow, and sufficient woody riparian vegetation within 100 m of the active channel to provide winter food and dam-building materials (Allen, 1983; McComb, Sedell, & Buchholz, 1990; Pollock, Heim, & Werner, 2003). BRAT incorporates these preferred attributes to estimate beaver-carrying capacity in terms of number of dams per kilometer of channel, categorized as none (0 dams/km), rare (0–1), occasional (1–4), frequent (5–15), and pervasive (>15) (Macfarlane et al., 2017). BRAT segments streams into 300 m lengths and then cleans the data to include only perennial and intermittent (not ephemeral) channels.

One benefit of BRAT is the ability to input datasets publicly available for the United States without the need for field verification. The primary inputs are the National Hydrography Dataset (last updated March 2019), LANDFIRE (national vegetation layer with 30 m spatial resolution, last updated 2016), base- and peak-flow equations derived from the US Geological Survey regional regressions, and national digital elevation models from the US Geological Survey National Elevation Dataset (approximately 10 m spatial resolution, last updated February 2019). LANDFIRE also provides vegetation layers based on best estimates of reference conditions prior to European settlement and land uses such as grazing or timber harvest that alter land cover. We refer to this layer as historical vegetation.

Although using publicly available datasets facilitate ease of use, the spatial resolution and accuracy of these datasets can create errors when using BRAT to estimate beaver-carrying capacity in relatively small watersheds. Vegetation layers are particularly problematic, given the 30-m spatial resolution of LANDFIRE and the presence of narrow riparian vegetation zones that can support beavers along smaller channels. Consequently, we used additional techniques to estimate riparian vegetation, as detailed below.

3.3 | Modification of BRAT vegetation inputs

We used image classification to improve the spatial resolution of riparian vegetation data that form one of the primary inputs for BRAT modelling. Image classification automatically groups pixels into desired classes or themes that the user specifies (Lilliesand, Kiefer, & Chipman, 2015). This technique works well for land cover because of the ability to automatically classify data across large spatial areas (Lu & Weng, 2007). Image classification techniques include object-based (e.g., Dragut & Blascke, 2006) and pixel-based (e.g., Moosavi, Talebi, & Shirmohammadi, 2014) analysis. Pixel-based image analysis uses spectral patterns to identify pixels with similar spectral reflectance or emissivity and groups pixels together into the same class (Lilliesand et al., 2015). Object-based image analysis (OBIA) examines localized groups of pixels when assigning a pixel to a class (Lilliesand et al., 2015). These segments account for both the shape and the spectral response of a group of pixels, facilitating a more realistic classification that resembles actual objects on Earth's surface.

Image analysis can be further distinguished as either unsupervised (e.g., Stepinski & Bagaria, 2009) or supervised (e.g., Phinn, Roelfsema, & Mumby, 2012) classification techniques (Lilliesand et al., 2015). Unsupervised classification analyzes unknown pixels in an image and clusters them into classes based on their spectral response and/or localized groups. The analyst then observes the classes and assigns them names from prior knowledge of the field site (Lu & Weng, 2007). Supervised classification utilizes a training dataset of known classes that the analyst specifies prior to image analysis. Classes are then created for the image by using the training data and searching for similar properties.

Support vector machines are a widely used form of supervised classification that represent a per-pixel, non-parametric technique (Lu & Weng, 2007). This approach does not rely on assuming a Gaussian distribution because statistical calculations are not used to determine classes. Instead, support vector machines create linear hyperplanes that maximize the margin between classes (Chapelle, Haffner, & Vapnik, 1999). Because a Gaussian distribution is not assumed, smaller, skewed training sets can be used for classifications (Lu & Weng, 2007).

In addition to the default vegetation layer input from LANDFIRE, we created two alternative vegetation layers. The first alternative used support vector machine pixel-based supervised classification on a principal component analysis of National Agriculture Imagery Program (NAIP) images from 2017. This imagery has 1-m spatial resolution. We created a training dataset from the principal component analysis according to beaver preferences for vegetation (Figure 3). We subsequently refer to this approach as pixel-based.

The second alternative vegetation layer was created using support vector machine OBIA supervised classification on the same principal component analysis of NAIP imagery. We used several segment attributes to determine classes: color, mean raster digital number, standard deviation, number of pixels, compactness, and rectangularity. Using multiple attributes improves the accuracy of classification by enhancing the ability to group pixels. We subsequently refer to this approach as OBIA.

We assessed the accuracy of each classification by visually interpreting the NAIP imagery based on our ground observations of the field site. We then used these comparisons in a confusion matrix to assess the relative accuracy of LANDFIRE, pixel-based, and OBIA vegetation data (Kornse, 2020). A confusion matrix assesses the match between instances in an actual class and instances in a predicted class. For the riparian vegetation in this study, the confusion matrix assessed the accuracy of the three different vegetation inputs relative to actual vegetation mapped on the ground.

4 | RESULTS

4.1 | BRAT results using LANDFIRE, pixel-based, and OBIA vegetation data

In comparison to ground-based observations, the vegetation layer derived from LANDFIRE data had the least accurate classification of vegetation, as reflected in a lower percentage of matching with ground-mapped vegetation (Figure 4, Table 1). Pixel-based classification was more accurate than LANDFIRE, but OBIA classified vegetation most closely matched ground observations.

Differences in vegetation input resulted in divergent estimates of beaver-carrying capacity using BRAT. With LANDFIRE data, 9% of the Dale Creek stream network was in the occasional category and 53% in the frequent category (Figure 5, Table 2), for example, whereas pixel-based classification resulted in 81% and 19% in the occasional and frequent categories, respectively, and OBIA classification resulted in 63% and 33% of the stream network in the occasional and frequent categories. In general, the more accurate OBIA vegetation classification resulted in reduced estimates of beaver-carrying capacity at the watershed scale because of a greater percentage of total stream length categorized by BRAT as occasional relative to LANDFIRE vegetation inputs (Figure 5). Given the dearth of contemporary beaver activity, this assessment seems appropriate. These changes can also be illustrated in a more spatially explicit manner (Figure 6), which revealed that pixel-based vegetation classification resulted in more stream segments decreasing by two categories compared to LANDFIRE. Both pixel-based and OBIA classifications resulted in different portions of the stream network increasing or decreasing in carrying capacity when compared to

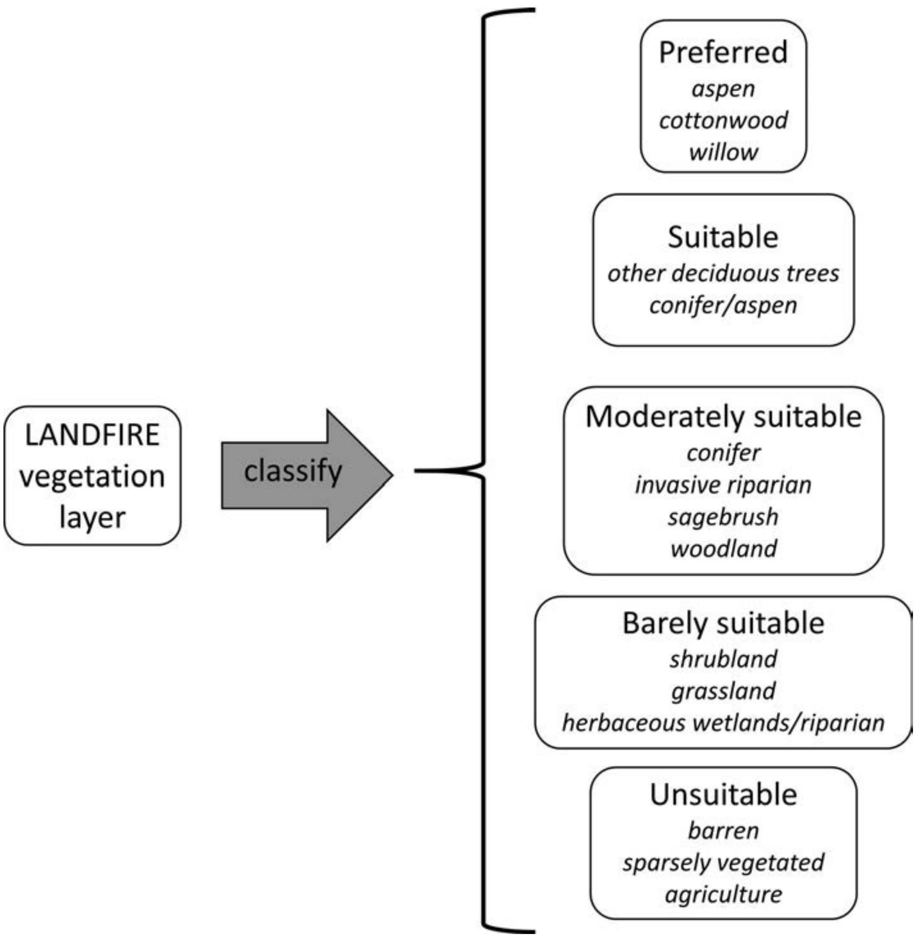

FIGURE 3 Illustration of how vegetation characteristics are delineated into categories based on known preferences of beaver and ability of different types of vegetation to support dam-building activities. With field-based prior knowledge of riparian vegetation in the Dale Creek watershed, we used these vegetation categories to create the training dataset used in pixel-based and OBIA classifications. (After Figure 1, Vegetation Input Rasters, BRAT-Riverscapes website, Utah State University, http://brat.riverscapes.xyz/Documentation/Tutorials/2-Preprocessing). BRAT, Beaver Restoration Assessment Tool; OBIA, object-based image analysis

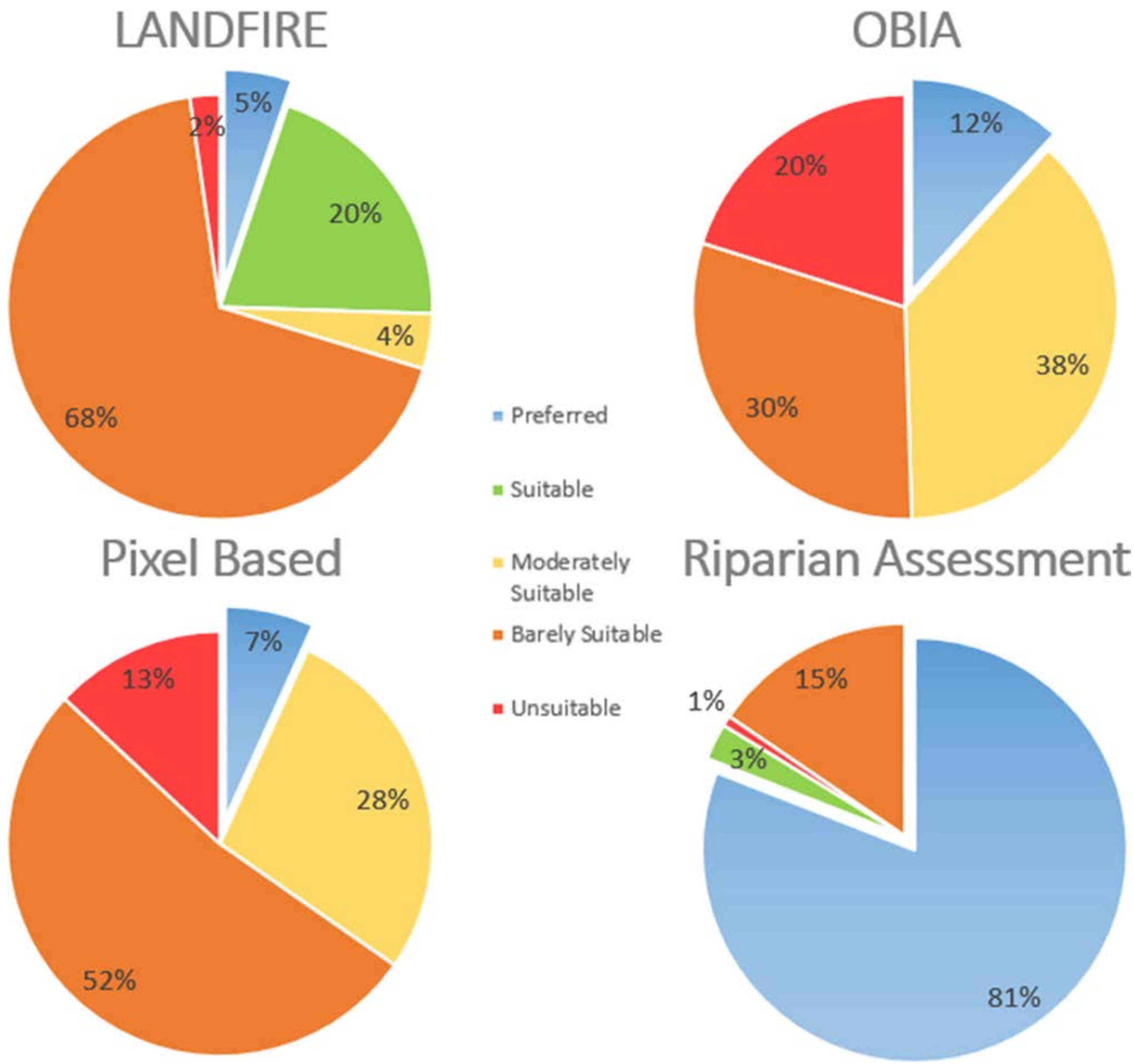

FIGURE 4 The proportions of vegetation in reference to how suitable the material is for beaver use compared between LANDFIRE, pixel-based image classification, OBIA image classification, and ground observations during field assessment [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Confusion matrix accuracy for LANDFIRE, pixel-based, and OBIA vegetation classification summary relative to field data and NAIP imagery

Vegetation Data	LANDFIRE	Pixel-based	OBIA
Accuracy	52%	64%	82%

Abbreviations: NAIP, National Agriculture Imagery Program; OBIA, object-based image analysis.

LANDFIRE results (Table 3). When separated by stream order, OBIA predicted greater carrying capacity on second- to fourth-order streams than LANDFIRE (Figure 7).

4.2 | Estimates of contemporary versus historical beaver-carrying capacity

As with the comparison of BRAT-modelled contemporary carrying capacity using different vegetation inputs, we used our ground-based mapping of past beaver activity as a basis for comparing BRAT-modelled historical carrying capacity. For most dam-carrying capacity categories, BRAT-modelled historical conditions suggested greater beaver occupancy than we found evidence for during field surveys (Table 2). These differences were greatest for zero- to second-order channels (Table 3). In contrast, field surveys indicated greater historical presence of beaver on third- and fourth-order channels than estimated by BRAT (Figure 7).

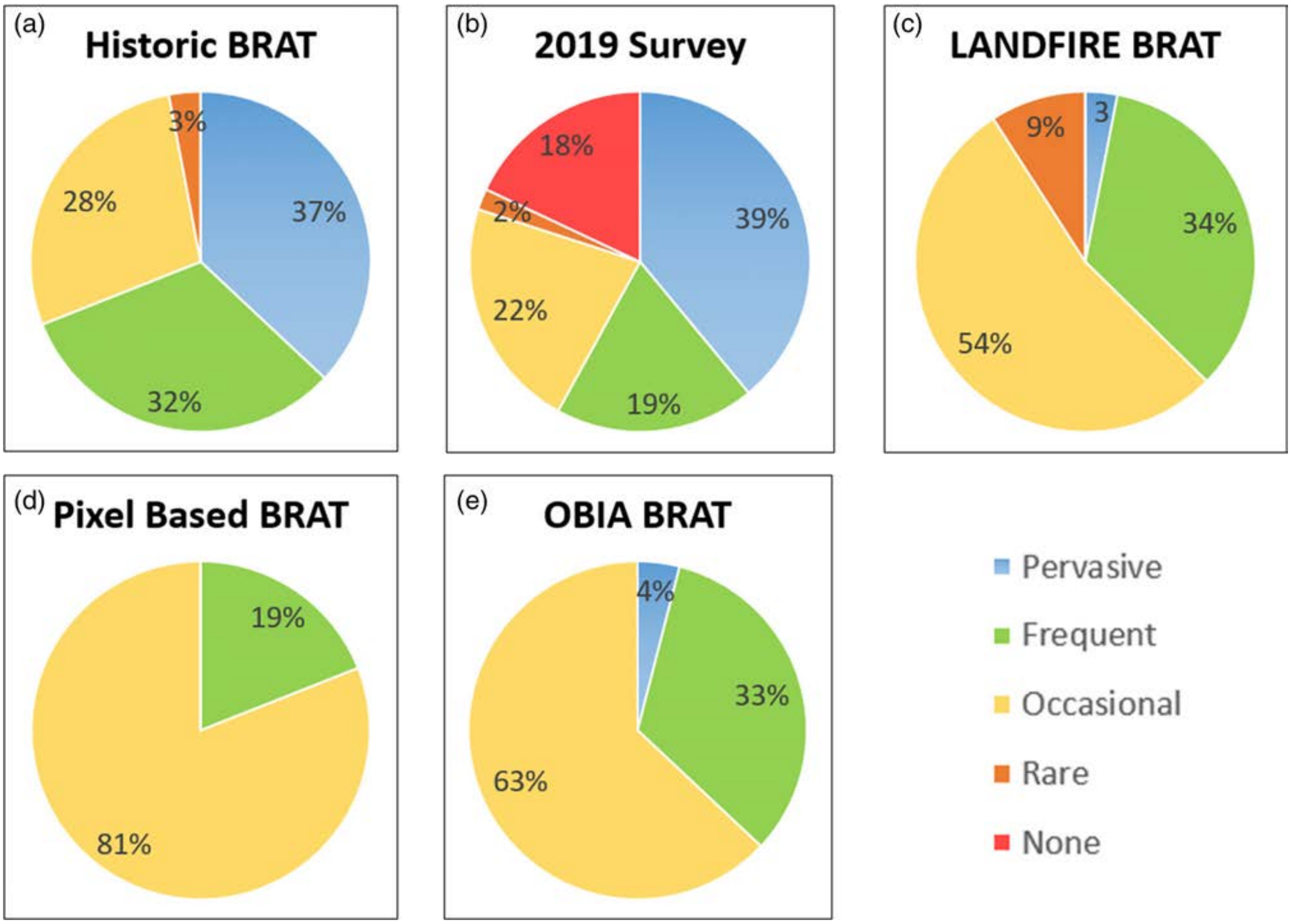

FIGURE 5 Representation of changes in percentage of total stream length within each BRAT-estimated category of beaver-carrying capacity for historical carrying capacity based on (a) BRAT historic (LANDFIRE) vegetation inputs and (b) field evidence and contemporary carrying capacity based on (c) LANDFIRE, (d) pixel-based, and (e) OBIA vegetation inputs to BRAT [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Proportion of total Dale Creek stream network in BRAT-estimated beaver-carrying capacity categories using different types of vegetation inputs

BRAT Class	Field Survey	Historic BRAT (LANDFIRE)	Contemporary BRAT (LANDFIRE)	Contemporary BRAT (pixel-based)	Contemporary BRAT (OBIA)
None	18	0	0	0	0
Rare	2	3	3	0	0
Occasional	22	28	9	81	63
Frequent	19	32	53	19	33
Pervasive	39	37	3	0	4

Abbreviations: BRAT, Beaver Restoration Assessment Tool; OBIA, object-based image analysis.

5 | DISCUSSION AND CONCLUSIONS

5.1 | Changes in BRAT-estimated carrying capacity in relation to vegetation input data

The coarser spatial resolution of LANDFIRE vegetation data prevented recognition of vegetation important for beaver-carrying capacity, such as the zone of riparian willows along the main channel. LANDFIRE also incorrectly classified much of the riparian zone as deciduous trees other than willow and aspen and incorrectly classified upland vegetation. The finer spatial resolution of the NAIP imagery allowed pixel-based classification to detect narrow bands of riparian willow, but this method failed to recognize continuous groups and therefore included substantial noise in the classification. The OBIA classification performed best relative to ground observations because of the ability to segment pixels into groups based on objects.

These differences in accuracy of vegetation categorization strongly influenced BRAT estimates of beaver-carrying capacity.

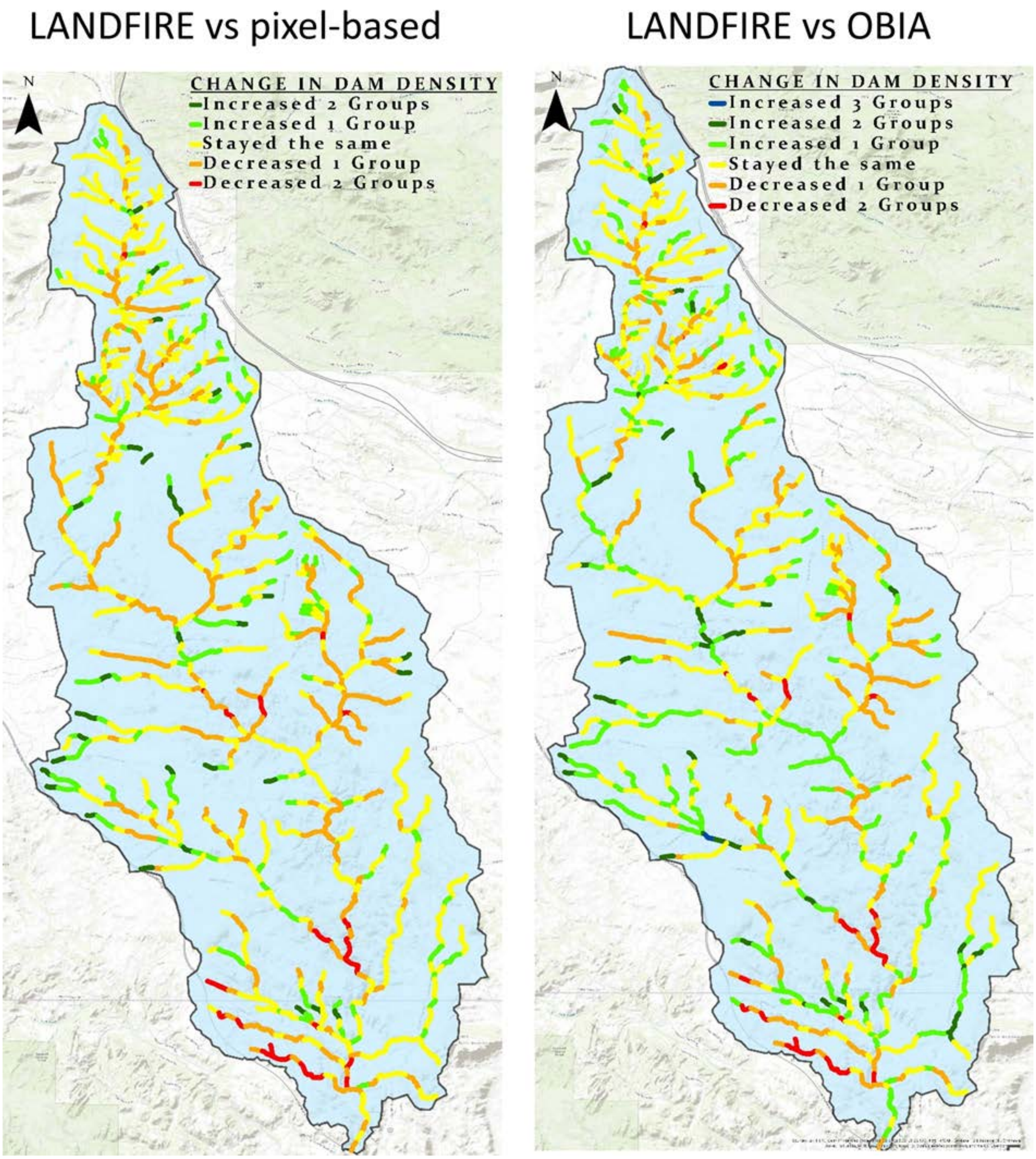

FIGURE 6 Changes in BRAT results using different vegetation inputs. (a) LANDFIRE versus pixel-based. (b) LANDFIRE versus OBIA [Color figure can be viewed at wileyonlinelibrary.com]

In locations where riparian willow and aspen were correctly identified, BRAT estimates increased by at least one category of dam density relative to LANDFIRE results. Similarly, where upland vegetation was correctly classified as sagebrush rather than brushland, dam density category increased. Decreases in BRAT estimates of carrying capacity occurred where floodplain vegetation was corrected from deciduous trees to herbaceous grasslands.

5.2 | Estimates of historic and contemporary beaver activity

Comparison of BRAT-estimated carrying capacity using LANDFIRE data for contemporary and historical conditions suggested that beaver-carrying capacity in the Dale Creek watershed has declined through time based on changes in the "pervasive" category (Tables 2 and 3). Given the known history of intensive riparian

TABLE 3 Proportion of the total length of streams within each stream order in the Dale Creek stream network in BRAT-estimated beaver-carrying capacity categories using different types of vegetation inputs

	Field Survey (% Total Stream Order Length)					Historic BRAT (LANDFIRE)					Contemporary BRAT (LANDFIRE)					Contemporary BRAT (Pixel-Based)					Contemporary BRAT (OBIA)				
Order and %	N	R	O	F	P	N	R	O	F	P	N	R	O	F	P	N	R	O	F	P	N	R	O	F	P
0 50	40	3	36	14	17	0	5	42	31	22	0	12	57	28	3	0	0	78	22	0	0	0	70	29	1
1 23	10	3	30	24	33	0	1	18	38	43	0	6	51	38	5	0	0	87	13	0	0	0	64	33	3
2 14	8	0	19	19	54	0	1	7	34	58	0	6	48	43	3	0	0	87	13	0	0	0	60	34	6
3 6	0	0	10	25	65	0	0	4	45	51	0	4	56	40	0	0	0	90	10	0	0	0	36	60	4
4 7	0	0	0	10	90	0	1	3	19	77	0	5	45	46	4	0	0	77	23	0	0	0	33	46	21

Note: In first column, % refers to percentage of total stream length within that order.
Abbreviations: BRAT, Beaver Restoration Assessment Tool; F, frequent; N, none; O, occasional; OBIA, object-based image analysis; P, pervasive; R, rare.

grazing by cattle and contemporary observations of intensive riparian grazing by moose and elk, this loss of beaver-carrying capacity through time seems reasonable.

The primary difference between BRAT estimates of beaver-carrying capacity and field mapping of past extent of beaver occupation was that the field survey found no evidence of beaver activity in many stream reaches, whereas BRAT suggested that beaver should have been present in every portion of the stream network. As noted in other contexts, the absence of evidence is not evidence of absence. Land uses including intensive cattle grazing, construction of unpaved roads and associated culverts, and construction of fences and corrals to control cattle could have obliterated evidence of past beaver activity. In addition, BRAT estimates the maximum carrying capacity and beaver might not have been at maximum capacity because of predation, disease, or other biological factors. Because of the absence of contemporary beaver activity throughout much of the stream network, we do not have a full-proof test of the accuracy of BRAT's estimates for historic beaver-carrying capacity.

We do, however, have a recent test of carrying capacity, thanks to the activities of beaver reintroduced to one stream reach along the mainstem creek late in Summer 2018. When we surveyed the site in September 2019, the beaver had built 21 dams along a 1,000-m length of Dale Creek (fourth order). Using OBIA vegetation input, BRAT estimated occasional or frequent dam categories for different segments of this site, whereas the beaver obviously considered the habitat of higher quality and built enough dams to place the stream segment in the pervasive category. This suggests that even with the improved vegetation inputs, BRAT may underestimate maximum contemporary carrying capacity on the mainstem of Dale Creek. The long-term viability of this beaver colony is of course not yet known.

5.3 | Implications for beaver reintroduction

The spatially explicit results from BRAT modelling suggested significant losses in beaver-carrying capacity across all stream orders in the Dale Creek watershed. These changes were especially pronounced in lower-order streams. Field evidence and historic BRAT estimates suggested that more than half of the total length of second-order streams are in the pervasive category, for example, whereas contemporary OBIA-based BRAT estimates indicated only 6% of second-order streams in this category (Table 3). The success of recently reintroduced beaver in colonizing the fourth-order mainstem suggests that the riparian vegetation that remains along the higher-order streams in the network may nonetheless be capable of sustaining beaver populations. The lack of woody riparian vegetation in many of the heavily grazed lower-order streams, in contrast, likely limits or precludes beaver occupancy of these sites until the riparian vegetation recovers (Baker, 2003; Baker, Peinetti, Coughenour, & Johnson, 2012). Grazing exclosures, or exclosures and active replanting of woody riparian species, would help riparian vegetation to recover in these areas.

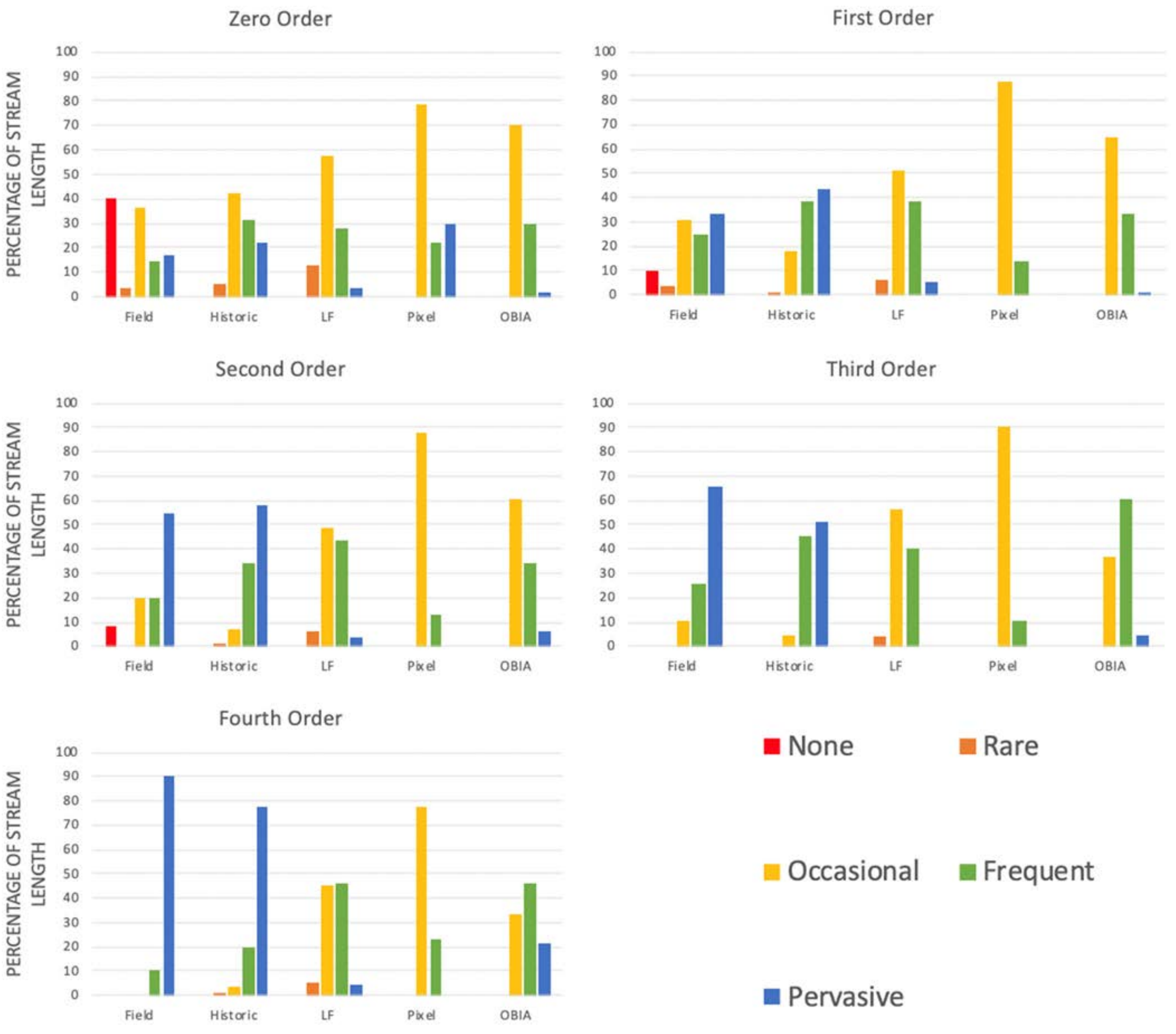

FIGURE 7 Changes in BRAT results for different stream orders based on historical and contemporary conditions with different vegetation inputs [Color figure can be viewed at wileyonlinelibrary.com]

Although beaver have been able to build dams along the mainstem, the slightly incised, single-thread contemporary channel and adjacent semiarid grassland of the former floodplain probably represent a simplified river corridor relative to historic conditions. Comparable portions of stream networks with sufficient woody riparian vegetation typically have a multi-thread channel planform with beaver dams on secondary channels and old ponds and vegetated berms across the floodplain (Laurel & Wohl, 2019; Polvi & Wohl, 2012). Re-establishment of analogous conditions along the mainstem Dale Creek probably requires more sustained beaver occupancy, as dams accumulate sediment upstream and raise the streambed, helping to establish lateral connectivity with the floodplain (Pollock, Beechie, & Jordan, 2007). The restoration of a wet, spatially heterogeneous floodplain may also require grazing exclosures and potentially active riparian planting, however, because the relatively narrow band of willows present along much of the mainstem is probably not sufficient to support construction of multiple dams on secondary channels. Consequently, depending on the scale of fencing considered feasible, reintroduction could focus on segments of headwater channels or higher-order channels.

Our results indicated that BRAT modelling can provide useful input when planning beaver reintroduction or stream restoration designed to foster beaver reoccupation. Using default options such as LANDFIRE vegetation data in BRAT can provide a rapid overview of the spatial distribution and abundance of potentially suitable beaver habitat in a stream network. Stream segments with high potential could then be assessed with greater accuracy by using lidar topographic data, for example, or pixel-based or OBIA vegetation classification. Image classification of vegetation can be relatively rapid for drainage areas less than 500 km^2 or with relatively little variability in vegetation. For larger watersheds or those with greater spatial variation in vegetation, LANDFIRE can be used to identify subareas for image classification of vegetation.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Allen, A.W. (1983) *Habitat suitability index models: Beaver*. Fort Collins, CO: U.S. Fish and Wildlife Service.

Baker, B. W. (2003). Beaver (*Castor Canadensis*) in heavily browsed environments. *Lutra*, *46*, 173–181.

Baker, B. W., Peinetti, H. R., Coughenour, M. B., & Johnson, T. L. (2012). Competition favors elk over beaver in a riparian willow ecosystem. *Ecosphere*, *3*, 1–15.

Burchsted, D., Daniels, M., Thorson, R., & Vokoun, J. (2010). The river discontinuum: Applying beaver modifications to baseline conditions for restoration of forested headwaters. *Bioscience*, *60*, 908–922.

Capesius, J. P., & Stephens, V. C. (2009). Regional regression equations for estimation of natural streamflow statistics in Colorado. *U.S. Geological Survey Scientific Investigations Report*, *2009-5136*, 46.

Chapelle, O., Haffner, P., & Vapnik, V. N. (1999). Support vector machines for histogram-based image classification. *IEEE Transactions on Neural Networks*, *10*(5), 1055–1064.

Dragut, L., & Blascke, T. (2006). Automated classification of landform elements using object-based image analysis. *Geomorphology*, *81*, 330–344.

Hood, G. A., & Bayley, S. E. (2008). Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation*, *141*, 556–567.

Hood, G. A., & Larson, D. G. (2015). Ecological engineering and aquatic connectivity: A new perspective from beaver-modified wetlands. *Freshwater Biology*, *60*, 198–208.

Johnston, C. A. (2014). Beaver pond effects on carbon storage in soils. *Geoderma*, *213*, 371–378.

Kornse, Z. (2020). *Prioritization of beaver (Castor canadensis) reintroduction sites within semi-arid grassland rivers in the Great Plains*. (MS thesis) Colorado State University, Fort Collins, CO.

Laurel, D., & Wohl, E. (2019). The persistence of beaver-induced geomorphic heterogeneity and organic carbon stock in river corridors. *Earth Surface Processes and Landforms*, *44*, 342–353.

Lilliesand, T. M., Kiefer, R. W., & Chipman, J. W. (2015). *Remote sensing and image interpretation*. Hoboken, NJ: John Wiley and Sons.

Lu, D., & Weng, Q. (2007). A survey of image classification methods and techniques for improving classification performance. *International Journal of Remote Sensing*, *28*, 823–870.

Macfarlane, W. W., Wheaton, J. M., Bouwes, N., Jensen, M. L., Gilbert, J. T., Hough-Snee, N., & Shivik, J. A. (2017). Modeling the capacity of riverscapes to support beaver dams. *Geomorphology*, *277*, 72–99.

McComb, W. C., Sedell, J. R., & Buchholz, T. D. (1990). Dam-site selection by beavers in an eastern Oregon basin. *Great Basin Naturalist*, *50*, 273–281.

Mills, E. A. (1913). *In beaver world*. Boston: Houghton Mifflin Company.

Moosavi, V., Talebi, A., & Shirmohammadi, B. (2014). Producing a landslide inventory map using pixel-based and object-oriented approaches optimized by Taguchi method. *Geomorphology*, *204*, 646–656.

Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of north American streams by beaver. *Bioscience*, *38*, 753–762.

Naiman, R. J., Melillo, J. M., & Hobbie, J. E. (1986). Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, *67*, 1254–1269.

Packard, F. M. (1947). A survey of the beaver population of Rocky Mountain National Park, Colorado. *Journal of Mammalogy*, *28*, 219–227.

Phinn, S. R., Roelfsema, C. M., & Mumby, P. J. (2012). Multi-scale, object-based image analysis for mapping geomorphic and ecological zones on coral reefs. *International Journal of Remote Sensing*, *33*, 3768–3797.

Pollock, M. M., Beechie, T. J., & Jordan, C. E. (2007). Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. *Earth Surface Processes and Landforms*, *32*, 1174–1185.

Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, C., Weber, & Volk, C. (2014). Using beaver dams to restore incised stream ecosystems. *BioScience*, *64*, 279–290.

Pollock, M. M., Heim, M., & Werner, D. (2003). Hydrologic and geomorphic effects of beaver dams and their influence on fishes. In S. V. Gregory, K. Boyer, & A. Gurnell (Eds.), *The ecology and management of wood in world rivers* (Vol. 37, pp. 213–233). Bethesda, MD: American Fisheries Society Symposium.

Pollock, M.M., Lewallen, G.M., Woodruff, K., Jordan, C.E., & Castro, J.M., Eds. (2017). *The beaver restoration guidebook*, v. 2.0. U.S. Fish and Wildlife Service, Portland, OR.

Pollock, M. M., Naiman, R. J., Erickson, H. E., Johnston, C. A., Pastor, J., & Pinay, G. (1995). Beaver as engineers: Influences on biotic and abiotic characteristics of drainage basins. In C. G. Jones & J. H. Lawton (Eds.), *Linking species and ecosystems* (pp. 117–126). Boston, MA: Springer.

Polvi, L. E., & Wohl, E. (2012). The beaver meadow complex revisited – The role of beavers in post-glacial floodplain development. *Earth Surface Processes and Landforms*, *37*, 332–346.

Rosell, F., Bozser, O., Collen, P., & Parker, H. (2005). Ecological impact of beavers Castor fiber and Castor Canadensis and their ability to modify ecosystems. *Mammal Review*, *35*, 248–276.

Shaw, S. P., & Fredine, C. G. (1971). Wetlands of the United States: Their extent and value to waterfowl and other wildlife. In *U.S. Fish and Wildlife Service circular* (Vol. 39). Washington, DC.

Soil Survey Staff. (2020). Natural Resources Conservation Service, US Department of Agriculture. Web Soil Survey. Available online at: https://websoilsurvey.sc.egov.usda.gov/. Accessed [February 2020].

Stephens, J. C., Allen, L. H., & Chen, E. (1984). Organic soil subsidence. *Geological Society of America Reviews in Engineering Geology*, *6*, 107–122.

Stepinski, T. F., & Bagaria, C. (2009). Segmentation-based unsupervised terrain classification for generation of physiographic maps. *IEEE Geoscience and Remote Sensing Letters*, *6*, 733–737.

Strahler, A. N. (1952). Hypsometric (area-altitude) analysis of erosional topography. *Geological Society of America Bulletin*, *63*, 1117–1142.

Stringer, A. P., & Gaywood, M. J. (2016). The impacts of beavers Castor spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. *Mammal Review*, *46*, 270–283.

Ver Ploeg, A.J., & McLaughlin, J.F. (2010). Preliminary Geologic Map of the Sherman Mountains West Quadrangle, Albany County, Wyoming. U.S. Geological Survey, 1:24,000 scale.

Vileisis, A. (1997). *Discovering the unknown landscape: A history of America's wetlands*. Washington, DC: Island Press.

Weber, N., Bouwes, N., Pollock, M. M., Volk, C., Wheaton, J. M., Wathen, G., … Jordan, C. E. (2017). Alteration of stream temperature by natural and artificial beaver dams. *PLoS One*, *12*, e0176313.

Wegener, P., Covino, T., & Wohl, E. (2017). Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism. *Water Resources Research*, *53*, 4606–4623.

Wohl, E., Dwire, K., Sutfin, N., Polvi, L., & Bazan, R. (2012). Mechanisms of carbon storage in mountainous headwater rivers. *Nature Communications*, *3*, 1263.

Wohl, E. E. (2001). *Virtual Rivers: Lessons from the mountain rivers of the Colorado front range*. New Haven, CT: Yale University Press.

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