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Modeling the capacity of riverscapes to support beaver dams

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ABSTRACT

The construction of beaver dams facilitates a suite of hydrologic, hydraulic, geomorphic, and ecological feedbacks that increase stream complexity and channel–floodplain connectivity that benefit aquatic and terrestrial biota. Depending on where beaver build dams within a drainage network, they impact lateral and longitudinal connectivity by introducing roughness elements that fundamentally change the timing, delivery, and storage of water, sediment, nutrients, and organic matter. While the local effects of beaver dams on streams are well understood, broader coverage network models that predict where beaver dams can be built and highlight their impacts on connectivity across diverse drainage networks are lacking. Here we present a capacity model to assess the limits of riverscapes to support dam-building activities by beaver across physiographically diverse landscapes. We estimated dam capacity with freely and nationally-available inputs to evaluate seven lines of evidence: (1) reliable water source, (2) riparian vegetation conducive to foraging and dam building, (3) vegetation within 100 m of edge of stream to support expansion of dam complexes and maintain large colonies, (4) likelihood that channel-spanning dams could be built during low flows, (5) the likelihood that a beaver dam is likely to withstand typical floods, (6) a suitable stream gradient that is neither too low to limit dam density nor too high to preclude the building or persistence of dams, and (7) a suitable river that is not too large to restrict dam building or persistence. Fuzzy inference systems were used to combine these controlling factors in a framework that explicitly also accounts for model uncertainty. The model was run for 40,561 km of streams in Utah, USA, and portions of surrounding states, predicting an overall network capacity of 356,294 dams at an average capacity of 8.8 dams/km. We validated model performance using 2852 observed dams across 1947 km of streams. The model showed excellent agreement with observed dam densities where beaver dams were present. Model performance was spatially coherent and logical, with electivity indices that effectively segregated capacity categories. That is, beaver dams were not found where the model predicted no dams could be supported, beaver avoided segments that were predicted to support rare or occasional densities, and beaver preferentially occupied and built dams in areas predicted to have pervasive dam densities. The resulting spatially explicit reach-scale (250 m long reaches) data identifies where dam-building activity is sustainable, and at what densities dams can occur across a landscape. As such, model outputs can be used to determine where channel–floodplain and wetland connectivity are likely to persist or expand by promoting increases in beaver dam densities.

1. Introduction

Due to the suite of hydrologic, hydraulic, geomorphic, and ecological feedbacks associated with the dam-building activities of beaver, both *Castor canadensis* in North America and *Castor fiber* in Europe and Asia, are widely recognized as ecosystem engineers (Burchsted et al., 2010; Gurnell, 1998; Naiman et al., 1988; Rosell et al., 2005; Warren, 1927). As such, beaver dam building activities affect the lateral, longitudinal, vertical and temporal connectivity of stream channels, floodplains, and adjacent uplands. Beaver dams increase lateral connectivity by linking stream channels, floodplains, and adjacent uplands subsequently increasing longitudinal discontinuities downstream (Burchsted et al., 2010). Beaver dams can enhance vertical connectivity by increasing exchanges between surface and ground water (Majerova et al., 2015). Longitudinally, beaver dams disrupt the delivery of water, sediment, wood and nutrients (Wohl, 2013b), potentially dramatically altering the connectivity of upstream sediment sources to downstream sinks and providing greater variation in the residence time in sinks for sediment storage associated with beaver dams. Whereas dam breaches,

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blow-outs or abandonments affect the temporal connectivity of fluvial systems. Intact beaver dams enhance hydrological connectivity between channels and their surrounding floodplains and hillslopes (Polvi and Wohl, 2013; Wohl, 2013a). Beaver dams profoundly influence floodplain and terrace development within large alluvial river valley by forming complex beaver meadows (Westbrook et al., 2011). Beaver blend lateral boundaries between channels, floodplains, and uplands, expanding the riparian zone across valley bottoms (Westbrook et al., 2011). Beaver dams force multithreaded channels that increase stream and riparian complexity (Polvi and Wohl, 2013), often increasing habitat quality and availability for aquatic and terrestrial flora and fauna (Bartel et al., 2010), including amphibians, fish, mammals, and birds (Bartel et al., 2010; Medin and Warren, 1991; Stevens et al., 2007; Westbrook et al., 2006; Wright et al., 2002). Beaver dams create wetlands, decreasing the longitudinal distance between wetlands, and increasing belowground hydrologic connectivity along riverscapes, even during extreme drought (Cunningham et al., 2007; Hood and Bayley, 2008; Remillard et al., 1987). Beaver dams also slow runoff, extend streamflow duration, and subirrigate downstream valley bottoms allowing for the establishment, expansion, and maintenance of riparian vegetation (Bird et al., 2011; Majerova et al., 2015; Runyon et al., 2014; Westbrook et al., 2006). Dam removal and/or failure may similarly alter fluvial systems by inducing sediment evacuation and channel entrenchment while removing the hydrology that forms wetland ecosystems (Butler and Malanson, 2005).

Pollock et al. (2007, 2014) suggested that beaver can be used to restore degraded, incised streams as their dams trap sediment and raise streambed elevations. This beaver-induced streambed sedimentation can expedite the natural process of incised stream recovery, which may otherwise take hundreds to thousands of years, reducing the timeframe of recovery to years to decades. However, whether beaver dams can accelerate incised stream recovery likely depends on many other factors. Levine and Meyer (2014) documented rapid flushing of most of the stored in-channel sediment when beaver dams breached, with no persistent aggradation. Persico and Meyer (2009, 2013) found that beaver-induced aggradation over 100–1000 year timescales was limited to 2 m in Yellowstone and Grand Teton National Parks at reaches suitable for beaver damming.

As early as the 1930s, resource managers recognized beaver for their ability to enhance floodplain connectivity through their dam-building and restore watersheds, and relocated beaver to degraded areas to reduce soil, vegetation, and water loss (e.g. Scheffer, 1938). In 1949 the Idaho Department of Fish and Game parachuted beaver from aircraft into what is now the Frank Church Wilderness in an effort to control soil erosion, improve trout habitat, and minimize spring flooding (Heter, 1950). Current stream restoration efforts involving beaver primarily focus on recovering beaver populations (Andersen and Shafroth, 2010; Andersen et al., 2011; Burchsted et al., 2010) or live trapping nuisance beaver and relocating them to areas where they can be used as a passive restoration tool (Albert and Trimble, 2000; Macdonald et al., 1995; McKinstry et al., 2001). Recently, DeVries et al. (2012) suggested emulating beaver with restoration structures that function similarly to beaver dams. Similarly, Pollock et al. (2014); Pollock et al. (2012), suggested using beaver dam analogues to mimic natural beaver dams where possible, hypothetically attracting beaver to maintain and improve those structures as their own dams. These beaver conservation and restoration efforts are hypothesized to buffer the hydrologic impacts of climate change (Bird et al., 2011), enhance aquatic and riparian habitat, and increase the uptake and retention of carbon, nitrogen, and other nutrients (Wohl and Beckman, 2014).

With stream restoration facing scrutiny for its high costs (Bernhardt et al., 2005), questionable results (Palmer, 2009), and limited spatial extents relative to the extent of degradation, beaver and their ecosystem engineering activities provide an affordable, effective alternative to human-engineered stream restoration projects. These projects are cost-effective because beaver undertake the labor and maintenance of their dams, building dynamic habitats as they build habitat heterogeneity. However, effective and appropriate use of beaver still requires careful planning. Using beaver to restore streams is appealing not only because of the cost savings when compared to traditional approaches that reshape stream channels with heavy equipment, but also because beaver have evolved as important drivers of geomorphic and hydrologic processes in these ecosystems (Polvi and Wohl, 2013; Westbrook et al., 2011). Consequently, beaver are increasingly being used as a critical component of both passive and active stream and riparian restoration strategies (Bird et al., 2011; DeVries et al., 2012; Green and Westbrook, 2009; Polvi and Wohl, 2013) as well as written into national and state level watershed management policy (e.g. Melillo et al., 2014; UDWR, 2010).

Although examples of initial successes in using beaver for restoration are encouraging (Albert and Trimble, 2000; Apple et al., 1984; Pollock et al., 2014) the enthusiasm surrounding the simplicity and cost-effectiveness of beaver may lead to unrealistic expectations about beaver's ability to restore streams and, in particular, restore channel–floodplain connectivity. Not all streams can support high levels of beaver dam activity (Persico and Meyer, 2009), and in many contexts, their engineering activities may be in direct conflict with other management priorities (e.g. agriculture, urban land-use, forestry, and irrigation) making them a potential nuisance (Bhat et al., 1993; Jensen et al., 2001). This evokes the question: where is it appropriate to employ beaver as a restoration agent by promoting their dam-building activities? Levine and Meyer (2014) draw attention to the specific issue of the potential links between channel incision and beaver loss/removal, as well as the assertion by (Pollock et al., 2007) that beaver restoration could reverse such degradation by promoting aggradation in the ponds and restoring lateral connectivity. Levine and Meyer (2014) specifically sought to explore the longevity of such gains and found that in their study system the persistence of deposition behind beaver dams was limited by frequent breaching. We agree with Levine and Meyer (2014) that better quantitative data, and improved expectation management are urgently needed to help scientists and managers avoid unnecessarily using beaver in inappropriate situations (i.e. environments that cannot support their dam building activities), but also to highlight the types of environments in which beaver dam building activity may be an appropriate restoration tool. In short, throughout a drainage network, what sorts of environments may support longer-lived dams that disrupt longitudinal sediment supply connectivity by promoting sinks (whether short-lived, or long-lived) that alter the timing and delivery of such sediment in fluvial systems?

Beaver, unlike many species of conservation interest, have relatively simple habitat requirements. Beaver can survive under an impressive diversity of conditions, ranging from boreal forest (Naiman et al., 1988) to deserts (Andersen and Shafroth, 2010). In simple terms, beaver need water and woody vegetation local to their lodges, which allow them to forage in safety from predators (Müller-Schwarze and Sun, 2003). These needs can be fully met in some environments such as ponds, lakes, rivers, and perennial streams, where, if water depth is sufficient to maintain underwater entrances to their lodges, building dams is not necessary. For example, beaver are found throughout major rivers with large rapids like the Grand Canyon of the Colorado (Breck et al., 2012), but they do not dam these rivers' main channels, nor do they need to for survival. However, where habitat is not as naturally suitable, beaver will build dams to maintain deep water pools around lodges, providing protection from predators, and improving access to woody food and building materials. Such activities are most common in lower order streams (i.e. wadeable streams) or side channels of major rivers, where water may be too shallow to maintain underwater lodge entrances and/or store underwater food caches for access under winter ice (Baker and Hill, 2003; Müller-Schwarze and Sun, 2003).

The earliest efforts to evaluate existing and potential beaver habitat for the western US began in the 1940s with qualitative beaver habitat suitability studies (e.g. Atwater, 1940; Packard, 1947). Slough and Sadleir (1977) used regression relationships to develop a beaver habitat classification system in British Columbia. Allen (1983) was one of the first to establish a quantitative beaver habitat suitability index (HSI) model that evaluated the suitability of beaver habitat based on key environmental variables thought to affect beaver populations. For riverine environments, Allen's (1983) model included stream gradient, average water fluctuation, percent tree and shrub canopy closure, tree size class frequency, shrub canopy height, and woody vegetation composition. Extensive testing of Allen's (1983) model and other statistical approaches followed, attempting to evaluate relationships between beaver density and various physical, environmental, and vegetative parameters (Beier and Barrett, 1987; Howard and Larson, 1985; Mccomb et al., 1990; Suzuki and McComb, 1998). Results from these studies suggest that HSI-based models can be accurate at distinguishing suitable beaver habitat from unsuitable habitat within a short temporal window (Mccomb et al., 1990). However, such empirical HSI models tend to be system specific with limited potential to extrapolate their results to other watersheds (Robel et al., 1993). Moreover, as Baldwin (2013) argues using "absence as proxy for environmental inappropriateness" is "problematic" because it assume a species' absence is due to a lack of preference, "rather than to past and ongoing predation by non-humans and humans."

Here we present a model that predicts the capacity of a landscape to support beaver's most dominant ecosystem effect: dam building. Our objectives were to (1) test our underlying hypotheses regarding the controls on the upper limit of beaver dam distributions; (2) evaluate the model's effectiveness at predicting upper limits of beaver dam densities over a large and diverse geographic area; (3) validate model to predictions using observations of dams in diverse physiographic settings; and (4) provide a large scale (i.e. regional to sub-continental) planning tool to develop reasonable expectations for input into where beaver reintroduction and dam building might be a viable stream, riparian and aquatic conservation approach, and where beaver-based restoration approaches might falter. Our modeling efforts center on the ability of the environment to support dams and dam-building activity, rather than either beaver habitat suitability (e.g. Allen, 1983) or beaver population estimates (e.g. Broschart et al., 1989) for several reasons. First, the most dramatic impacts of beavers' ecosystem engineering activities on streams stem from their dams, rather than their lodges, bank burrows, or other environmental manipulations (Burchsted et al., 2010). The frequency, density, and size of their dams, rather than beaver population density, drives the extent of positive hydrologic, geomorphic, and biotic feedbacks that create diverse aquatic and terrestrial habitats (Johnston and Naiman, 1990). These same dam-mediated hydrogeomorphic changes are exactly what process-based stream restoration efforts attempt to emulate and/or exploit (Bird et al., 2011). Thus, beaver dams are arguably a better index of the relative impact of beaver as a restoration agent. Second, predicting limitations to the feasibility of dam building and dam persistence are driven by easily defined hydraulic, geomorphic, and vegetation constraints. Third, in order to inform potential strategies for translocation of beaver to key conservation locations, a broad scale evaluation of suitable locations is important. Ideally, these evaluations would rely on broad-scale, widely- and freely-available landscape data.

We hypothesize that controls on the occurrence and upper limit (i.e. capacity) of beaver dams are primarily driven by the availability of water and woody vegetation. Moreover, we postulated that data for these variables limiting dam construction and persistence were readily approximated over drainage networks across the United States and are available in publicly available GIS formats. We concur with Gibson and Olden (2014) who advocate that because most of the desired ecological feedbacks of beaver activity depend on dam construction, '*accurate predictions of where and in what densities beavers are capable of building and maintaining dams*' is a critical focus when considering beaver-mediated ecosystem effects.

2. Study area

Beaver dam capacity was estimated across 40,561 km of streams including 27,345 km in Utah and 13,216 km in neighboring states of Nevada, Idaho, Wyoming, Colorado, New Mexico, and Arizona (Fig. 1). This large and diverse study area covers 315,047 km^2, which range from alpine meadows to desert canyons, across which a wide range of stream conditions and beaver densities could be reasonably expected to occur. We used examples from four physiographically diverse watersheds (Fig. 1) to ascertain whether the model predictions were coherent and logical. The validation watersheds (each an eight digit USGS hydrologic unit code watershed) were the Fremont, Logan-Little Bear, Price, and Strawberry. The watersheds are well distributed over the study area to capture the diversity of habitats that exist and represent 3425 km of the 40,561 km of rivers and streams analyzed (i.e. 8%). The Fremont Watershed is located in south-central Utah and drains the High Plateaus ecoregion of the Wasatch Plateau and then carves through the Shale Deserts and Semiarid Benchlands and Canyonlands ecoregions (Woods et al., 2001). The Logan-Little Bear watershed is located in northern Utah and drains the Wasatch Montane Zone ecoregion of the Bear River Mountain Range into the Cache Valley ecoregion (Woods et al., 2001). The Price Watershed is located in eastern Utah with headwaters in the Escarpment ecoregion and trunk streams that cut through the Shale Deserts and Semiarid Benchlands and Canyonlands ecoregions (Woods et al., 2001). The Strawberry Watershed is located in central Utah and drains the Wasatch Montane Zone and Semiarid Foothills ecoregions before flowing through the Semiarid Benchlands and Canyonlands ecoregions (Woods et al., 2001). Not only do these watersheds represent a broad range of climate, geology and ecoregions, they also reflect very different beaver management strategies ranging from active discouragement to passive encouragement.

3. Methods

3.1. Beaver dam capacity model

Our estimates of beaver dam capacity came from seven lines of evidence, including: (1) a reliable water source; (2) streambank vegetation conducive to foraging and dam building; (3) vegetation within 100 m of edge of stream to support expansion of dam complexes and maintain large beaver colonies; (4) likelihood that dams could be built across the channel during low flows; (5) the likelihood that a beaver dam on a river or stream is likely to withstand typical floods; (6) a suitable stream gradient that is neither too low to limit dam density nor too high to preclude the building or persistence of building dams; and (7) a suitable river that is not too large to restrict the building or persistence of dams. We used publicly available datasets of national extent (Table 1) that provide direct approximations for these lines of evidence based largely on remotely-sensed imagery and regionally-derived empirical relationships. While we fully recognize that higher resolution inputs of higher accuracy and fidelity could result in more precise model outputs, we are most interested in testing the model's ability to produce accurate results from freely and broadly available datasets of coarser resolution. However, this does not preclude users from applying the model with higher precision data.

Model outputs are calibrated to typical field-observed dam densities and those reported in the literature, which are reported as high as 40 dams/km, or roughly one dam every 25 m. These high densities are only found where multiple colonies maintain large dam complexes, within which each complex may vary from 3 to 15 dams (Gurnell, 1998). We chose to model dams per kilometer because a) it is directly comparable to densities that can be calculated in GIS from field GPS measurements, b) densities can also be approximated with aerial imagery and/or overflights, and c) linear dam density is commonly reported in the literature (e.g. Cooke and Zack, 2008; Gurnell, 1998) so there are valid estimates for direct comparison.

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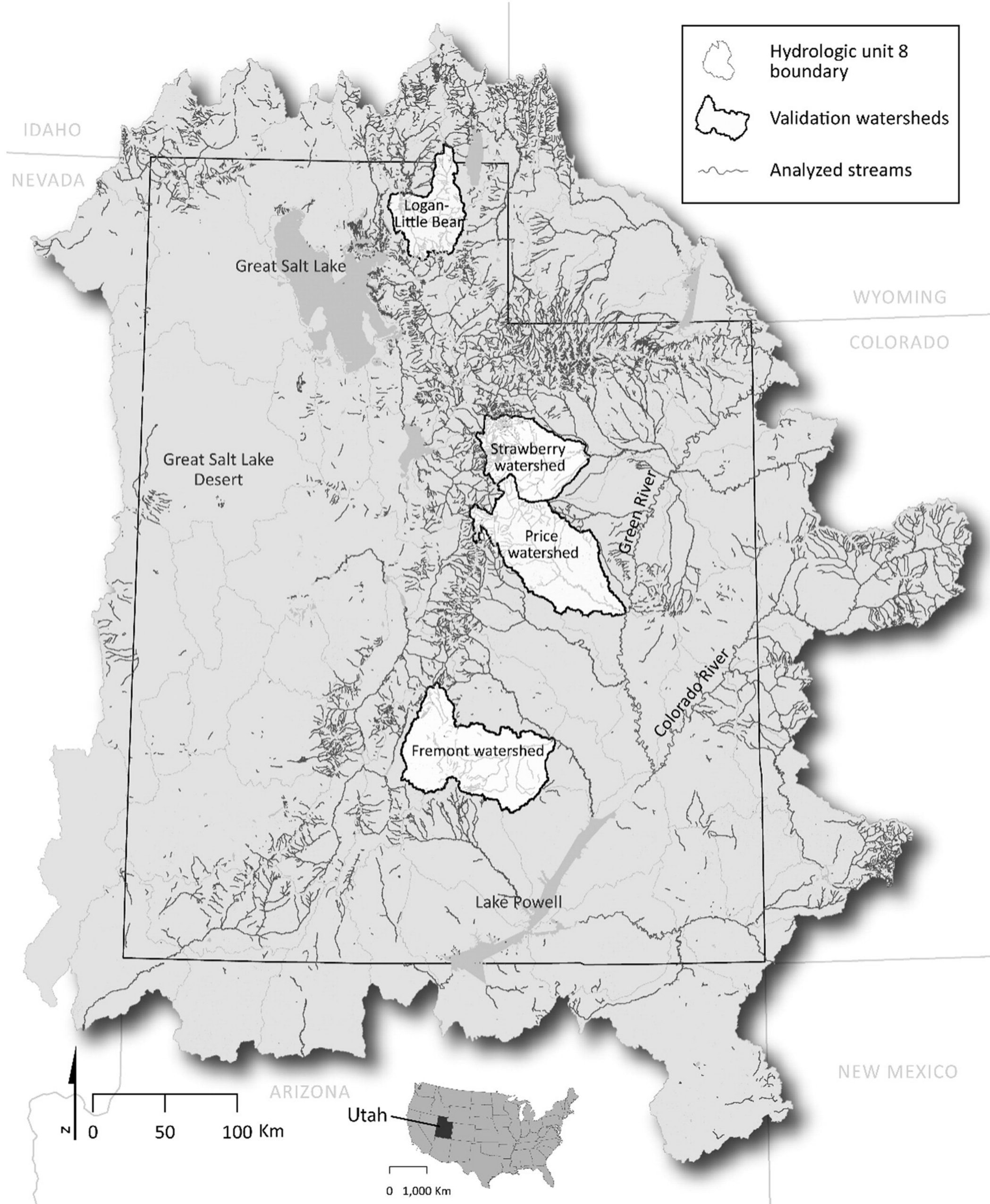

Fig. 1. Study area extent covering 40,561 km of streams including 27,345 km in Utah, and 13,216 km in neighboring states of Nevada, Idaho, Wyoming, Colorado, New Mexico and Arizona, that flow through common Hydrologic Unit Code (HUC) 8 watersheds. The four validation USGS HUC 8 watersheds are highlighted on the map in white.

3.1.1. Evidence of a reliable water source

Many researchers have reported occasional beaver presence on intermittent streams (Albert and Trimble, 2000; Ffolliott et al., 1976; Hood, 2011; Hood and Bayley, 2008; McKinstry et al., 2001). However, the vast majority of intermittent stream lengths are likely never used because of their unreliability as a water source (Allen, 1983; Buech, 1985; Persico and Meyer, 2013; Williams, 1965). To assess evidence of a stream within a network being a reliable water source for dam-building beaver we used the National Hydrologic Dataset (NHD) cartographically derived 1:24 000 drainage network (USGS, 2014). The NHD network differentiates between perennial, intermittent, and ephemeral watercourses. To assess the accuracy of this classification we compared stream flow between late spring and autumn imagery in Google Earth. We found that the perennial designation was reliable at capturing streams with perennial flow, but that this designation also occasionally included some intermittent streams. We used these perennial designated streams and their associated intermittent streams for modeling. We segmented the drainage network longitudinally into 250 m long segments, because a) this was a reasonable length over which to approximate

Table 1
Input data used to represent the lines of evidence of the beaver dam capacity model.

Input data	Criteria	Source
Streams	Perennial water	USGS National Hydrography Dataset http://nhd.usgs.gov/
LANDFIRE 2011 (EVT and BPS)	Riparian vegetation	LANDFIRE land cover data http://www.landfire.gov/
USGS baseflow equations	Dam could be built	Wilkowske et al. (2008) http://pubs.usgs.gov/sir/2008/5230/
USGS 2-year peak flow equations	Dam could withstand floods	Kenney et al. (2008) http://pubs.usgs.gov/sir/2007/5158/
10 m DEM	Evidence of stream gradient	USDA NRCS Geospatial Data Gateway http://datagateway.nrcs.usda.gov/

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reach-averaged slope from a 10 m DEM (digital elevation model, USGS, 1999), and b) 250 m segments produced a reasonable length along which to sample 30 m LANDFIRE vegetation data within buffers and get a representative sample. Moreover, this segmentation provides an appropriate spatial scale over which to illustrate the longitudinal patterns and connectivity of stream segments capable of supporting dam-building activity to varying degrees.

3.1.2. Evidence of woody vegetation for building material

3.1.2.1. Beaver forage and building material preferences. We classified LANDFIRE 2011 (first made available in 2013), a nationwide 30 m Landsat satellite imagery-based landcover classification (LANDFIRE, 2014), into beaver dam-building material preference categories. Denney (1952) investigated the woody plant preferences of beaver throughout North America and found, in preferential order, aspen (Populus tremuloides), willow (Salix spp.), cottonwoods (*Populus* spp.), and alder (*Alnus* spp.) to be the most preferred browse species. Several studies confirm that aspen, willow, and cottonwood are preferred forage and dam-building material (Kimball and Perry, 2008; Warren, 1926), other research shows a strong association between beaver presence and willow (Baker and Hill, 2003; Mortenson et al., 2008; Tallent et al., 2011) as well as dam presence and riparian trees (Mccomb et al., 1990). When preferred materials are not available, herbaceous wetland vegetation like cattail (*Typha* spp.; Andersen and Shafroth, 2010) and upland woody vegetation (Warren, 1927), or sagebrush (*Artemisia* spp.; Apple et al., 1985), can be used for dam construction. Based on these preferences, we assigned a single numeric suitability value from 0 to 4 to each of the land cover classes, with zero representing unsuitable food/building material and four representing preferred food and building material. The result was a look-up table of LANDFIRE land cover classes and associated beaver preference values that were applied to raster data on a cell-by-cell basis.

(1) *Streamside vegetation buffers.* — Riverscapes with narrow riparian corridors limit beaver dam construction opportunities relative to those with expansive riparian areas and/or adjacent deciduous forests with preferred woody browse (e.g. aspen). To represent this important distinction, we generated two buffers along the drainage network in which we assessed beaver dam-building preference values:

- A 30 m buffer representing the streamside vegetation (Fig. 2; step 3a); and
- A 100 m buffer representing the maximum harvest distance (Fig. 2; step 3b).

We based these buffer distances on documented distances from water that beaver typically travel to harvest woody stems for dam and lodge construction, and winter food caches. Many studies indicate that most of the woody species utilized by beaver occur within 30 m of the edge of water (Barnes and Mallik, 2001; Hall, 1960; Jenkins, 1980). Allen (1983) considered a 200 m forage buffer, but conceded that a majority of foraging occurs within 100 m. Within our validation sites, ~150 m was the maximum harvest distance we observed at a few locations, but at thousands of other locations 100 m was the upper limit. Riparian vegetation scores within each of the buffers were averaged to calculate a mean score (range: 0–4) per stream segment (Fig. 3).

The two lines of evidence regarding building material availability were combined using a Fuzzy Inference System (FIS; herein the *vegetation FIS*) to collectively estimate the dam building density that a riverscape can presently support (Fig. 4). FIS allow 'computing with words,' whereby multiple lines of evidence are combined mathematically with simple rule tables, and categorical ambiguity and uncertainty between categories are explicitly accounted for by representing the output and all inputs as continuous variables with overlapping membership functions for each category (Openshaw, 1996; Zadeh, 1996). Moreover, fuzzy habitat models are more flexible and easily applied without invalidating necessary assumptions of traditional habitat models (Mocq et al., 2013; Schneider and Jorde, 2003). We developed an expert-based rule system (Table 2 for vegetation), but rely on continuous numeric inputs and provide continuous numeric output calibrated to empirical data (Adriaenssens et al., 2003; Klir and Yuan, 1995). Accordingly, the buffered polygon segments with their associated distribution of categorical building material preference values (0–4; unusable to preferred) were converted to continuous values by calculating the mean of all categorical values per segment. These values were then extracted from the buffers and mapped onto the drainage network resulting in two new fields added to the NHD drainage network's attribute table: a stream bank vegetation preference score and a riparian to upland fringe preference vegetation score.

The FIS model was developed and run using the Fuzzy Logic Toolbox 2.0 in Matlab (Jang and Gulley, 2009;Supplement 1). The rule table, the specification of membership functions, and the resulting outputs are shown in Table 3. The input membership functions were centered on the categorical values (1, 2, 3, and 4) used in dam-building material classification (Fig. 4). In contrast, we calibrated the output membership function to values reported in the literature and that we have field-documented throughout the western US:

- None — 0 dams: *segments deemed not capable of supporting dam building activity*
- Rare — >0–1 dam/km: *segments barely capable of supporting dam building activity*; *likely used by dispersing beaver*
- Occasional — >1–4 dams/km: *segments that are not ideal*, *but can support an occasional dam or small colony*
- Frequent — >4–15 dams/km: *segments that can support multiple colonies and dam complexes*, *but may be slightly resource limited*
- Pervasive — >15–40 dams/km: *segments that can support extensive dam complexes and many colonies.*

Note, while crisp ranges are described above and used for cartographic convenience in displaying the continuous dam density output predictions of the model categorically, Fig. 4 shows the actual overlap in membership between these categories used in the vegetation FIS. This vegetation FIS was applied on each stream segment (Fig. 3) and the output was an aggregated membership function that represents the full range of uncertainty in predicting dam capacity per kilometer (Fig. 2). That output membership function was defuzzified using its centroid, so that a crisp, single-value, continuous output in dams per kilometer was reported. This vegetation FIS output was based solely on the availability of building materials (Fig. 4).

3.1.3. Evidence that a beaver dam can be built and will likely persist

While the vegetation FIS represents the primary control on local dam capacities, other fluvial geomorphic factors can act to prevent this capacity from being realized. Local channel geomorphology, and the range of hydraulics experienced over different flows, determine specific locations where dam construction is possible (i.e. baseflows) and whether those dams are likely to persist through high flows (Andersen and Shafroth, 2010). Pollock et al. (2014) reviewed how stream power influences beaver dams and outlined conceptually how beaver damming modifies both absolute and unit stream power. Persico and Meyer (2009, 2013) investigated geomorphic constraints on beaver damming and their findings suggest that higher stream powers limit the ability of beaver to maintain dams through high flows (see also, Mccomb et al., 1990). Although imperfect, stream power provides a simple and tractably calculated proxy for the energy expended per unit time and unit channel length (Worthy, 2005). Stream power is the product of slope (S) and discharge (Q):

$$\Omega = \rho \cdot g \cdot Q \cdot S \quad (1)$$

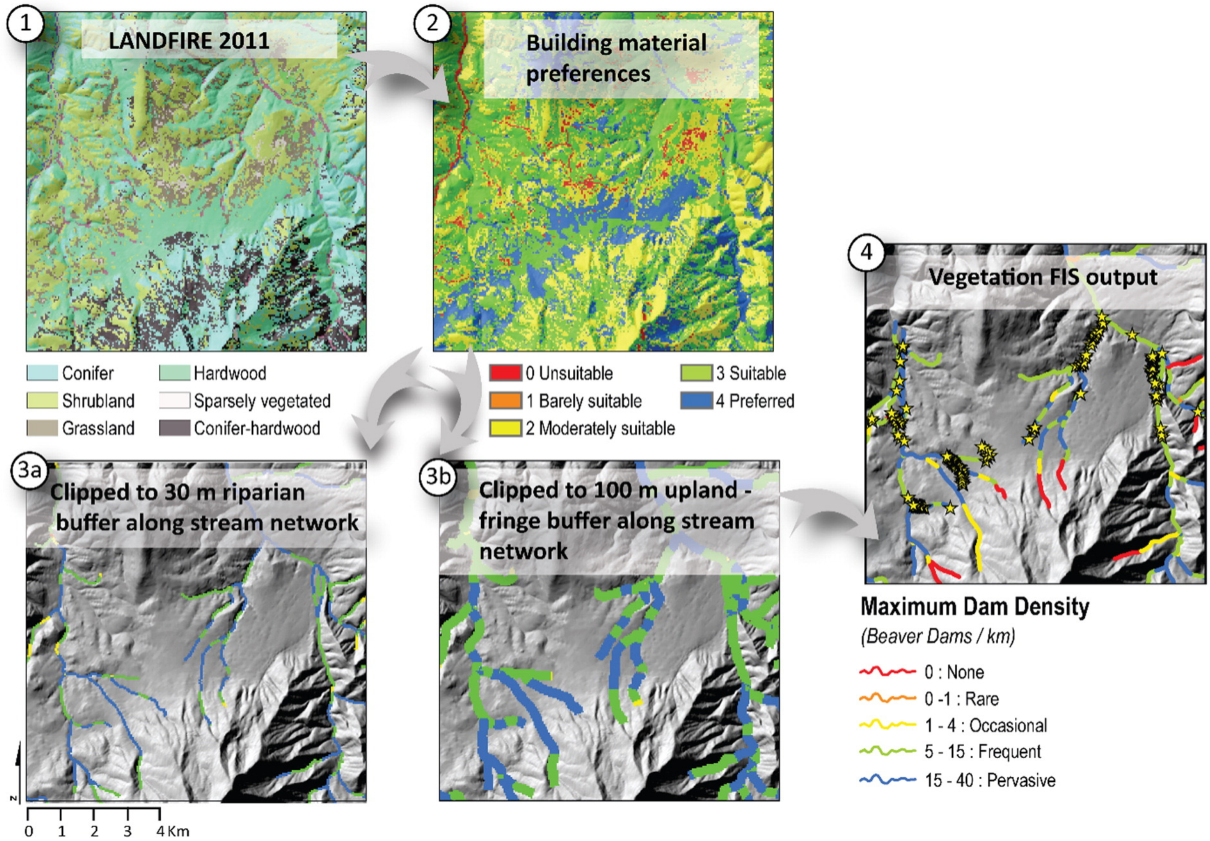

Fig. 2. Network scale illustration of the workflow for determining the capacity of riverscapes to support beaver dam-building activity, based solely on the availability of suitable building material in close lateral connectivity to the channel. Vegetation data (1), is classified based on beaver preferences (2). We then average these suitability classes within two reach-scale buffers, a streamside buffer (30 m) in 3a and a riparian/upland buffer (100 m) in 3b. Both are then combined using a FIS to estimate the maximum dam density (4) based on vegetation preferences (Fig. 4). The vegetation FIS output is an input into the combined capacity FIS (Fig. 6).

Where Ω is total stream power (watts/m), ρ is the density of water (1000 kg/m^3), g is acceleration due to gravity (9.8 m/s^2), Q is discharge (m^3/s), and S is the channel slope. Stream power (Ω) is readily calculable for any segment of stream if Q is known, because S can be derived from a DEM and drainage network and the density of water (ρ) and gravity (g) are constants. As Pollock et al. (2014) pointed out, the relationship between likelihood of a beaver dam to persist and the driving forces acting on it, unit stream power (ω — watts/m^2) is arguably a more appropriate and accurate measure to describe relative differences in the forces beaver dams experience:

$$\omega = \Omega / w \tag{2}$$

where w is flow width. The hydraulic geometry of any cross-section of stream to which Eq. (2) is applied can vary dramatically with flow stage (more so in streams with floodplains, less so in incised streams).

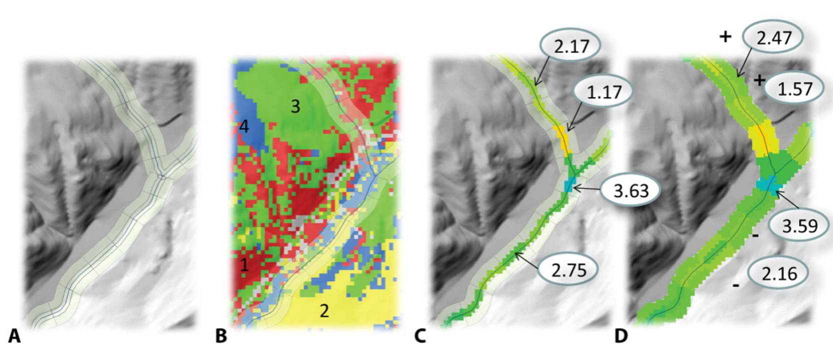

Fig. 3. Reach scale illustration of derivation of streamside vs. riparian vegetation scores from 30 vs. 100 m stream network buffers. A shows the 30 m and 100 m buffers, which we used to summarize intersecting pixels from 30 m resolution classified LANDFIRE raster in B. Dam building suitability are shown in B and range from 0 (unsuitable; gray) to 4 (optimal; blue) with red for 1, yellow for 2, and green for 3. C & D contrast the buffer averaged values for the 30 m buffer (C) and the 100 m buffer (D). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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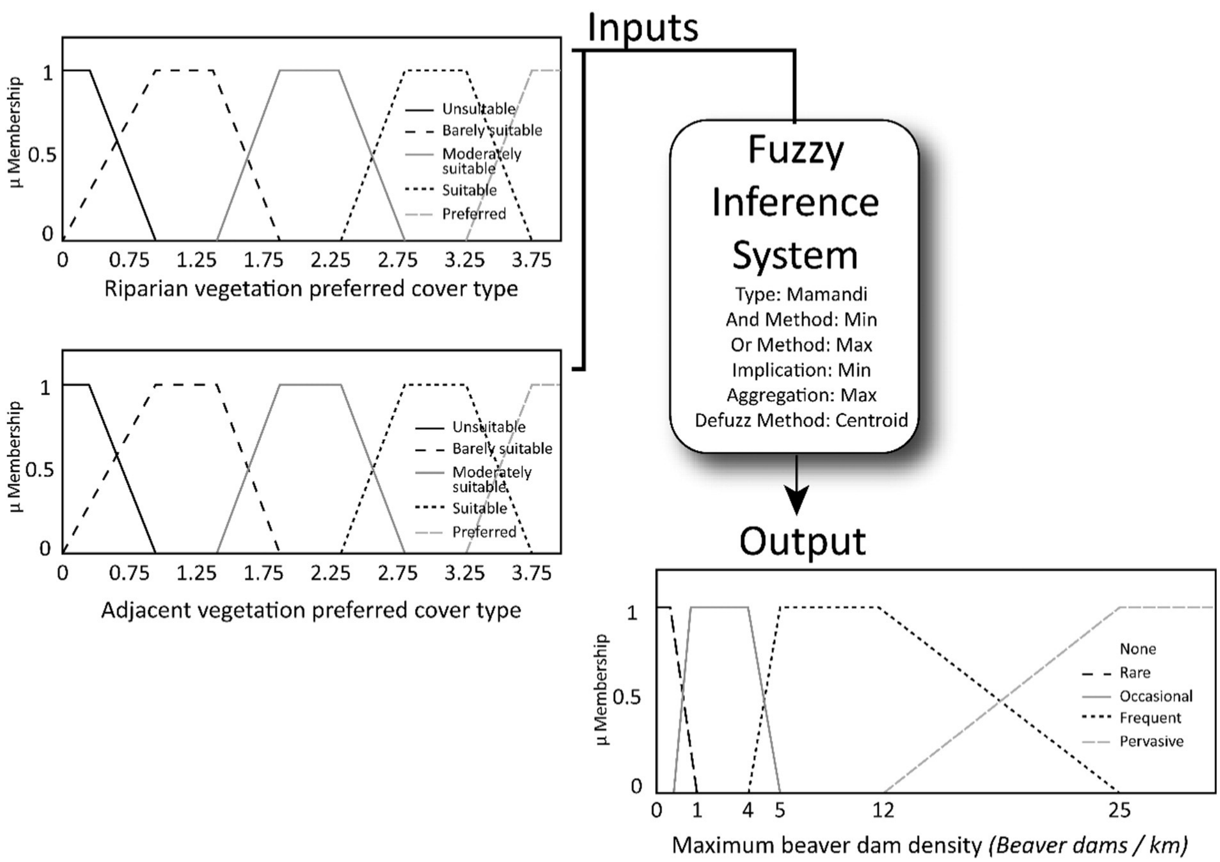

Fig. 4. Vegetation Fuzzy Inference System for capacity of riverscape to support dam building beaver activity based only on vegetation available as a building material. This shows the specification of fuzzy membership functions with overlapping values for categorical descriptors in inputs and the output.

Moreover, as argued in Pollock et al. (2014), through their dam building activity beaver themselves manipulate both stage and width. Thus, beaver can modify the impact of the same flood at a given location. Unfortunately, without higher resolution topography (e.g. LiDAR) and explicit hydraulic models to simulate flow width at different discharges (including the hydraulic impacts of beaver dams), it is not typically

Table 2
Rule table for two input fuzzy inference system that models the capacity of the riverscape to support dam building activity (in dam density) using the suitability of streamside vegetation and suitability of riparian/upland vegetation as inputs.

	If	Inputs			Output	
		Suitability of streamside vegetation		Suitability of riparian/upland vegetation		Dam density capacity
Rules	1	Unsuitable	&	Unsuitable	, then	None
	2	Barely suitable	&	Unsuitable	, then	Rare
	3	Moderately suitable	&	Unsuitable	, then	Occasional
	4	Suitable	&	Unsuitable	, then	Occasional
	5	Preferred	&	Unsuitable	, then	Occasional
	6	Unsuitable	&	Barely suitable	, then	Rare
	7	Barely suitable	&	Barely suitable	, then	Occasional
	8	Moderately suitable	&	Barely suitable	, then	Occasional
	9	Suitable	&	Barely suitable	, then	Frequent
	10	Preferred	&	Barely suitable	, then	Frequent
	11	Unsuitable	&	Moderately suitable	, then	Occasional
	12	Barely suitable	&	Moderately suitable	, then	Rare
	13	Moderately suitable	&	Moderately suitable	, then	Frequent
	14	Suitable	&	Moderately suitable	, then	Frequent
	15	Preferred	&	Moderately suitable	, then	Pervasive
	16	Unsuitable	&	Suitable	, then	Rare
	17	Barely suitable	&	Suitable	, then	Frequent
	18	Moderately suitable	&	Suitable	, then	Frequent
	19	Suitable	&	Suitable	, then	Frequent
	20	Preferred	&	Suitable	, then	Pervasive
	21	Unsuitable	&	Preferred	, then	Occasional
	22	Barely suitable	&	Preferred	, then	Frequent
	23	Moderately suitable	&	Preferred	, then	Frequent
	24	Suitable	&	Preferred	, then	Pervasive
	25	Preferred	&	Preferred	, then	Pervasive

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Table 3
Rule table for three input fuzzy inference system that model the capacity of the riverscape to support dam building activity (in dam density) using the vegetative dam density capacity (output of Table 2 model), baseflow stream power, and the two-year flood stream power.

	If	Inputs								Output
		Vegetative dam density capacity (FIS)		Baseflow stream power		2-year flood stream power		Reach slope (%)		Dam density capacity
Rules	1	Unsuitable	&	–	&	–	&	–	, then	None
	2	–	&	Cannot build dam	&	–	&	–	, then	None
	3	–	&	–	&	–	&	Cannot build dam	, then	None
	4	Rare	&	Can build dam	&	Dam persists	&	–	, then	Rare
	5	Occasional	&	Can build dam	&	Dam persists	&	–	, then	Occasional
	6	Frequent	&	Can build dam	&	Dam persists	&	Can build dam	, then	Frequent
	7	Frequent	&	Can build dam	&	Dam persists	&	Probably can build dam	, then	Occasional
	8	Pervasive	&	Can build dam	&	Dam persists	&	Really flat	, then	Pervasive
	9	Pervasive	&	Can build dam	&	Dam persists	&	Can build dam	, then	Pervasive
	10	Pervasive	&	Can build dam	&	Dam persists	&	Probably can build dam	, then	Occasional
	11	Rare	&	Can build dam	&	Occasional breach	&	–	, then	Rare
	12	Occasional	&	Can build dam	&	Occasional breach	&	–	, then	Occasional
	13	Frequent	&	Can build dam	&	Occasional breach	&	Can build dam	, then	Frequent
	14	Frequent	&	Can build dam	&	Occasional breach	&	Probably can build dam	, then	Occasional
	15	Pervasive	&	Can build dam	&	Occasional breach	&	Really flat	, then	Occasional
	16	Pervasive	&	Can build dam	&	Occasional breach	&	Can build dam	, then	Frequent
	17	Pervasive	&	Can build dam	&	Occasional breach	&	Probably can build dam	, then	Occasional
	18	Rare	&	Can build dam	&	Occasional blowout	&	–	, then	Rare
	19	Occasional	&	Can build dam	&	Occasional blowout	&	–	, then	Occasional
	20	Frequent	&	Can build dam	&	Occasional blowout	&	Can build dam	, then	Frequent
	21	Frequent	&	Can build dam	&	Occasional blowout	&	Probably can build dam	, then	Occasional
	22	Pervasive	&	Can build dam	&	Occasional blowout	&	Really flat	, then	Occasional
	23	Pervasive	&	Can build dam	&	Occasional blowout	&	Can build dam	, then	Frequent
	24	Pervasive	&	Can build dam	&	Occasional blowout	&	Probably can build dam	, then	Occasional
	25	Rare	&	Can build dam	&	Blowout	&	–	, then	None
	26	Occasional	&	Can build dam	&	Blowout	&	–	, then	Rare
	27	Frequent	&	Can build dam	&	Blowout	&	Can build dam	, then	Rare
	28	Frequent	&	Can build dam	&	Blowout	&	Probably can build dam	, then	None
	29	Pervasive	&	Can build dam	&	Blowout	&	Really flat	, then	Rare
	30	Pervasive	&	Can build dam	&	Blowout	&	Can build dam	, then	Occasional
	31	Pervasive	&	Can build dam	&	Blowout	&	Probably can build dam	, then	Rare
	32	Rare	&	Probably can build dam	&	Occasional breach	&	–	, then	Rare
	33	Occasional	&	Probably can build dam	&	Occasional breach	&	–	, then	Occasional
	34	Frequent	&	Probably can build dam	&	Occasional breach	&	Can build dam	, then	Frequent
	35	Frequent	&	Probably can build dam	&	Occasional breach	&	Probably can build dam	, then	Occasional
	36	Pervasive	&	Probably can build dam	&	Occasional breach	&	Really flat	, then	Occasional
	37	Pervasive	&	Probably can build dam	&	Occasional breach	&	Can build dam	, then	Frequent
	38	Pervasive	&	Probably can build dam	&	Occasional breach	&	Probably can build dam	, then	Occasional
	39	Rare	&	Probably can build dam	&	Occasional blowout	&	–	, then	Rare
	40	Occasional	&	Probably can build dam	&	Occasional blowout	&	–	, then	Occasional
	41	Frequent	&	Probably can build dam	&	Occasional blowout	&	Can build dam	, then	Occasional
	42	Frequent	&	Probably can build dam	&	Occasional blowout	&	Probably can build dam	, then	Rare
	43	Pervasive	&	Probably can build dam	&	Occasional blowout	&	Really flat	, then	Occasional
	44	Pervasive	&	Probably can build dam	&	Occasional blowout	&	Can build dam	, then	Frequent
	45	Pervasive	&	Probably can build dam	&	Occasional blowout	&	Probably can build dam	, then	Occasional
	46	Rare	&	Probably can build dam	&	Blowout	&	–	, then	None
	47	Occasional	&	Probably can build dam	&	Blowout	&	–	, then	Rare
	48	Frequent	&	Probably can build dam	&	Blowout	&	Can build dam	, then	Rare
	49	Frequent	&	Probably can build dam	&	Blowout	&	Probably can build dam	, then	None
	50	Pervasive	&	Probably can build dam	&	Blowout	&	Really flat	, then	Rare
	51	Pervasive	&	Probably can build dam	&	Blowout	&	Can build dam	, then	Occasional
	52	Pervasive	&	Probably can build dam	&	Blowout	&	Probably can build dam	, then	Rare

practical to base a large-scale network model like this one on unit stream power. For example, Hough-Snee et al. (2015) used unit stream power as a predictor of instream large wood, but were unable to extrapolate their model to a network scale due to a lack of reliable stream width and channel form measurements. Many of these measurements (gradient, channel width) are closely correlated to stream power, indicating that to build a network model, stream power would have sufficed (Hough-Snee personal communication). Instead, we developed our relationships based on stream power, but note that users could modify these relationships and drive the model on unit stream power if they had a reliable means of estimating stage-dependent width.

In this paper, we calculated stream power based on a local derivation of slope and flow accumulation area from 10 m resolution USGS DEMs. We estimated slopes by sampling the lowest elevation from a 10 m USGS DEM near the top and bottom of our 250 m long reach segments, differencing those elevations and dividing by reach segment length (i.e. typically c. 250 m). Discharge was estimated using USGS regional curves developed for the state of Utah (Kenney et al., 2008; Wilkowske et al., 2008) that relate Q to upstream drainage area and elevation values at a given location to produce a time-integrated estimate of the average impact of stream power. Upslope drainage area was derived at the top of each stream segment directly from the 10 m USGS DEMs using a flow accumulation geoprocessing algorithm. The next question is: what representative flows should stream power be derived for? The answer depends on what question is being asked of stream power.

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3.1.3.1. Base flow stream power: evidence that a beaver dam can be built. To infer whether it was likely that beaver could physically build a dam during low-flow conditions, we calculated stream power at baseflow. Using Wilkowske et al. (2008) for each USGS Geohydrologic Region (region) in Utah, we approximated baseflow with a commonly available flow statistic — the discharge exceeded 80% of the time for the month with the lowest runoff (Q_{p80}). An example of a typical form of these equations is illustrated for region 6:

$$Q_{p80} = 9.4102^{-2} \cdot A^{0.7404}$$

where A is drainage area in km^2. This Q_{p80} estimate is then substituted into the stream power equation and used to infer the following categories:

- Can build dam
- Can probably build dam
- Cannot build dam

The 'cannot build dam' category was based on distributions of Q_{p80} stream power derived for parts of the drainage network that had

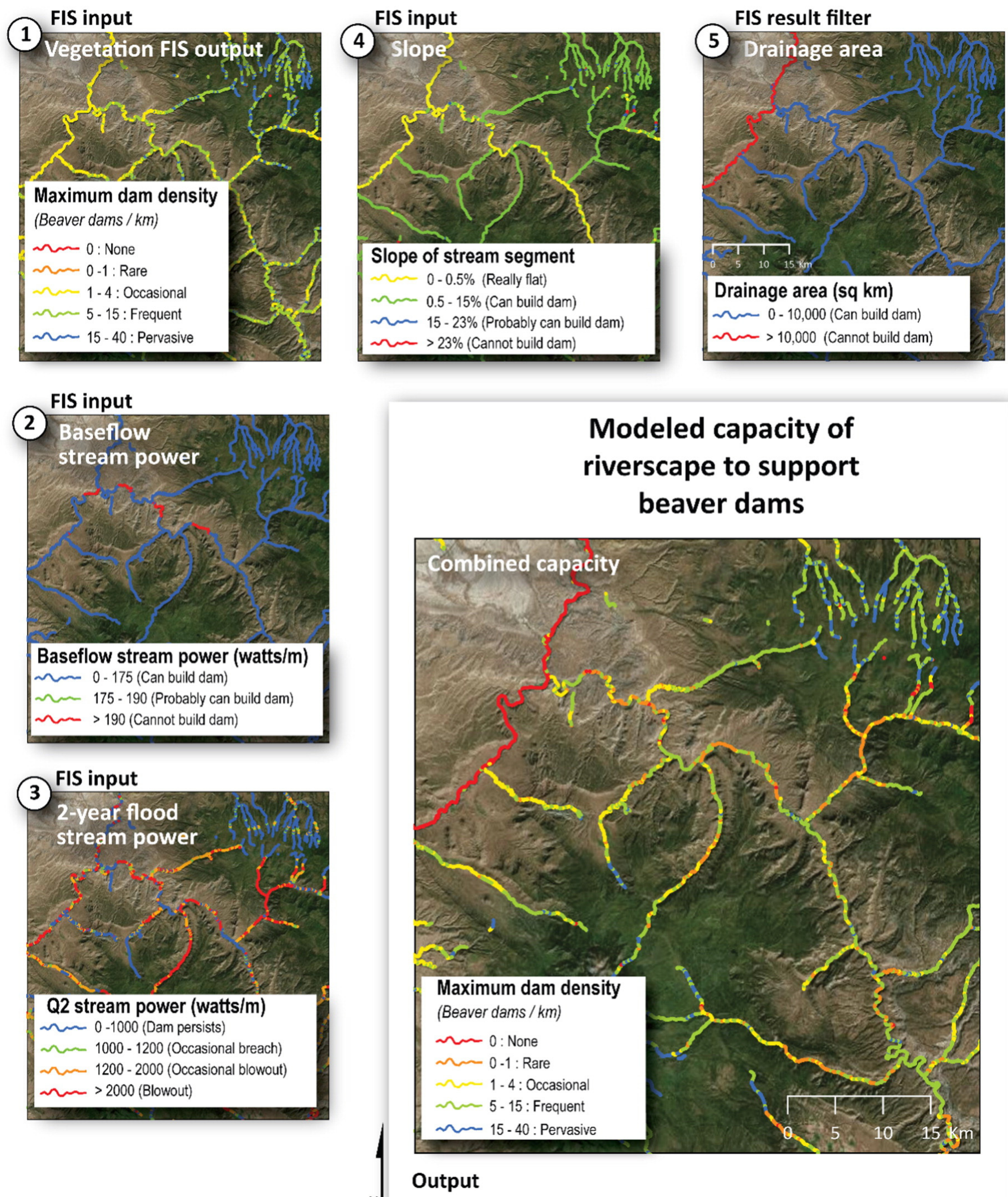

Fig. 5. Methodological illustration of inputs (1–5) and output for the combined capacity model of riverscape capacity to support beaver dam-building activity. Model output was expressed as dam density (dams/km).

vegetation suitable to support beaver, and may even have evidence of beaver activity, but had no evidence that beaver dams ever existed. Such reaches were typically higher gradient, or of larger stream order (i.e. >3–4) and had high baseflow stream powers. By contrast, the 'can build dam' category was based on stream power distributions derived for areas where beaver have frequently constructed persistent dams. Those segments with only occasional dam activity were used to calibrate the 'can probably build dam' category. The overlap in the stream power distributions were used to represent the overlap in the fuzzy membership functions in the baseflow stream power input (Fig. 5; step 2). We calibrated the baseflow stream power thresholds based on the derived low flow stream powers at 2852 dam locations.

3.1.3.2. Two year flood: evidence that a beaver dam will likely persist. To infer the likelihood that a beaver dam would persist once built, the two-year recurrence interval peak flood (Q_2) stream power was calculated using formulae from Ries et al. (2005). An example of a typical form of these equations is illustrated for region 6:

$$Q_2 = 4150\,A^{0.553} \cdot (El/1000)^{2.45}$$

Where A is drainage area in km^2 and El is elevation in meters. This Q_2 estimate is then substituted into the stream power equation and used to infer the following linguistic categories:

- Dam persists — *regardless of peak flow, the dam remains in-tact*
- Occasional breach of dam — *peak flows may cause a partial breach of a dam* (i.e. *only part of the height of the dam is breached, and part remains intact*), *which is easily repaired by beaver*
- Occasional blow out of dam — *peak flows may occasionally cause a dam to completely blow out* (i.e. *the full height of the dam is washed away*), *and may be abandoned, but the frequency of this occurrence is low*
- Blow out — *peak flows will certainly lead to a blow out*

Distributions of stream power were derived using the Q_2 estimates and reach-averaged slope to develop empirical relationships for each of the fuzzy categories based on where specific dams experiencing roughly Q_2 flows exhibited each of the above categories. The ambiguous overlap between the categories was explicitly accounted for with overlapping fuzzy membership functions (Fig. 5; step 3 and Fig. 6).

3.1.4. Evidence of suitable stream gradient

Numerous studies have found that dam presence is strongly associated with low stream gradient (Baker and Hill, 2003; Burchsted and

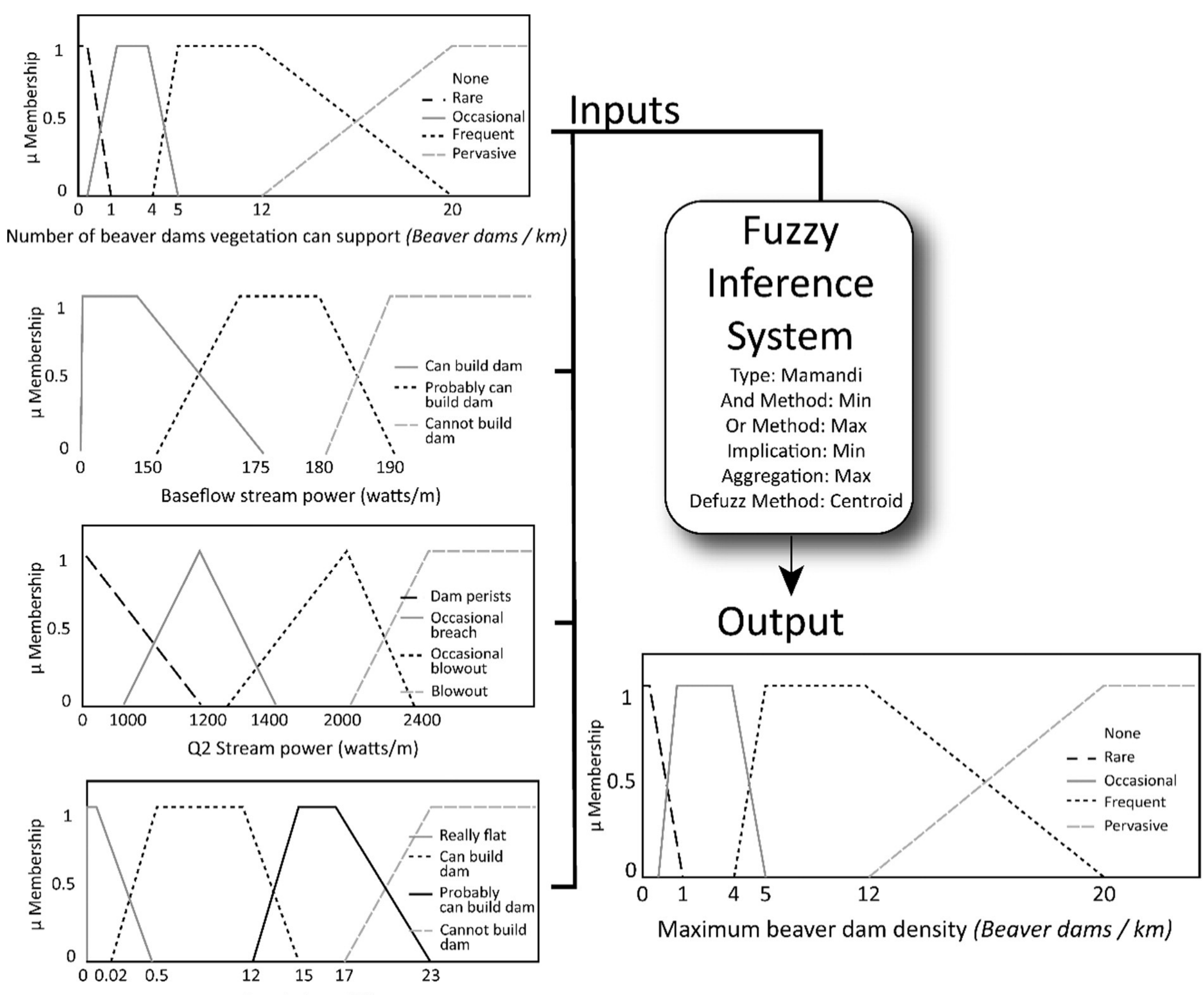

Fig. 6. Combined capacity Fuzzy Inference System for capacity of riverscape to support dam building beaver activity. This shows the specification of fuzzy membership functions with overlapping values for categorical descriptors in inputs and the output.

Daniels, 2014; Curtis and Jensen, 2004; Mccomb et al., 1990). Moreover, investigators (Allen, 1983; Gurnell, 1998) have noted upper slope thresholds as a limitation for beaver dam construction. For example, in Colorado, Retzer (1956) reported never finding beaver colonies on streams where slope exceeds 15%. However, Persico and Meyer (2009) found slope thresholds that were a function of upstream drainage area. Although our stream power input implicitly considers reach slope, exceptionally low slope areas generally occur further downstream in a drainage network where drainage areas are larger (Brierley et al., 2013; Fryirs and Brierley, 2010; Schumm and Khan, 1972). Subsequently, stream power alone fails to discriminate and identify these very low slope reaches adequately. For our capacity model, we established slope thresholds based on 2852 beaver dam locations where we looked at outliers in slope. No beaver dams occurred at streams where slope was >23% but some sparse dams were found between 17% and 23%. Therefore, we set conditional logic slope thresholds in the model as follows: if a stream segment had a slope greater than 23% the segment was classified as 'beaver cannot build a dam' and if a stream segment had a slope greater than 17% the segment's beaver dam capacity was reduced to the next lowest category (Fig. 5; step 4).

Exceptionally low slope reaches (i.e. slopes <0.0002) can also limit dam densities. Most primary beaver dams (i.e. ones that support a lodge) are roughly a meter in height and can reach heights well above three meters (Gurnell, 1998), with secondary dams typically at least 30–50 cm in height. As dam backwater distance upstream is a function of both channel slope and dam height, even a 50 cm high dam in a 0.0002 slope channel has a 250-m backwater (hence, four dams per kilometer in this example). Beaver build secondary dams to extend their foraging and building material harvesting range upstream and/or downstream of a primary dam. Thus, in lower slope areas, they simply do not need as many dams to accomplish this. To accommodate this, we lowered dam capacities by one category (e.g. from *frequent* to *occasional*) in reaches with 'very low' slopes (<0.0002) to produce more realistic dam densities in such reaches.

3.1.5. Evidence that river is too large to allow dams to be built and to persist

The depth and width of large streams prevents dam persistence during high flows (Mccomb et al., 1990). During our pilot study (Macfarlane and Wheaton, 2013), we found that stream power alone was insufficient at determining when a river was too large to allow dams to be built and persist. Therefore, a maximum upstream drainage threshold value was added that assumes that above a specified value a beaver could not build a dam (Fig. 5; step 5). From validation data we determined that for USGS Geohydrologic Region 6 the drainage threshold should be 10 000 km^2 because large-scale water withdrawal in these streams greatly reduces discharge (e.g., Escalante, San Rafael, Virgin and Price rivers). For all other USGS Geohydrologic regions in the study area a drainage threshold of 4600 km^2 was assigned.

3.2. Combined model

The seven lines of evidence, described in Sections 3.1.1 to 3.1.5, were combined within a combined capacity FIS to estimate the maximum beaver dam density (dams/km) of riverscapes (Fig. 6). The FIS captured and synthesized observations that are difficult to adequately represent in a traditional HSI model, but can easily be made with words. For example, most experts on the ecology of beaver would probably agree with the following statements that reflect final group membership conditions (Polvi and Wohl, 2013):

- If building materials do not exist, it does not matter what baseflows or peak flows are, there will be no dams (Table 3, rule 1).
- If baseflow stream power is too high, it does not matter what building materials are available or what peak flows are, there will be no dams (Table 3, rule 2).
- If a site is bounded by expansive aspen or cottonwood forest, then dams can be built at baseflows; where those dams persist at high flows, pervasive stable colonies and dam complexes will exist (Table 3, rule 5).

Table 3 represents the combined capacity FIS rule table that was developed by expert judgment with reference to the literature and Fig. 6 shows the membership functions for inputs and the output. Fig. 5 shows an example of how these five inputs are combined to produce beaver dam capacity estimates. Each ~250 m reach segment has a predicted capacity in terms of maximum number of dams. Thus, density estimates are multiplied by the maximum number of dams by the segment length. These capacity numbers are then summed to estimate the total capacity of the system.

3.3. Model validation

Three forms of model validation were used to assess the performance of the capacity model:

1. Are spatial predictions coherent and logical?
2. Do dam capacity estimates predict observed dam density?
3. Does the electivity index (*EI*) increase proportionately from the *none* to the *pervasive* class?

To facilitate model validation, actual dam counts were collected using a combination of on-the-ground surveys (e.g. Lokteff et al., 2013), aerial overflights (e.g. Macfarlane et al., 2013), and virtual reconnaissance in Google Earth. For the Fremont, Logan-Little Bear, Strawberry, and Price watersheds, we conducted detailed dam count censuses using Google Earth to navigate up and down every stream in the drainage network at an altitude of roughly 500–600 m above ground. When potential dams were identified, a technician zoomed in and assessed other lines of visual evidence (e.g., pond shape, evidence of dam, riparian harvest, and/or skid trails). When likely beaver dams were identified, locations were recorded. Each point was given an accuracy estimate of *very high*, *high*, *medium*, and *low* based on the likelihood that the identified feature was actually a beaver dam. To corroborate these observations, dam locations with medium and low status were independently reexamined in Google Earth to determine if the dam should remain in the dataset. The resulting dam location data was used for model validation.

Our expectations were that 1) dams should not persist in areas that cannot support dams (e.g. stream power too high, no dam building vegetation), and 2) because beaver can be selective and mobile, dam building activities will occur in proportion to the ability of the environment to support dams, hence dam capacity is a proxy for stream quality for dam building. However, because beaver are far below carrying capacity due to legacy trapping, management and extirpation effects, we would expect several locations to be absent of beaver and their dams regardless of the stream's potential capacity. Therefore, we first evaluated whether dams were built in segments the model predicts dams should not be present (i.e. dams observed in segments predicted as *none*). We then restricted our comparison between segments where either a dam was observed and predicted, or where a dam was not observed nor predicted (i.e. if no dams were observed but predicted, we did not include this in the comparison) to prevent over-inflation of zero observations.

For each watershed we compared the average density of predicted dam capacity of all segments in each output membership class to the average density of observed dams in these same segments averaged by classes. In addition, for all segments, we used quantile regressions to compare predicted capacity to observed densities due to the heterogeneous nature of the variance in observations (Cade and Noon, 2003). Quantile regression has been used to evaluate habitat models in describing abundance, with upper percentiles (e.g. 75th, 90th) providing much clearer evidence of habitat limitations than the mean, which is heavily influenced by low density observations through factors not included in

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the models (Terrell et al., 1996, Dunham et al., 2002, Eastwood et al., 2003). While our model attempts to describe limitations to dam building, several factors that result in beaver populations and dam densities below these limits were not accounted for in the model. Because we expect several locations that are capable of supporting dam building activities to have very low densities of beaver dams, regression-based validations between expected and observed dam densities are unlikely to be meaningful.

Finally, to assess whether or not beaver dam-building was preferentially taking place in segments with higher capacity estimates, an EI was calculated. Following Pasternack (2011) an electivity index *EI*, was calculated for each segment type (i):

$$EI_i = \frac{(n_i/\sum n_i)}{(l_i/\sum l_i)} \tag{3}$$

where n_i is the number of beaver dams surveyed in segment type i and l_i is the length of that segment type. The *EI* essentially normalizes utilization by availability, and a value less than one indicates avoidance of a particular habitat, whereas a value greater than one indicates preference for a habitat. If the capacity model is effectively segregating actual dam densities then the following would be expected: an *EI* close to zero for the 'none' and 'rare' classes, less than one for the 'occasional' class, greater than one for the 'frequent' class, and much greater than one for the 'pervasive' class.

4. Results

4.1. Model output

The capacity model suggests that Utah and adjacent watersheds have the capacity to support tremendous quantities of beaver dams,

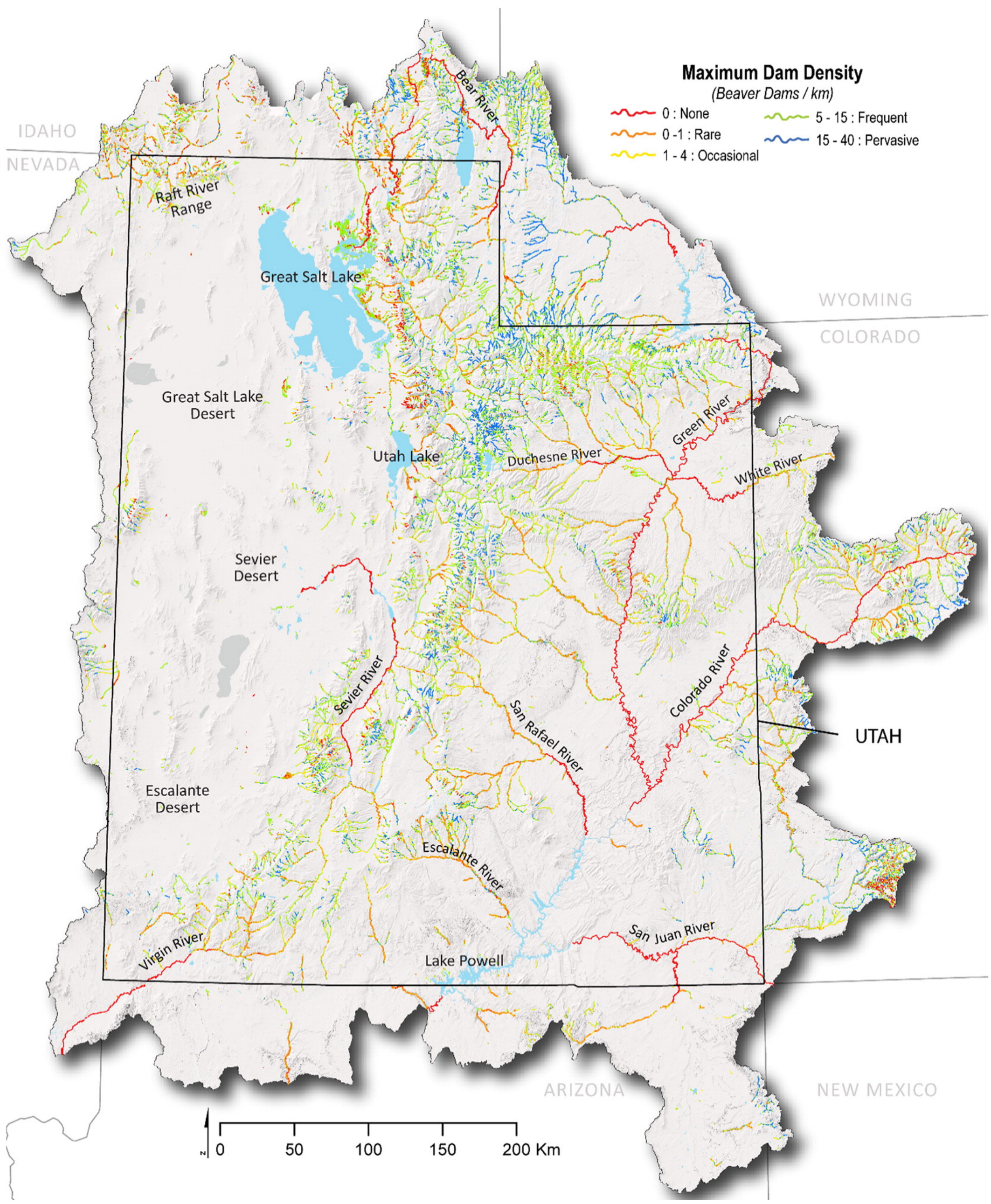

Fig. 7. Modeled existing beaver dam capacity at the reach scale (250 m segment) for all perennial streams within the study area. An interactive Keyhole Markup Language (.kmz) version is available in the Supplement 2.

Table 4
Summary of existing beaver dam gross modeled capacity estimates by capacity categories.

Category	Stream length (km)	% of stream network	Estimated dam capacity
Pervasive	6219	15%	147,644
Frequent	18,162	45%	186,184
Occasional	8234	20%	21,544
Rare	3307	8%	922
None	4639	12%	–
Total	40,561		356,294

with an estimated current capacity of 356,294 dams, or roughly 8.3 dams/km (based on 2011 imagery; Fig. 7; Supplement 2; Table 4). In Utah alone, our model predicts a capacity of 226,939 beaver dams and Macfarlane et al. (2014) estimated there are somewhere between 20,000 and 40,000 actual beaver dams currently in the state based on extrapolating areas with existing dam counts and using the capacity model. For context, there are 39 major man-made dams (above 15 m) throughout Utah (USGS, 2006), so regardless of precise number of beaver dams, they are very prevalent when compared to man-made dams and the capacity of the drainage network to support them is substantial.

The modeled dam density is relatively evenly distributed throughout the study area, with a slightly greater proportion of total capacity in northern regions associated with higher elevations and precipitation (Fig. 7; Supplement 2). The 4639 km of streams in the *none* category primarily reflects the biggest mainstem rivers in the region (e.g. the Colorado, Green, and Bear Rivers) that are simply too wide and deep for beaver to build dams across main channels. We note that dams are found on some smaller side channels of these rivers where active floodplains still exist, and beaver often maintain bank lodges throughout these regions. Also, in steep headwater streams and gorges, stream power is too high for beaver dams to be built. At 45% of the stream network (Table 4), the *frequent* dam density represents the largest single category.

4.2. Model validation

For all four validation watersheds (Fig. 1), we did not observe any beaver dams where the model predicted *none*. In fact, of the 1143 segments with observed dams, only 15 (<0.01%) exceeded the capacity estimates. The over predictions in these few segments was generally easily attributed to inaccuracies in the underlying LANDFIRE vegetation classification. In general, the average densities of observed dams by categories ranked as expected as did *EIs* (Table 5). In all watersheds, *none*, *rare*, and *occasional EI* estimates suggest avoidance, and only *pervasive EI* estimates suggest beaver seeking out those habitats beyond their availability (i.e. a preference). In the *frequent* category, the *EI* was neutral except in the Fremont, where it was avoided (Table 5), which may be related to predation including trapping and other forms of lethal removal. We found a total of 2852 dams across the four validation watersheds. The actual dam densities are only a small fraction of estimated capacity (from 1% to 16%) suggesting that there are many streams and rivers capable of supporting more dam-building beaver than currently exist on the landscape (Table 5). Note that the model makes no attempt to account for historic extirpation and overtrapping of beaver, which was extensive throughout the study area (Dolin, 2010), nor does it account for ongoing and current efforts to discourage nuisance beaver.

4.2.1. Fremont watershed

In the Fremont watershed only 52 dams were identified and were limited to the northwestern corner of the watershed in the High Plateaus (Table 5; Appendix A, Fig. 1). The capacity estimate for the watershed was 5945, suggesting that less than 1% of dam capacity is

Table 5
Existing number of dams and modeled capacity estimates for the four validation watersheds.

Segment type	Stream length	% of drainage network	Surveyed dams	Estimated capacity	Average surveyed dam density	Average predicted capacity	% of modeled capacity	Electivity index
	km	*%*	*# of dams*	*# of dams*	*dams/km*	*dams/km*	*%*	
Fremont watershed								
None	19.4	3%	0	0	0.00	0.0	0%	0.00
Rare	141.1	18%	0	41	0.00	0.3	1%	0.00
Occasional	205.6	26%	5	531	0.03	2.6	9%	0.36
Frequent	313.6	40%	14	3129	0.04	10.0	53%	0.67
Pervasive	97.2	13%	33	2246	0.30	23.3	38%	5.07
Subtotal	777	NA	52	5947	0.07	7.7	1%	NA
Logan-Little Bear watershed								
None	17.8	3%	0	0	0.00	0.0	0%	0.00
Rare	76.4	11%	8	21	0.30	0.3	0%	0.06
Occasional	105.3	15%	103	270	1.30	2.5	4%	0.60
Frequent	389.4	56%	675	4002	1.90	10.3	58%	1.06
Pervasive	112.1	16%	355	2626	3.30	23.8	38%	1.95
Subtotal	701	NA	1141	6919	1.63	9.9	16%	NA
Price watershed								
None	2.5	0%	0	0	0.00	0.0	0%	0.00
Rare	49.8	5%	2	37	0.01	0.3	0%	0.17
Occasional	154.1	16%	19	733	0.06	2.7	9%	0.77
Frequent	499.6	52%	41	4458	0.08	9.6	57%	0.96
Pervasive	259.2	27%	27	2641	0.20	22.8	34%	2.71
Subtotal	965	NA	89	7869	0.09	8.2	1%	NA
Strawberry watershed								
None	9.5	1%	0	0	0.00	0.0	0%	0.00
Rare	127	13%	8	15	0.10	0.3	0%	0.10
Occasional	271	28%	110	412	0.70	2.7	3%	0.44
Frequent	466	47%	867	5117	1.60	10.3	43%	1.07
Pervasive	109	11%	585	6260	2.30	24.3	53%	1.40
Subtotal	982	NA	1570	11,804	1.60	12.02	13%	NA
Total across all validation watersheds	3425	NA	2852	32,539	0.83	9.50	9%	NA

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currently utilized by beaver. Beaver appear to have been eliminated from the remaining watercourses of the watershed. The capacity model appears to identify frequent and pervasive beaver dams in the portion of watershed where beaver do exist (Appendix A, Fig. 1). U M Creek in the Fremont Watershed is an example of where the modeled capacity for dam density accurately describes actual dam densities (Appendix A, Fig. 2).

4.2.2. Logan-Little Bear watershed

The capacity model estimates 6919 dams watershed-wide, suggesting that the Logan-Little Bear watershed is currently at 16% of total estimated capacity (Table 5). Estimated capacity and actual dam counts for the Logan-Little Bear watershed are shown in Appendix A, Fig. 3. A total of 1141 dams were counted with dams concentrated in high-elevation, mountainous regions of the watershed. Very few dams were identified in Cache Valley where human population and anthropogenic impacts are highest in the watershed (Appendix A, Fig. 3). The distribution of dams relative to predicted categories are highlighted in aerial imagery and maps in tributaries of the Logan River. In Franklin Basin (Appendix A, Fig. 3, part A), the capacity estimate appears to effectively rank all categories of dam densities (none, rare, occasional, frequent, and pervasive). Temple Fork also illustrates that the model produced dam density patterns that resemble observed densities (Appendix A, Fig. 4). Using surveys from Lokteff et al., 2013, areas predicted as not able to support beaver are areas where we have not observed active dams nor historic evidence of dams. Most of Temple Fork and Spawn Creek were predicted to support occasional to frequent dams, and these densities are observed at both streams. Dam capacity is limited primarily by the lack of extensive riparian vegetation or aspen owing to a long history of livestock grazing at Temple Fork. A cattle exclosure was installed in 2005 around the Spawn Creek tributary as part of a passive restoration strategy, and riparian vegetation continues to recover (Hough-Snee et al., 2013). Several new dams were constructed in lower Spawn Creek from 2011 to 2015, an area predicted to have frequent dam density.

In the middle of Spawn Creek is an area flanked by extensive aspen forests that has supported multiple stable colonies. Within this aspen forest, between 8 and 20 (currently 18) active dams have persisted since the 1950s, all in an area less than 0.5 km in length (Appendix A, Fig. 4). These exact reach segments were predicted as being able to support *pervasive* dam densities. On Temple Fork, where grazing is still permitted, there are currently 14 beaver dams in the 3 km upstream from the Spawn Creek confluence (4.6 dams/km). Along this 3 km reach our model predicted a mixture of *occasional*, *frequent* and *pervasive* beaver dam densities and this was what we observed, illustrating that the model sufficiently identified these various supplies of preferred food and building material, and changes in stream power that allow various levels of dam building to exist (Appendix A, Fig. 4).

4.2.3. Price watershed

In the Price watershed only 89 dams were identified and were isolated to a few streams (Table 5; Appendix A, Fig. 5). Beaver appear to have been eliminated from large portions of the watershed (Appendix A, Fig. 5). The distribution and density of actual dams relative to predicted densities highlights good model performance. For example, the model effectively identified an area where beaver are colonizing the stream segments identified as *frequent* (Appendix A, Fig. 6). The existing capacity estimate for the watershed was 7688, revealing that only 1% of the existing capacity was being utilized by dam-building beaver (Table 5).

4.2.4. Strawberry watershed

For the Strawberry watershed a total of 1570 dams were identified in the census, the highest amount recorded of the four watersheds. These dams were distributed fairly evenly across the watershed (Table 5; Appendix A, Fig. 7). Appendix A, Fig. 8 shows that the capacity model was effectively identifying frequent and pervasive dam density segments. The existing capacity was 11,804 dams; therefore, the watershed is currently at 13% of existing capacity (Table 5). This watershed has the potential to support a high number of segments with pervasive dams.

Throughout all of the four validation watersheds (Fig. 1) the predicted capacity and observed densities across segments exhibited an anticipated classic wedge shape distribution (Terrell et al., 1996). In this distribution, the model identifies limits to dam building but not to other factors preventing beaver from establishing in some segments. We observed a strong significant relationship between average predicted capacity density and average observed density in each of the validation watersheds (Fig. 8). We found a strong positive relationship between predicted capacity and observed densities across segments, with slopes significantly greater than zero for the 50th, 75th, and 90th percentiles (Table 6; Fig. 9). These results suggest that the model is precise in describing stream segment potential to support dams. While some observations occur above the 90th percentile line for any given predicted value approximately only 10% of the values are above this line (e.g. for predicted capacity between 9 and 12, of the 184 points in Fig. 9, 19 are above the 90th percentile line).

5. Discussion

Our primary hypothesis underpinning the capacity model was that beaver dam distributions on perennial streams and rivers are fundamentally controlled by the distribution of preferred riparian vegetation, and secondarily limited by local flow regime, and stream gradient. The lines of evidence used in the model reflect this hypothesis, and our validation of model performance provides a reasonable, but non-exhaustive test of this hypothesis.

5.1. Critiquing the capacity model's performance

Although subtle nuances in beaver behavior and site-specific conditions may ultimately influence whether or not beaver build dams at a particular location, our findings support the premise that the primary controls on beaver dam density can be simply reduced to vegetation and water availability. While a more complicated and/or more computationally intensive model (e.g. an agent-based model coupled with hydraulic and hydrologic models) may highlight the importance of temporal dynamics and/or more specific attributes (behavior, predator response, etc.), the idea that a few key components can be used to approximate upper limits on dam distributions through time is both simple and appealing. Traditional HSI models are also very simple and can perform reasonably well in the localities for which they are developed. However, they do not always accurately predict beaver dam distributions outside the sample locations where the model was developed (Baldwin, 2013). The FIS approach used here is crucial to effective model performance from a parsimonious, generalizable framework. Fuzzy Inference Systems are much less sensitive to input precision than traditional statistical approaches and do not necessitate the large quantities of empirical data that traditional habitat models do (Marsili-Libelli et al., 2013; Munoz-Mas et al., 2012).

Patterns of dam capacity and observed dam density by category meet our hypothesized expectations (see also Appendix A and Supplement 2 for site-specific examples). These averages include many segments where dam density is far below capacity (i.e. slope of the regression <1.0; Fig. 9). Across entire watersheds, the total number of dams was <1–16% of capacity. This might be negatively interpreted as the model is over-predicting the number of dams that can reasonably be supported in a watershed. One explanation is that if beaver rapidly deplete woody food and building materials, there could be a negative feedback by beaver lowering capacities locally (Beier and Barrett, 1987). However, we have documented (unpublished data) the opposite taking place in semi-arid regions where by raising water tables, beaver

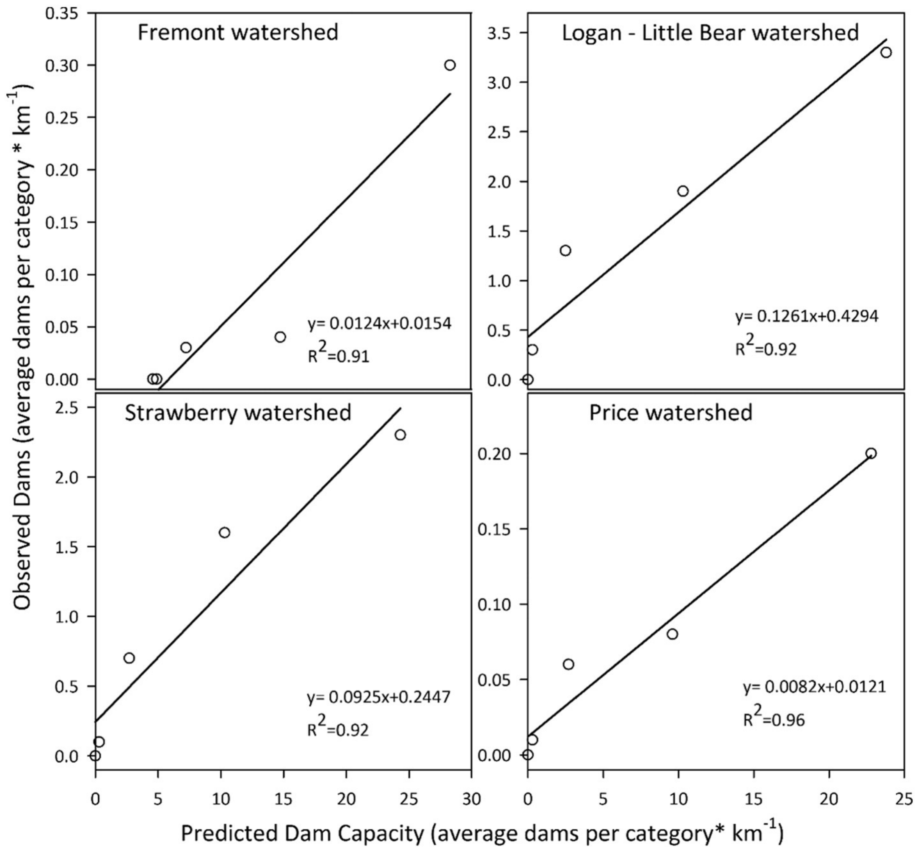

Fig. 8. The predicted dam capacity density, averaged by each category (*none*, *rare*, *occasional*, *frequent*, and *pervasive*) versus the actual observed density averaged by each category.

dramatically expand the riparian zone and create a positive feedback that expands woody vegetation. Moreover, many researchers have documented positive responses of riparian woody species to harvest from beaver (Harrison, 2011; Hood and Bayley, 2009; McColley et al., 2011). In many localities, beaver act like rotational crop farmers, working an area hard for two to five years, and then letting it rest and recover for two to ten years before returning to work it again. Beaver were historically extirpated and have not yet returned to many of the areas

Table 6
Summary of the intercept and slope parameters, and the standard error, confidence intervals, t value and probability that the parameter estimate is different from zero, from the 50th, 75th, and 90th percentiles for each validation watershed based on the quantile regressions.

Watershed	Percentile	Parameter	Estimate	Standard error	90% Confidence limits		t Value	Pr > |t|
Fremont	50th	Intercept	−0.206	0.000	−0.206	−0.206	−4.53E + 14	<.0001
		Capacity	0.720	0.000	0.720	0.720	3.5E + 14	<.0001
	75th	Intercept	−0.544	0.078	−0.672	−0.416	−7.01	<.0001
		Capacity	1.900	0.269	1.457	2.342	7.07	<.0001
	90th	Intercept	−0.605	0.038	−0.667	−0.543	−16.12	<.0001
		Capacity	2.112	0.128	1.901	2.323	16.49	<.0001
Logan-Little Bear	50th	Intercept	−0.121	0.057	−0.214	−0.027	−2.13	0.0338
		Capacity	0.645	0.021	0.611	0.680	31.05	<.0001
	75th	Intercept	0.000	0.037	−0.061	0.061	0	1
		Capacity	1.259	0.043	1.188	1.330	29.09	<.0001
	90th	Intercept	2.187	1.496	−0.277	4.650	1.46	0.1442
		Capacity	2.132	0.230	1.754	2.511	9.28	<.0001
Price	50th	Intercept	−0.121	0.057	−0.214	−0.027	−2.13	0.0338
		Capacity	0.645	0.021	0.611	0.680	31.05	<.0001
	75th	Intercept	0.000	0.037	−0.061	0.061	0	1
		Capacity	1.259	0.043	1.188	1.330	29.09	<.0001
	90th	Intercept	2.187	1.496	−0.277	4.650	1.46	0.1442
		Capacity	2.132	0.230	1.754	2.511	9.28	<.0001
Strawberry	50th	Intercept	−0.173	0.031	−0.224	−0.121	−5.53	<.0001
		Capacity	0.602	0.012	0.582	0.622	49.57	<.0001
	75th	Intercept	0.000	0.453	−0.747	0.747	0	1
		Capacity	1.145	0.087	1.001	1.289	13.1	<.0001
	90th	Intercept	4.252	1.057	2.512	5.993	4.02	<.0001
		Capacity	1.421	0.124	1.216	1.625	11.42	<.0001

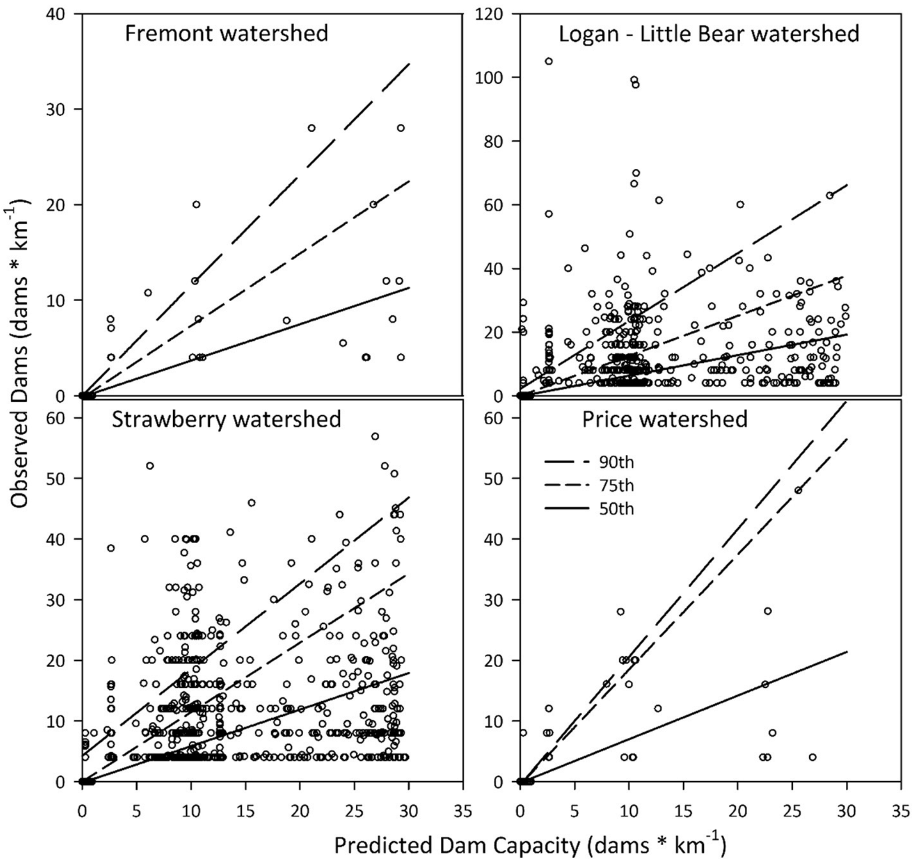

Fig. 9. Predicted dam capacity density for all segments in each watershed versus observed dam densities for reaches >0 observed dams and segments with 0 observed dams in segments predicted as zero (i.e. does not include segments with 0 observed dams and >0 predicted). Quantile regressions for 90th, 75th, and 50th, percentiles represented by long dashed, short dashed, and solid lines respectively.

where the capacity model was run (UDWR, 2010), whereas in other areas beaver have been actively discouraged. Thus, we argue that the low overall percent of predicted capacities at the watershed scale are not indicative of the model over predicting, but instead suggestive of the tremendous additional capacity most these streams have to support additional beaver dam building activity.

Quantile regression can be useful in identifying predictive relationships when factors that can greatly influence the densities are not modeled or measured (Cade and Noon, 2003). For example, legacy effects (e.g. trapping, hunting, water diversions, disease, and fire) can suppress mature beaver populations from reestablishing. While in the majority of segments, observed densities were below capacity, several segments were considerably higher than capacity (Fig. 9). These high observed dam densities may, in part, be artifacts of the scale of observation. Dams were counted in 250 m segments and summarized as dams/km. A 250 m segment may capture intensive dam building by a colony of beaver that is unlikely to extend across an entire kilometer. Behavioral interactions between multiple colonies could prevent high dam prevalence from occurring across adjacent segments. A 1 km moving average across adjacent segments may smooth out these higher observations. However, the slope of the 90th percentile was considerably greater than 1.0 and even the 75th percentile was greater than 1.0 for all validation watersheds, suggesting that dam densities can often exceed model predictions. Therefore, we believe that the model is not overestimating dam capacity and perhaps is even conservative in estimating dam capacity. Moreover, it is important to highlight that while in any given reach segment we may expect actual dam densities to approach capacity, we would never expect a whole system to be at capacity.

5.2. Management applications & future extensions

Resource managers are increasingly developing stream and riparian restoration plans that employ beaver (DeVries et al., 2012). The success of these restoration plans will depend in large part on the capacity of riverscapes to support dam-building beaver. Yet, beaver-based restoration plans have not adequately considered dam building capacity to date. It is improbable that beaver will thrive in every location that they are reintroduced (McKinstry and Anderson, 2003). Therefore, land managers urgently need to better understand where dam-building activity is sustainable and what dam densities can be expected at a given location. The simple, spatially-explicit beaver dam capacity model presented here is driven by nationally available datasets, and is able to consistently make capacity predictions that compare favorably to actual dam densities where beaver are building dams. These same modeled segments also segregate meaningfully by electivity indices, showing potential for applications elsewhere.

We suspect more refined spatial predictions may be possible with higher resolution datasets (e.g. LiDaR topography and high-resolution, classified multi-spectral imagery), but we also posit that in many instances the freely available nationwide datasets used here are more than adequate for describing both the dominant patterns and even making reasonable reach-specific predictions. Because our model effectively segregated the primary factors controlling beaver dam occurrence and densities, we infer that it is a powerful research, restoration, and conservation planning tool. This model output is already being used to help resource managers target specific locations for stream restoration through beaver reintroduction and/or conservation (Macfarlane and Wheaton, 2013; Portugal et al., 2015a;

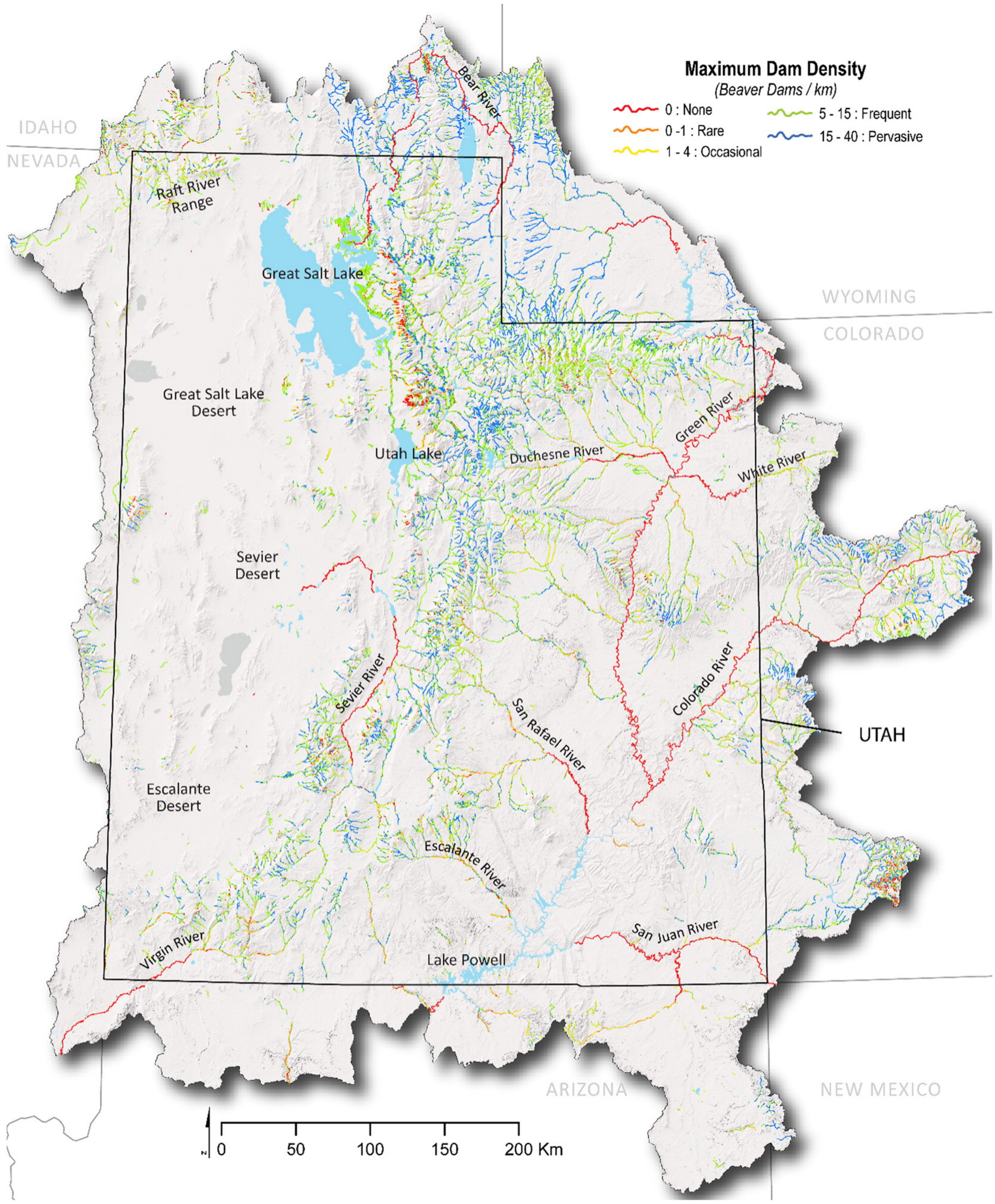

Fig. 10. Modeled historic beaver dam capacity (based on LANDFIRE Biophysical Settings (BpS) layer that represents the vegetation that may have been dominant on the landscape prior to Euro-American settlement) for comparison with Fig. 7.

Portugal et al., 2015b; Wheaton, 2013; Wheaton and Macfarlane, 2014). With accurate predictions of potential dam building capacities, researchers and managers are empowered to make reliable predications of a riverscape's potential responses to beaver, responses that are intended to improve riparian and aquatic habitat for species of concern (Collen and Gibson, 2001).

The capacity model could be run as a time-varying dynamical model. The vegetation could vary through time and actual time series of discharge could be used to drive these dynamics. If the model were to be run in this manner over short time scales (<5 years), flow variability would be the primary driver in deviations from the time-averaged model outputs reported here. However, over longer time scales where vegetation communities have shifted due to dramatic disturbance (e.g. timber harvest and fire) or more gradual impacts like browse pressure (e.g. from beaver, cattle, and elk), such outputs may produce very interesting patterns. For illustrative comparison purposes, we show a run of the model in Fig. 10 based on LANDFIRE historic vegetation predictions to facilitate comparison of current (Fig. 7) and historic capacities. Such historic capacity estimates can be used to build specific hypotheses on where beaver might have thrived prior to current human disturbance (Macfarlane and Wheaton, 2013). The model could also be run using future climate and hydrologic scenarios to forecast future beaver dam building capacity estimates and distributions.

Although we believe this model can be used as a line of evidence to effectively target areas for conservation and restoration using beaver dams, we recognize that a capacity model approach alone is insufficient for all planning activities. A major concern not considered in this model, is that many places where beaver might build dams are in direct conflict with humans (e.g., damming of irrigation canals and flooding of roads). To address areas of human–beaver conflict, a decision support system we call the Beaver Restoration Assessment Tool (BRAT) was developed by Macfarlane et al. (2014) and serves to help resource managers, restoration practitioners, wildlife biologists, and researchers assess the potential for beaver as a stream conservation and restoration agent across landscapes. The backbone to BRAT is the capacity model described here, while BRAT's decision support and planning tools use simple geospatial analyses and rule systems to account for the recovery potential of riparian habitat and potential for beaver dam-related human conflicts. The BRAT model output segregates the stream network into multiple conservation and restoration zones based on this intersection of a riverscape's capacity for beaver dams and the potential for human–beaver conflict (Macfarlane et al., 2014).

Many of the 40,561 km of streams and riparian zones modeled in this study are either threatened or impaired by a combination of altered flow regimes, water withdrawal, channel incision, sedimentation, and/or establishment of invasive plant species that displace native riparian vegetation (Goodwin et al., 1997; Poff et al., 2011; Stromberg et al., 2007). This degradation limits the amount of instream wood that can be contributed to and retained in channels. This reduction in wood decreases aquatic habitat complexity and instream cover for native fish (Keller et al., 2014). Our findings suggest that many of these same streams can support beaver dams at higher densities than they yield even in their current degraded states. If higher dam densities are promoted and realized, it is likely that the resulting increase in dams will dramatically improve in-stream habitat complexity and increase lateral hydrologic connectivity between channels and floodplains. This lateral connectivity will facilitate and maintain hydrophytic riparian vegetation (Wohl, 2013a) that contributes wood, both as instream large wood (Hough-Snee et al., 2014) and as dam-building material. These wood subsidies decrease longitudinal connectivity by creating geomorphic and hydraulic breaks impeding the downstream transport of wood in what is known as the river discontinuum (Burchsted et al., 2010).

5.3. Geomorphic implications & connectivity

Dam building by beaver creates discontinuous river and stream networks (Burchsted et al., 2010) that have been shown to alter the amount, and timing of water and sediment delivery (Gurnell, 1998; Naiman et al., 1988; Pollock et al., 2003). Ponding upstream of beaver dams reduces water velocity, encouraging fine sediment deposition (Butler and Malanson, 1995; Pollock et al., 2007) in the pond itself, and on the adjacent floodplain during high flows. Beaver ponds and dams can act as long-term sinks for both suspended and bedload sediment (Green and Westbrook, 2009) facilitating the storage of fine sediment and organic matter in valley bottoms (Burns and McDonnell, 1998; Wohl and Beckman, 2014). Beaver dams also cause an increase in overbank flooding, elevating water tables and enhancing channel–floodplain connectivity (Burchsted et al., 2010; Collins and Montgomery, 2001; Pollock et al., 2007; Wohl and Beckman, 2014). Such improved connectivity typically leads to an increase in the diversity and abundance of native riparian tree species such as aspen, willow, and cottonwoods (Wohl, 2013a; Wright et al., 2002) and an expansion of the riparian corridor (Westbrook et al., 2006; Westbrook et al., 2011) creating beaver meadows (Ives, 1942; Ruedemann and Schoonmaker, 1938). The transformation of single-thread channels in alluvial valley bottoms to heterogeneous beaver meadows increases instream wood loading that facilitates the development of complex instream habitat and channel planform (Polvi and Wohl, 2013). Although we did not explicitly model the impacts that beaver dams have on geomorphology, many of the impacts have been reviewed and studied extensively elsewhere (Butler and Malanson, 2005; Butler and Malanson, 1995; Gurnell, 1998; Persico and Meyer, 2009; Pollock et al., 2014; Westbrook et al., 2011). What the capacity model provides are spatial predictions of where those feedbacks on lateral connectivity and longitudinal connectivity have the potential to be most pronounced as a result of potential beaver dam building and maintenance.

6. Conclusions

We presented results of a new drainage network-based model of the capacity of streams and rivers to support beaver dam building activity. The model output is an upper limit or carrying capacity of beaver dams in dams per kilometer. The large spatial coverage that can be modeled with this network capacity model, as illustrated here for Utah and surrounding states is heretofore unprecedented. The model was run and validated successfully using free, widely available, public data to assess the upper limits of riverscapes to support beaver dam-building activities at the reach level. The model can be used to help identify, over large regions, where conservation and restoration actions utilizing beaver activity may be most likely to succeed. Beaver dam density was the focus instead of 'suitable beaver habitat', as dam building activity is the keystone process shaping lateral and longitudinal connectivity. It is this biotically-mediated connectivity that results in the cascade of ecological and hydrogeomorphic feedbacks that watershed conservation and stream restoration demand. When run with coarse resolution datasets, the model produces dam density and total maximum dam capacity estimates that compare favorably to actual beaver dam distributions, even across a large, climatically and physiographically diverse landscape where water and/or wood may be locally limiting.

We conclude that the spatially-explicit dam capacity outputs from this type of model provide researchers and resource managers with important reach-level (stream segment) information. Such information helps explain patterns of beaver dam building activity and could be used to make inference about past processes of valley bottom formation (Persico and Meyer, 2009, 2013) and future potential to use beaver reintroduction to maintain valley bottom and stream connectivity. Similarly, in areas where high beaver dam capacity is predicted, but beaver have been removed, trajectories of historic channel change can be inferred and used to assess riparian, wetland and stream condition. This could be crucial in exploring the potential hydrologic connectivity impacts of beaver dams, testing suggestions that beaver could help improve ecosystem resilience as a part of a climate change adaptation strategy. Moreover, the beaver dam capacity model provides a regional-scale planning tool capable of effectively identifying where beaver reintroduction and dam building might be a viable stream, riparian, and aquatic conservation approach, and where beaver-based restoration approaches may not be appropriate.

Acknowledgments

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Appendix A. Beaver dam capacity model validation maps showing capacity estimates and actual beaver dam counts for the four validation watersheds: Fremont, Logan-Little Bear, Price, and Strawberry

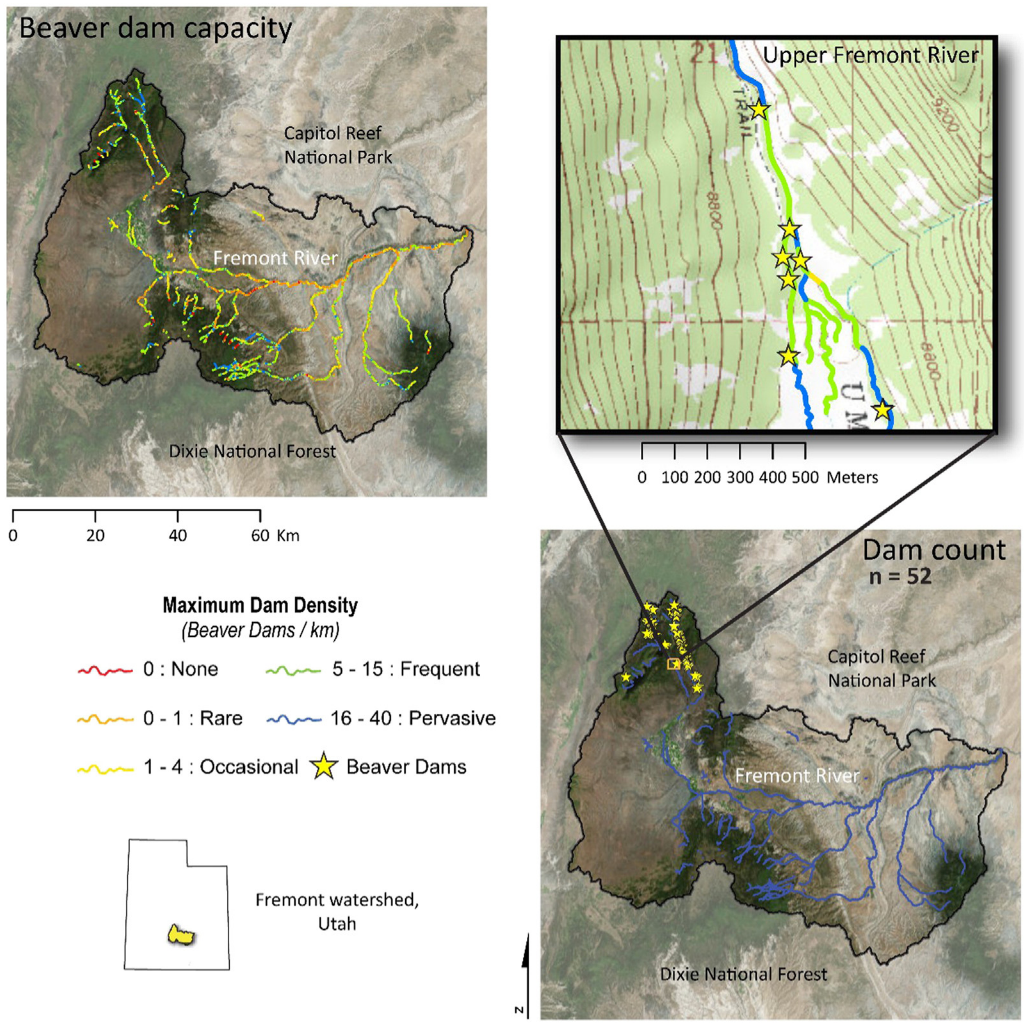

Fig. 1. Map shows the Fremont watershed, one of the validation watersheds, with capacity estimates and actual beaver dam counts.

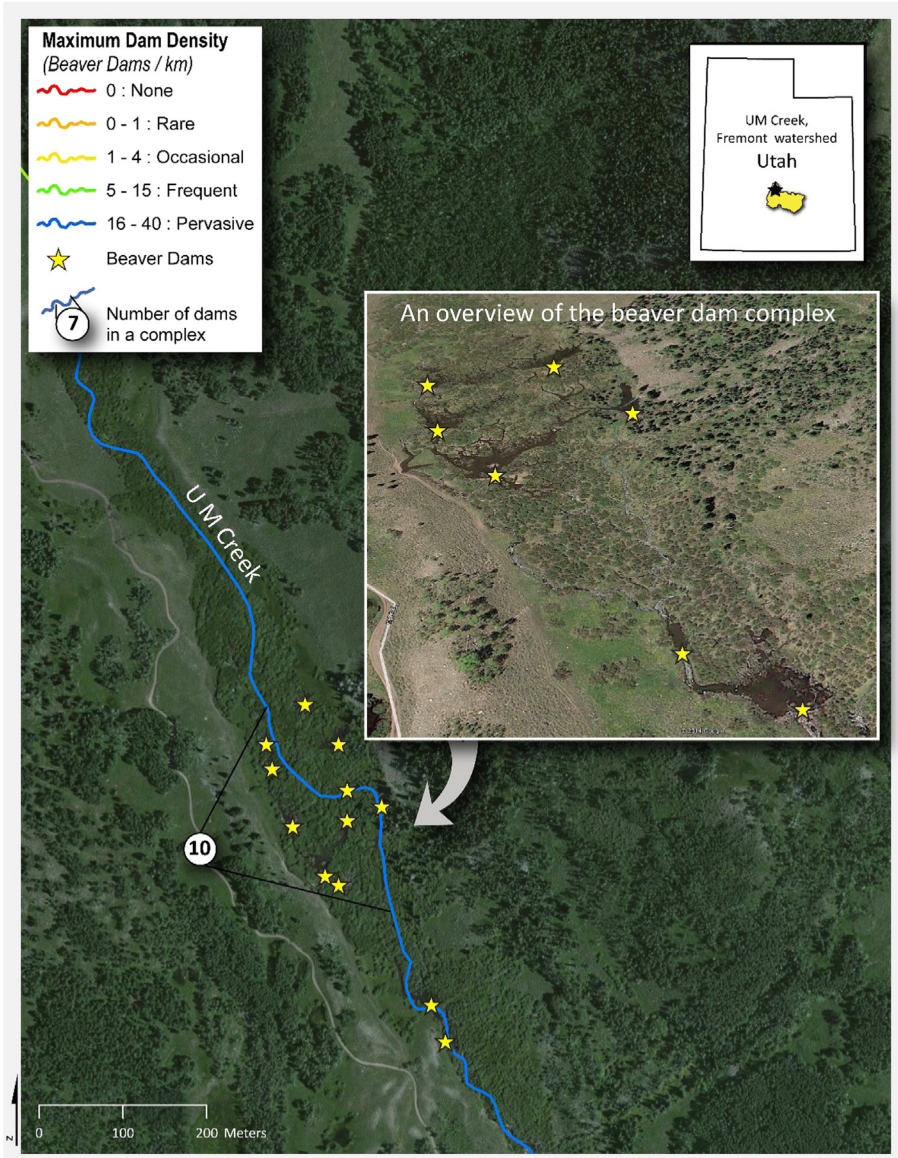

Fig. 2. Map shows capacity model performance on UM Creek in the Fremont watershed. Individual beaver dams are denoted with yellow stars. The Figure illustrates how the capacity model has effectively captured a high dam density segment. The model differentiated the segment where 10 dams exist as a *pervasive* density reach (250 m segment). Compared to the surrounding upstream and downstream segment, these segments boast a supply of willow within the 30 m buffer and aspen extends throughout the 100 m buffer. This illustrates that the model correctly identified this abundant supply of preferred food and building material, and predicted what is found within the segment—pervasive dam densities.

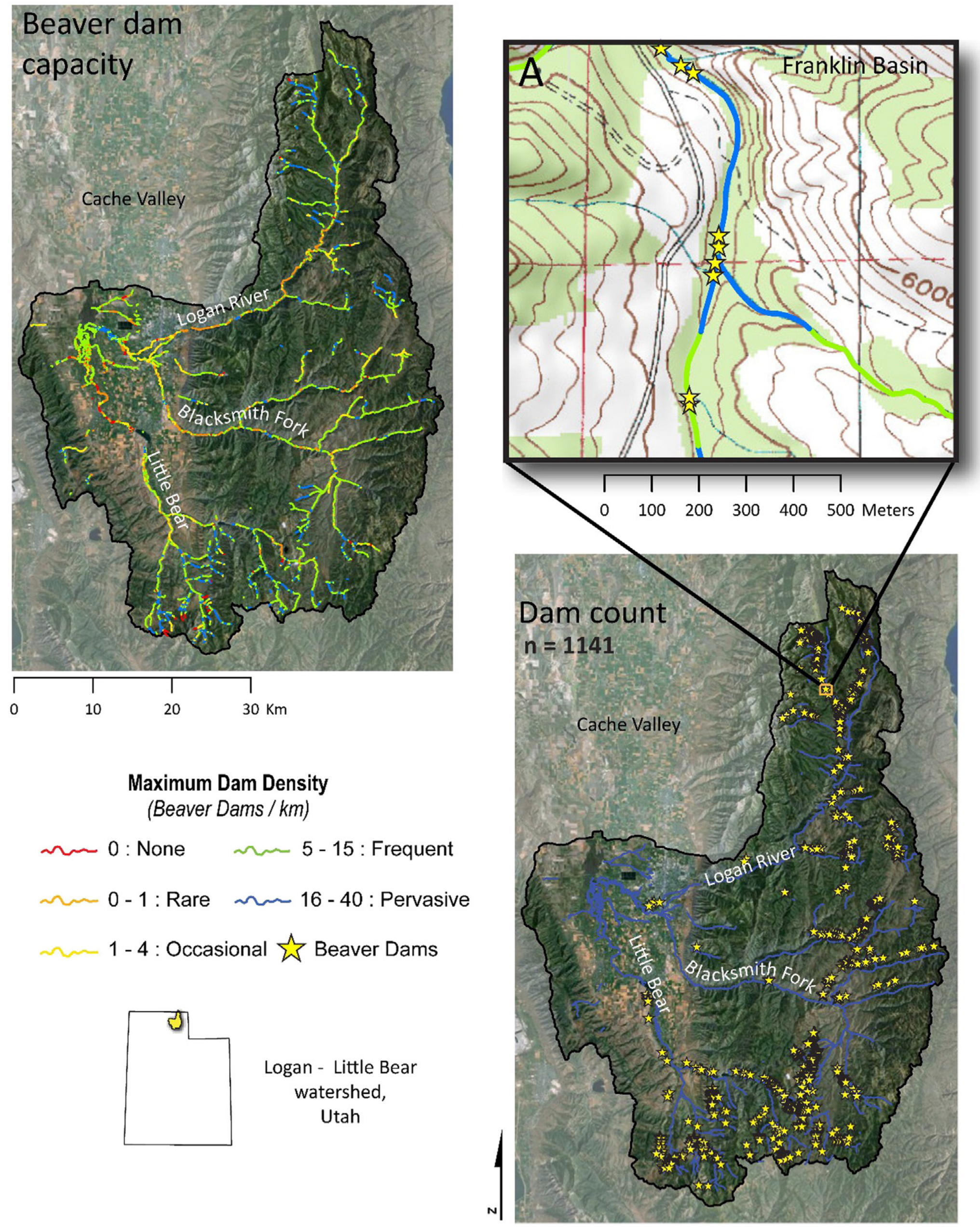

Fig. 3. Map shows the Logan-Little Bear watershed, one of the validation watersheds, with capacity estimates and actual beaver dam counts.

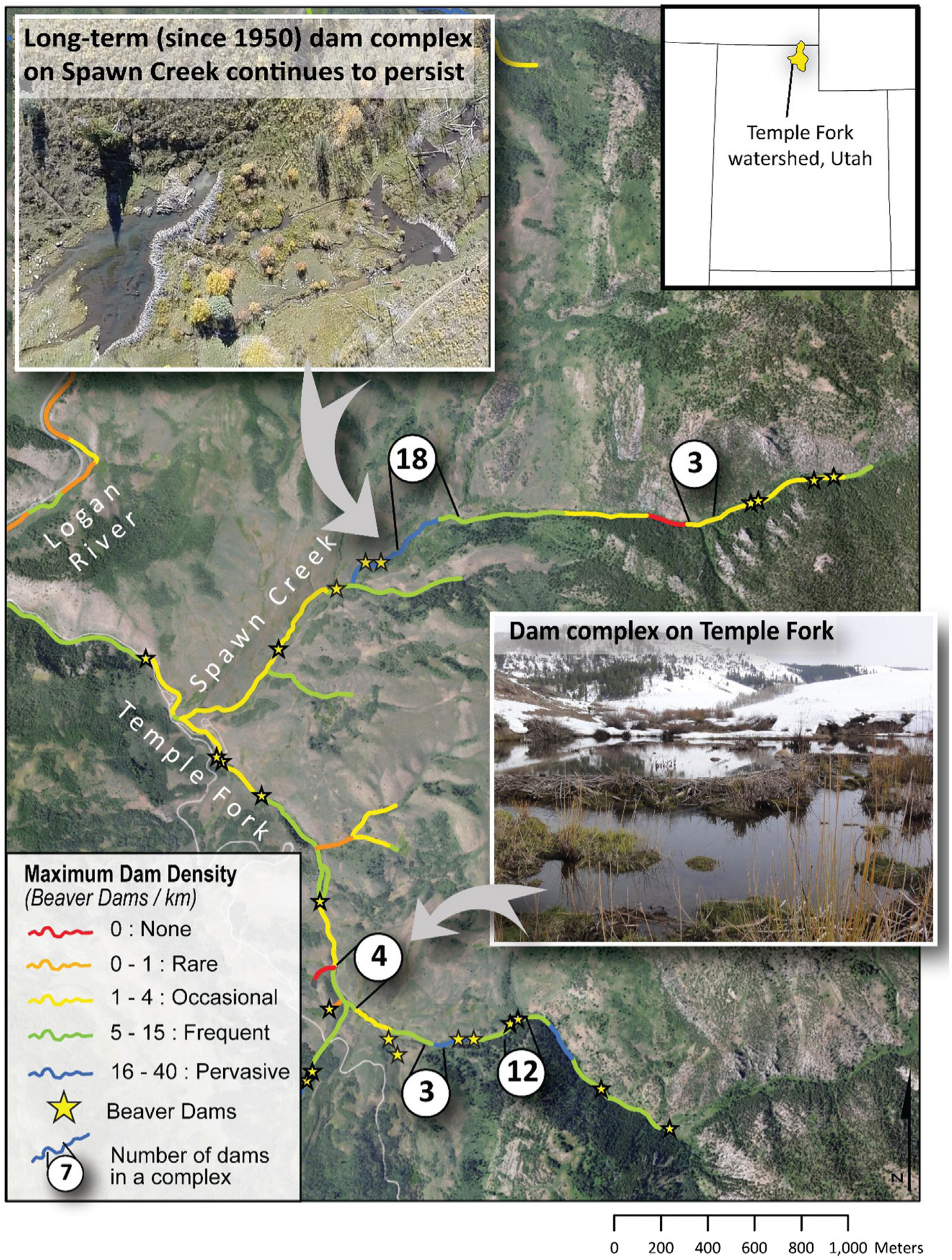

Fig. 4. Map shows capacity model performance in the Temple Fork watershed (tributary to Logan River). Individual beaver dams are denoted with yellow stars, whereas dam complexes are shown in circles (number in circle is count of dams) in discrete segments.

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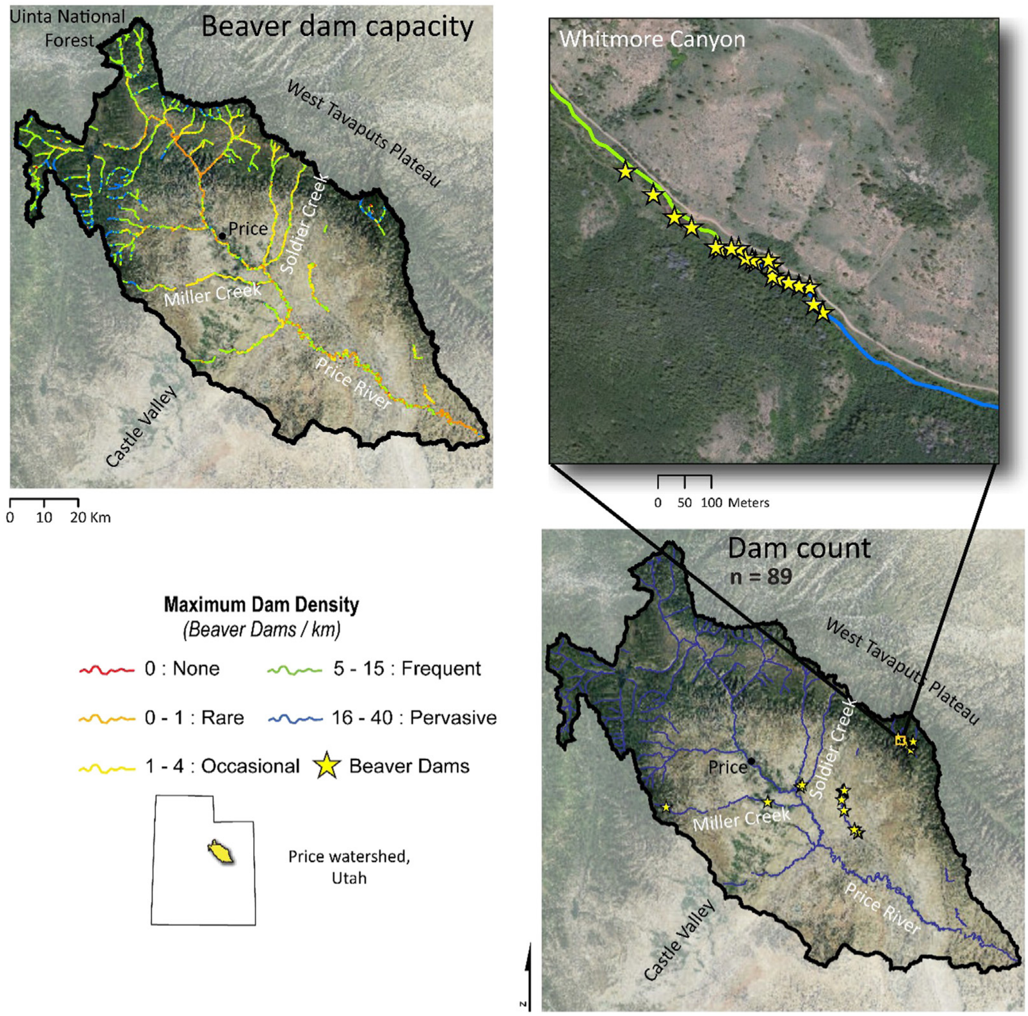

Fig. 5. Map shows the Price watershed, one of the validation watersheds, with capacity estimates and actual beaver dam counts.

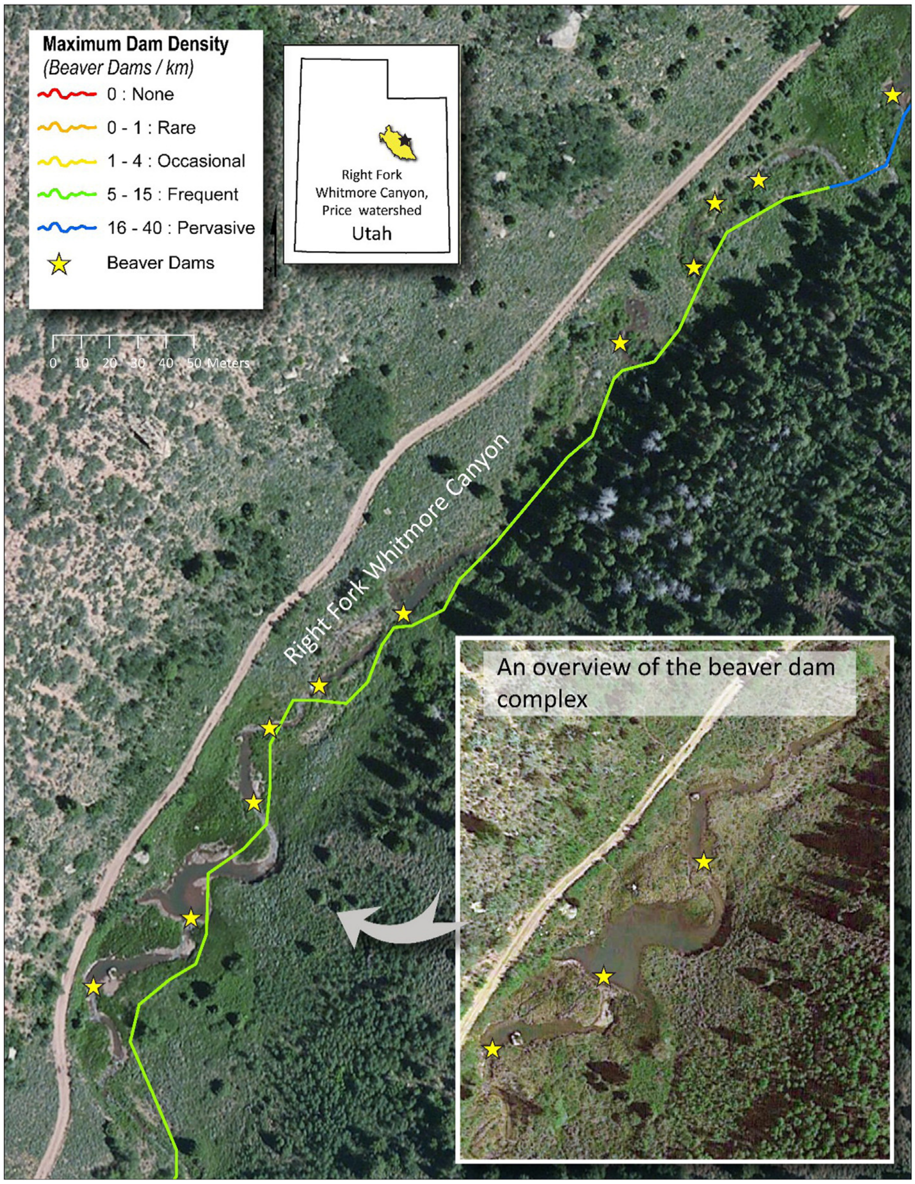

Fig. 6. Map shows capacity model performance on Right Fork of Whitmore Canyon in the Price watershed. Individual beaver dams are denoted with yellow stars. This figure illustrates how the capacity model has effectively captured frequent dam densities in an area that appears to be near capacity. Right Fork of Whitmore Canyon also confirmed that the spatial dam density patterns are coherent and logical and match what is found on the ground.

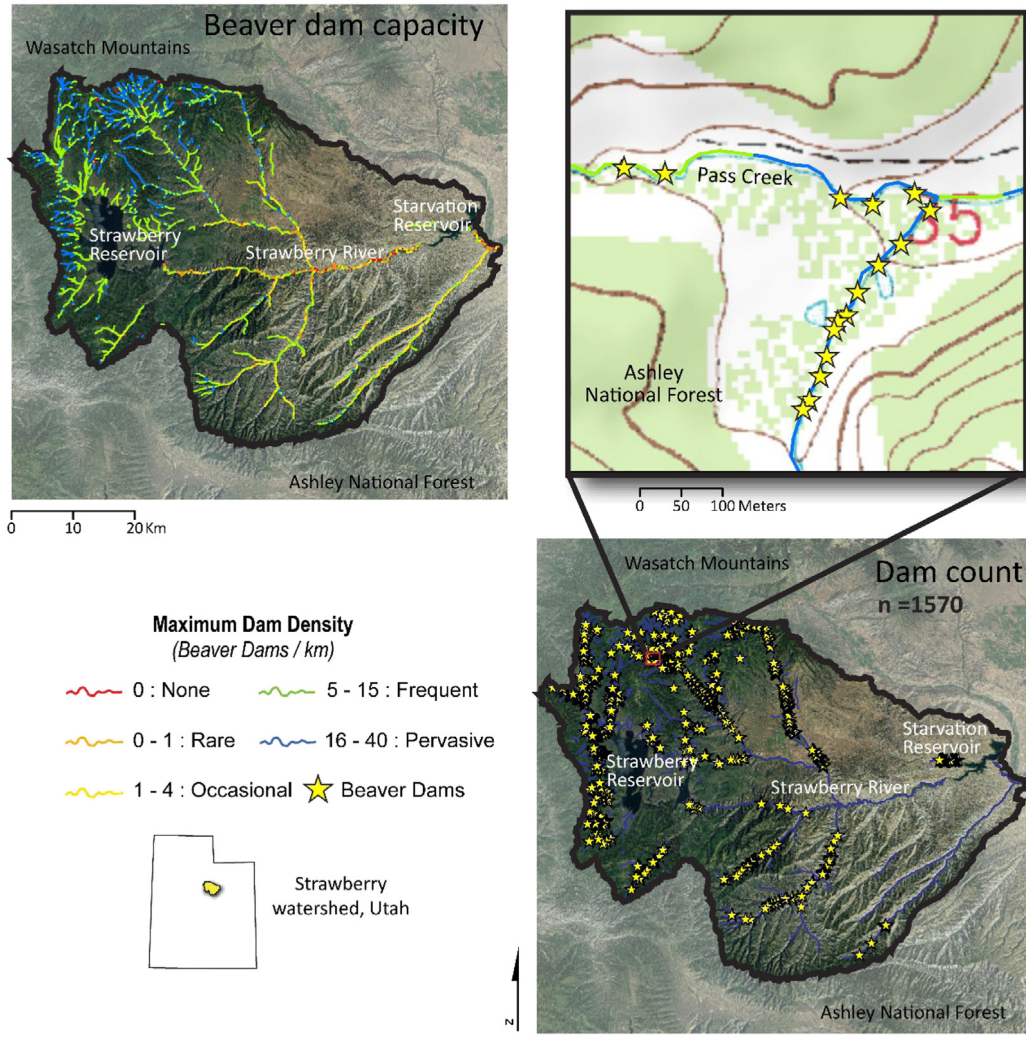

Fig. 7. Map shows the Strawberry watershed, one of the validation watersheds, with capacity estimates and actual beaver dam counts.

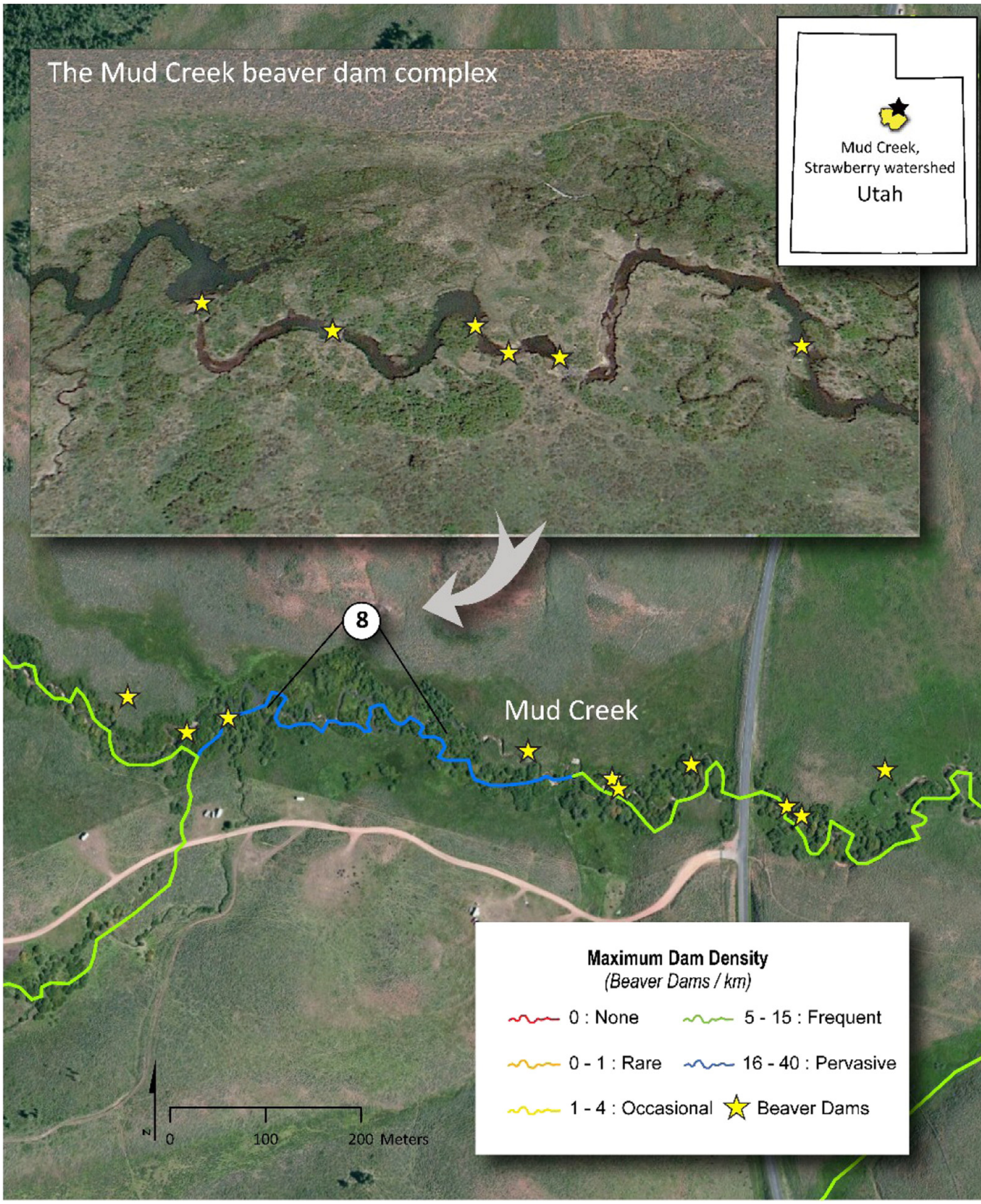

Fig. 8. Map shows capacity model performance on Mud Creek in the Strawberry watershed. Individual beaver dams are denoted with yellow stars, whereas dam complexes are shown in circles in discrete segments (number in circle is count of dams). The figure illustrates how the model has effectively differentiated pervasive and frequent dam density segments. The model differentiated the segment in the center of the photo from neighboring segments as being able to support *pervasive* dam densities (16–30 dams/km) compared to the surrounding upstream and downstream segments predicted to support *frequent* dam densities (5–15 dams/km). The center *pervasive* segment boasts a supply of willow and aspen within the 30 m buffer that extends throughout the 100 m buffer; whereas, the upstream and downstream segments have a narrower riparian corridor and a less extensive supply of preferred building material. This illustrates that the model sufficiently identified this abundant supply of preferred food and building material, and predicted very high dam densities where preferred material is extensive and lower dam densities where preferred material is less extensive.

Appendix B. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi: http://dx.doi.org/10.1016/j.geomorph.2015.11.019.

Supplement 1 includes Beaver dam capacity FIS models and MatLab scripts. Supplement 2 includes existing beaver dam capacity output in Keyhole Markup Language (.kmz) file format subset by USGS Geohydrologic Region.

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