Quantifying beaver dam dynamics and sediment retention using aerial imagery, habitat characteristics, and economic drivers

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RESEARCH ARTICLE

Quantifying beaver dam dynamics and sediment retention using aerial imagery, habitat characteristics, and economic drivers

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Abstract
Context The North American beaver (*Castor canadensis*) population experienced a precipitous decline in the early twentieth century, fueled by the economic value of their pelts and habitat loss from forestry and agricultural expansion. The historical response of beaver populations to changing stresses is difficult to quantify due to a lack of population data.
Objective Here we characterize beaver dam dynamics as a surrogate measure for population and analyze spatio-temporal relationships with landscape and management characteristics, and estimate the potential of watershed beaver dam activity to sequester sediment.
Methods We use aerial photos from >70 years along with GIS analysis to quantify counts, sizes, and distributions of beaver dams and impoundments over time, including site recurrence. Human predation pressure and young aspen area are used to predictively model temporal changes in dam count. Finally, we estimate sediment retention through time by applying our data to published relationships.
Results Our analyses reveal a remarkable correlation between watershed beaver dam dynamics and statewide records of beaver harvest. Beaver dams show a pattern of spatial clustering as the number of dams increased, mostly in tributaries directly connected to the main river, regardless of stream order. Our multiple linear regression model predicts dam counts from pelt prices and young aspen area, producing an excellent fit ($R^2 = 0.86$).
Conclusions We found evidence for beaver population recovery from near extirpation using relatively simple and widely-available measures. Methods we present can be used to estimate regional beaver population dynamics in other watersheds.

Keywords Aerial imagery · Spatial GIS analysis · Beaver population dynamics · Hydrology · Sedimentation

Introduction

The geomorphology of hydrologic systems is closely tied to past disturbances and their consequences, which plays out over decades to centuries. It has long been known that the dam-building activities of North American beavers (*Castor canadensis*) play an important role in the geomorphology of streams continent-wide. Human activities have disrupted the landscape through purposeful breaching of beaver dams, trapping beavers for trade, and altering beaver habitats. Quantifying the impacts of these disruptions, and of

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the now-rebounding beaver populations, has been difficult due to a limited understanding of the spatial and temporal dynamics of beaver populations.

Beaver dams create a mosaic of dynamic wetland patches that strongly alter the regional hydrology, ecology, and sediment flux within river systems (Johnston and Naiman 1987; Naiman et al. 1988; Johnston and Naiman 1990; Rosell et al. 2005). Beaver dams alter flows and store significant volumes of sediment (Fig. 1) (Butler and Malanson 2005; Wohl 2005; Green and Westbrook 2009). They also greatly alter regional ecosystem dynamics by increasing the amount of wetland habitat and beavers preferentially

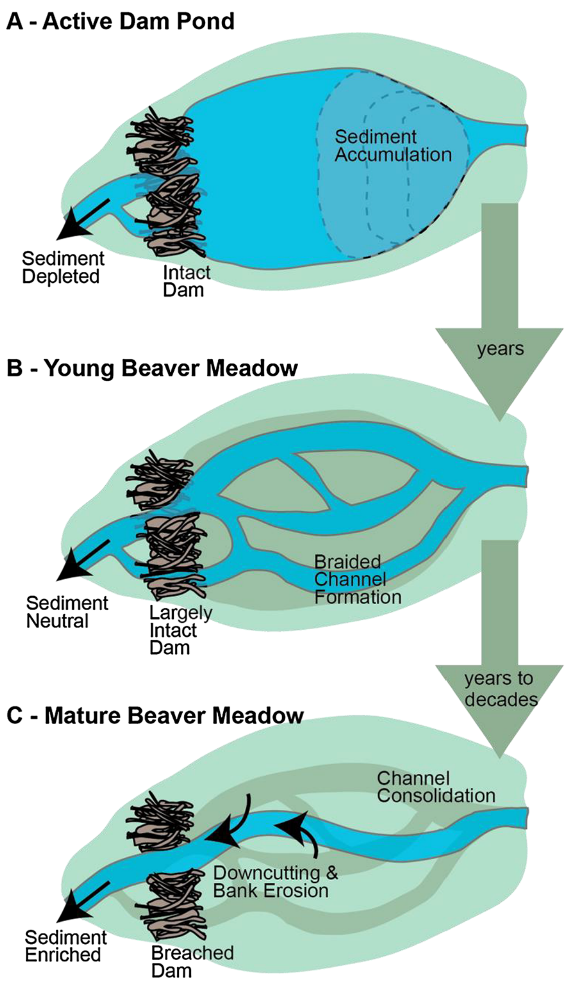


Fig. 1 Conceptual diagrams of beaver dam retention and release of sediment through lifecycle stages; **a** active pond filling, **b** young beaver meadow, and **c** mature beaver meadow. *Arrows* indicate approximate transition times in the watershed based on air photo analysis and examination of standing snags

utilize particular food sources, such as aspen and willow (Rosell et al. 2005; Cunningham et al. 2006; Martell et al. 2006; Demmer and Beschta 2008). As dams are breached by humans, or naturally deteriorate after abandonment, sediment supply to downstream river sections increases (Fig. 1c).

Previous studies have focused on relationships between beavers and specific ecological and hydrologic factors, with many focusing on regional land cover changes and habitat dynamics (Meentemeyer and Butler 1995; Fustec and Lode 2001; Cunningham et al. 2006; Martell et al. 2006; Host and Meysembourg 2009; Little et al. 2012). Far fewer studies have examined the decline and recovery of beaver populations with associated impacts on hydrology, geomorphology, and ecological stream conditions. In a large-scale historical reconstruction of colonial hydrology in the Northeastern United States, Pastore et al. (2010) note the decimation of the beaver population as a significant factor in altered hydrologic regimes, while Wohl (2013) found that the extirpation of beavers reduced carbon storage. As beaver populations recolonize their historic habitats, the patterns they exhibit have a strong influence on stream and wetland dynamics (Naiman et al. 1988; Johnston and Naiman 1990; Hood and Bayley 2008; Burchsted et al. 2010).

While several studies mention the impacts of twentieth century human activities on beaver populations and resulting landscape changes, few have quantified linkages between beaver populations and historical human activity and management (Martell et al. 2006; Little et al. 2012). Wohl (2005) noted the extensive impacts of trapping on Colorado Front Range beaver populations and stream geomorphology, however, the lack of historical records of beaver populations and stream changes precluded quantifiable linkages. Beaver responses to food distribution and habitat dynamics have been compared to local hunting data by Hyvönen and Nummi (2008), but their study period (1980–1998) was relatively short given the slow rate of change in many systems. We only identified one study that quantified long term linkages between beaver management (i.e., trapping), patch dynamics, and vegetation changes; Snodgrass (1997) found that trapping seemed to affect the percentage of active beaver ponds and the addition of new ponds. These studies show the importance of comparing historical beaver populations to historical human activities and management practices to understand the complex relationships between population dynamics and landscape changes.

There are few estimates of beaver-induced changes in watershed-scale sedimentation, primarily because it is difficult to accurately quantify regionally-specific storage rates. Butler and Malanson (1995) estimated that in Pre-European times, total beaver-related sediment storage in North American streams ranged from tens to hundreds of billions of cubic meters. They found that post-European trapping and decimation followed by beaver dam failure eventually led to large increases in sediment yield of North American streams. However, they report estimates of modern sediment retention that are still impressive, at a few billion cubic meters of stored sediment. A study on colonial millpond dams, which may be analogous to the sedimentation impacts of beaver dams, demonstrated the widespread and continued impact of sediment retention from those historical dams on the current geomorphology of Pennsylvania's hydrologic systems (Walter and Merritts 2008). These studies illustrated the need to further quantify how historical changes in beaver populations have affected the sediment yield and geomorphology of North American streams.

Most studies have focused on estimating sedimentation in single beaver ponds (Meentemeyer and Butler 1999; Butler and Malanson 2005; Pollock et al. 2007) although a few have moved towards estimates across whole watersheds and sequences of dams (McCullough et al. 2007; Green and Westbrook 2009; de Visscher et al. 2013). These studies revealed significant insights into predictive relationships between dam area and sediment volume (Butler and Malanson 2005; de Visscher et al. 2013), and declining sediment accumulation rate with increasing age of the dam (John and Klein 2004; Butler and Malanson 2005; Pollock et al. 2007). These relationships are crucial for creating accurate estimates of sediment storage.

Our study quantifies beaver dam dynamics over more than 70 years and links these patterns to human activities and landscape changes. We use remote sensing images to quantify changes in morphological proxies (dam ponds and beaver meadows) for beaver populations. We validate these proxies and analyze the spatio-temporal patterns of beaver population within a mid-sized watershed with historical trapping and logging. We examine linkages between these patterns and both historical trapping and habitat data. Specifically, we hypothesize that beaver populations and associated proxies (harvest and dam count) respond to management and regeneration of key habitats, primarily young aspen stands.

We focused on a single watershed to refine our understanding of the local influence of beavers, while capturing spatial patterns that are generalizable across larger spatial scales (e.g., statewide). We demonstrate the efficacy of a GIS approach to provide quantitative evidence for long-term dynamics and spatial patterns of beaver dams. By linking beaver dam counts with statewide beaver pelt harvest data, and estimated county level pelt harvest, we expand our findings and postulate general responses of beaver population to twentieth century human activities. In addition, mapping the dynamic distribution of beaver dams provides insight into historical beaver movement, including clustering, dam persistence, stream order, and slope. We then demonstrate that temporal beaver dam patterns appear to be linked to resource availability via aspen forest management practices and trapping pressure. Finally, these patterns are used to provide quantitative estimates of sediment retention through time as a function of beaver dam age. Identifying changes in regional beaver distribution is crucial to estimating sediment retention, understanding the progression of ecological relationships, and creating a template to model these long term relationships.

Methods

Site description

Michigan's Jordan River Watershed (JRW) is a state-designated scenic river prized for its recreational trout fishing and canoeing. Its upper portion runs through undeveloped state forest, and is characterized by a wide valley with many islands, channels, and sloughs. The lower navigable portion winds through a mixture of semi-developed private land and marsh before emptying into Lake Charlevoix in the town of East Jordan. The watershed covers approximately 333 km^2 in Antrim and Charlevoix counties, ranging in elevation from 177 to 415 m (Fig. 2). The land cover of this area is 61 % forest, 14 % woody wetlands, 12 % cultivated crops, and 8 % herbaceous/grassland, with developed land as the remaining 5 % (Fig. 2). The

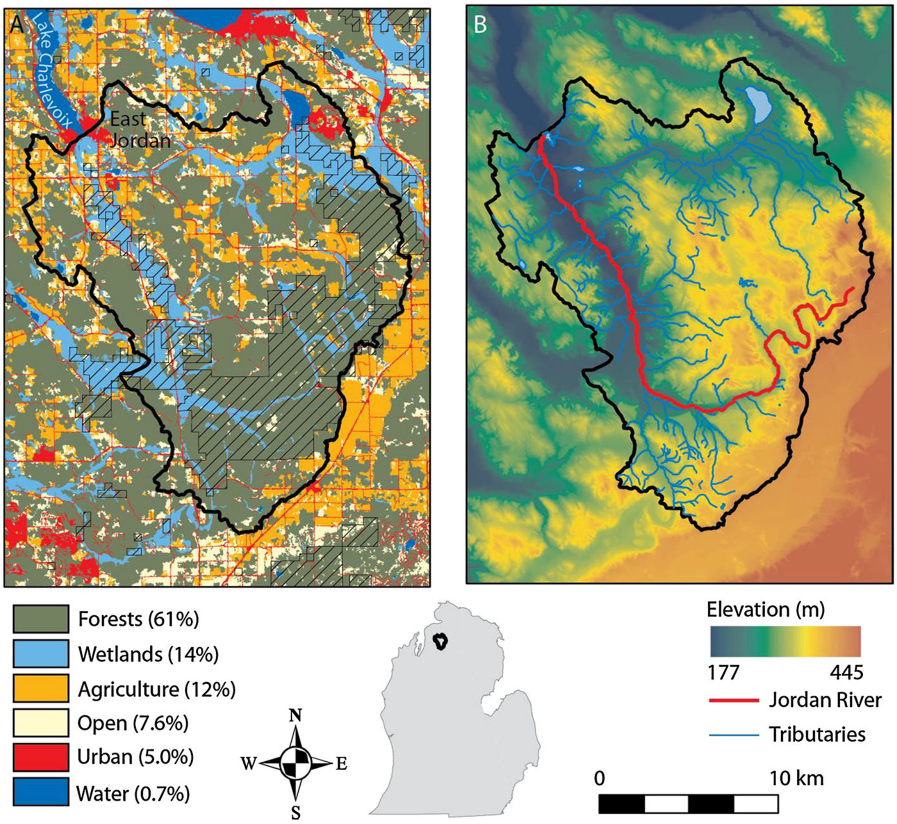


Fig. 2 Map of the Jordan River surface watershed (outlined on the Lower Peninsula of Michigan map) highlighting **a** land use/cover from the 2006 National Land Cover Dataset (Fry et al. 2011) and public lands (*black hatched areas*), and **b** elevation from 1 arc second National Elevation Dataset (Gesch et al. 2002)

forest composition within 1 km of the Jordan River is about 60 % northern hardwoods, 10 % aspen, and 7 % lowland conifers, with the remaining 23 % composed of various forest covers in smaller percentages (<4 %). From its headwaters to its outlet, the Jordan River flows for approximately 56 km.

Due to the underlying coarse-textured glacial sediments, the river is dominated by groundwater inputs and maintains a stable flow with minor increases after rainfall events. The proportion of flow in the Jordan River derived from groundwater sources, as measured by baseflow index, is 87–89 % (Wollock 2003). Forty-six years of USGS stream discharge data at the only gauge within the watershed (#04127800) show that the river rarely floods. The median and standard deviation of daily discharge are 177 and 38.7 m^3/s, respectively, and the maximum recorded daily discharge is just 4.7 times the median flow. This stability of flow is likely related to the longevity and persistence of beaver dams.

The Jordan River's history of trapping and logging, its stable hydrology, and the fact that its upper portion flows largely through state-managed forest make it an excellent demonstration site to examine the responses of beavers to historical beaver trapping and habitat dynamics. From anecdotal reports, the local beaver population was nearly extirpated during the booming fur trade around the turn of the twentieth century. Extensive logging from the 1880s to the 1920s further stressed the beaver population. Agriculture then expanded widely into marginal lands across the region, which subsequently fell out of agricultural management due to an economic downturn in the 1930s. In more recent decades, concerns over sediment load in the river led to various control measures and management strategies (e.g., sand traps), despite an incomplete knowledge of a historical reference condition (Persico and Meyer 2012), or of the role that an expanding beaver population might play in management of sediment transport and retention (Burchsted et al. 2010; Polvi and Wohl 2013).

Remote sensing and GIS

Aerial images from 1938, 1952/1955 (combined to obtain complete coverage), 1963, 1973, and 1981 from the Michigan State University Aerial Imagery Archive were digitized and georectified for the Jordan River watershed. The photos, with scales from 1:20,000 to 1:58,000, were scanned, imported into ArcMap, and referenced to a statewide dataset of roads from the Michigan Geographic Database Library using first-order polynomial transformation. The georectified images were then digitally mosaicked to create five complete synoptic coverages for the area, which we supplemented with five additional periods from Google Earth: 1993 and 1998/1999 aerial imagery, and 2005, 2006, and 2011 satellite imagery.

For each of these ten periods, we located and digitized morphological features related to beaver activity. We identified beaver dam features based on a set of characteristics among consecutive images: a flooded area that appears dry in previous periods; an abrupt transition back to unmodified channel at the downstream end of the impoundment; and the absence of nearby roads to exclude ponding from engineered flow constrictions (Fig. 3). If in subsequent years these features are no longer flooded, they were recorded as abandoned dams or beaver meadows. Similar methods have been used in other studies, with shallow flooded marsh or open water as indicators of beaver activity (Broschart et al. 1989; Johnston and Naiman 1990; Butler 1991; Townsend and Butler 1996; Snodgrass 1997; Meentemeyer and Butler 1999). Points were created for each beaver dam, and polygons were created for each beaver dam pond. Each dam was assigned two IDs in a database: one for the dam location, and another for each unique instance where

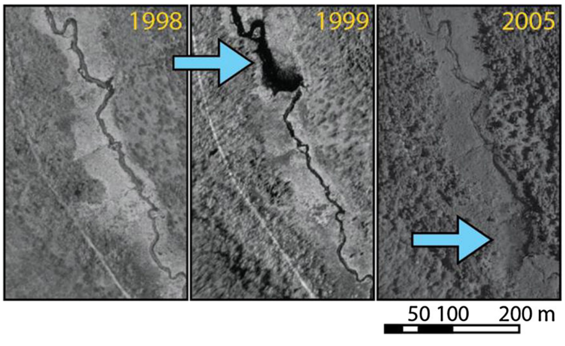


Fig. 3 Time sequence of aerial imagery illustrates the development and subsequent abandonment of beaver dams. In 1998 there are no dam features. A dam pond is present in the 1999 photo, to the right of the arrow. By 2005, the beaver pond has become a meadow and a new dam has appeared (new incidence) about 200 m downstream

the dam was identified (dam incidence). Thus, analysis of incidence IDs provides a temporal record of the total number of times a dam is present, while the location ID provides a spatial record of the different locations where dams occurred.

We did not attempt to discern whether flooded dams were active or abandoned due to the often gradual process by which abandoned dams fail and eventually drain, and the difficulty of identifying food caches signifying beaver activity. We also omitted non-dammed bank dens from our counts, since these are generally not identifiable by aerial/satellite imagery, and are negligible in terms of sediment storage. The Jordan's stable flow regime contributes to longer-term stability of beaver dams and increases the likelihood of full sampling by our ten periods, since catastrophic flooding and destruction of dams is unlikely. The Jordan River's stable flows also increase the likelihood that observed flooded areas are actually ponds behind beaver dams rather than seasonally flooded riparian areas unaffected by beaver.

In August 2011, we conducted a ground-truth survey of approximately 10 % of our identified dams. In all cases, a lodge or dam structure was confirmed in the field for each aerially-identified old or active beaver dam site. We also located three smaller dams that had not been identified via aerial imagery, due to their small size and proximity to roads and/or larger dam features. This suggests that our aerial imagery analysis underestimates the total number of beaver dams in any given year. However, our consistent application of identification methods likely assures that the overall trends in beaver population have been captured.

Comparing population estimates to harvest and pelt price data

Records of statewide annual beaver harvest (1931–2010, Michigan Department of Natural Resources [MDNR] tagged beaver tally and survey of trappers), number of trappers (1931–2010, MDNR, tally of licenses sold and survey of trappers), and historical beaver pelt prices (1930–2007, Wisconsin Department of Natural Resources Wildlife Surveys, prices CPI adjusted to 2007) were compared with our dam counts. In addition to bivariate correlations across the time series, these data were used to build and select multiple linear regression models to better understand variations in dam counts through time.

Dam site habitat analysis

We analyzed the spatio-temporal patterns of beaver dams to determine a range of characteristics associated with dam placement. First, we quantified the temporal recurrence of dams across the watershed to identify frequently inhabited sites. Second, within each image series, we tested the hypothesis that dam placement was spatially clustered rather than random. Finally, we examined landscape characteristics (i.e. slope, stream network position, and forest composition) that may affect dam site selection.

Dam site recurrence was quantified across multiple imagery years within the study period. A query of the count of incidence IDs for each location ID provides the temporal recurrence of occupation of a particular location across our 10 image sets. For this analysis we did not distinguish between re-colonization or continued occupancy across consecutive image sets.

To understand the spatial distribution of beaver dams over time, we tested the null hypothesis that the dams were randomly distributed. We first calculated the distance between the center point of each dam and its nearest neighboring dam for each year with data. We then applied an "average nearest neighbor" statistical analysis within ArcGIS, which compares the observed mean distance between dams for each year to the expected mean distance between dams if the distribution along the river was random. The analysis for each year then gives us a p value, which is the likelihood of random dam dispersal. We evaluated this ratio over time to test if the beaver dams began clustering directly following their near extirpation, or whether clustering developed with increasing population.

To study the impact of slope in beaver dam site selection, we identified the center of each dam pond in GIS, and created a circular 50 m buffer. We calculated the average slope within each buffer zone from the one arc-second USGS national elevations dataset (NED) DEM (resolution $\sim$30 m). The mean slopes surrounding each dam pond location were plotted against time to explore the influence of slopes on beaver dam site selection. As the typical impoundment (<100 m channel length) is far smaller than the typical distance between topographic contours in this region (500–1,000 m), we assumed that beaver dams themselves did not significantly influence measured DEM characteristics.

We evaluated dam locations against Strahler stream order (Strahler 1957) to evaluate whether and how site selection has changed over time. In addition to stream order, we assessed the role of stream connectivity in dam site selection by adding a "degree" designation to the original Strahler stream order. We measure the degree as the number of connections away from the main stem Jordan. For example, if a first order stream connects directly to the main stem, it is labeled "1st, 1°." Alternately, if a first order stream connects to a tributary that then connects to the Jordan, it is labeled "1st, 2°," and so on. Order and degree were assigned to all dams in the dataset, except for the 1938 and 1973 series, since the number of identified dams in those years was too small to provide an accurate distribution (see "Results" section). We then plotted the percentages of dams grouped by tributary order and degree of connectivity versus time.

To relate beaver population and spatial location to food-source preferences, we obtained a recent version (March 20, 2013) of the MDNR's forest inventory for the region (Dan Heckman, personal communication). The inventory contained polygons indicating the dominant species within a tree stand, and attributes of that stand including stand acres and year of stand origin (i.e., maximum age of the stand). Of the common beaver food resources (willow, poplar, aspen, etc.) only aspen were explicitly separated from other species in the stand inventory. We created a 1-km buffer of the Jordan River and its tributary network, and extracted the polygons within this buffer for further analysis. We then computed the total yearly area of all aspen stands with ages ranging from 1920 to 2011, grouped into age categories (0–9, 10–19, 20–29, and >30 years), and then compared this to the beaver dam counts within each imagery series. Aspen area was also used as an input to a multiple linear model describing beaver dam counts (described below).

Beaver dam count modeling

We built linear regression models to describe beaver dam counts using both human predation pressure and food resource availability. Human predation was estimated using statewide data of beaver harvest, pelt price, and trapping licenses. Food resources were described using aspen stand acreage within 1-km of the Jordan River network.

Beaver are known to prefer younger aspen as a food source (Thompson 1988; Naiman et al. 1988; Beier and Barrett 2013), however the available stand data are characterized by maximum stand age, rather than average stand age. Thus, to identify what age of aspen stand acreage should be included, we conducted cross-correlation analysis using Pearson correlation coefficients between beaver dam counts (estimated by this study) and the binned time series of aspen acreage (described above). The best-correlated combination of temporal lag and aspen age bin was then selected to serve as a predictor variable in a linear regression model.

The second aspect of this model is human predation, as described by three time-series datasets of beaver harvest, pelt price, and trapping licenses. Each of these statewide data series was used in combination with the time-lagged aspen data in a multi-parameter linear regression model on dam counts. We tested all combinations of one to four predictor variables (lagged aspen acreage, beaver harvest, pelt price, and trapping licenses) using 15 models. The model with the best fit to the data, as determined by adjusted R^2, had two variables:

$$N_{dam} = C_1 \times A_{t-n} + C_2 \times P_t + C_3 \qquad (1)$$

where N_{dam} is the number of dams at a given time t, A is the area of aspen (ha) of a given age group at time t-n, where n is the number of years lag selected by cross-correlation; P is the price of beaver pelts (in 2007 dollars) at time t, and; C_1, C_2, and C_3 are empirically fit coefficients. The constants were then fit using automated parameter optimization (rather than linear regression), subject to the constraint that $N_{dam} > 0$.

Sediment retention modeling

The GIS-derived inventory of beaver dams was used to generate two estimates of sediment retention in all beaver ponds at each time step. We estimated the age of each pond at its first appearance as half of the time interval between this occurrence and the previous image. In cases where the pond was not visible in an intermediate image, it was assumed that a new dam had been built. The average of all dam ages in our study was used as an estimate of age for the two identified dams in 1938, our first aerial image series. Equations developed by Butler and Malanson (1995) (Eq. 2) and Pollock et al. (2007) (Eq. 3) to estimate sediment retention were then applied to our dataset and the accumulated sediment was summed for all dams into a total for each year.

$$V_{B\&M} = Age \times Area \times e^{-2.99-0.71\ln(Age)}/100 \qquad (2)$$

$$V_{Pollock} = Age \times Area \times 0.3835 \times Age^{-0.9093} \qquad (3)$$

where V indicates the volume of sediment (m^3) predicted by each model, Age is the age of each pond in years, and $Area$ is the area of each pond (ha).

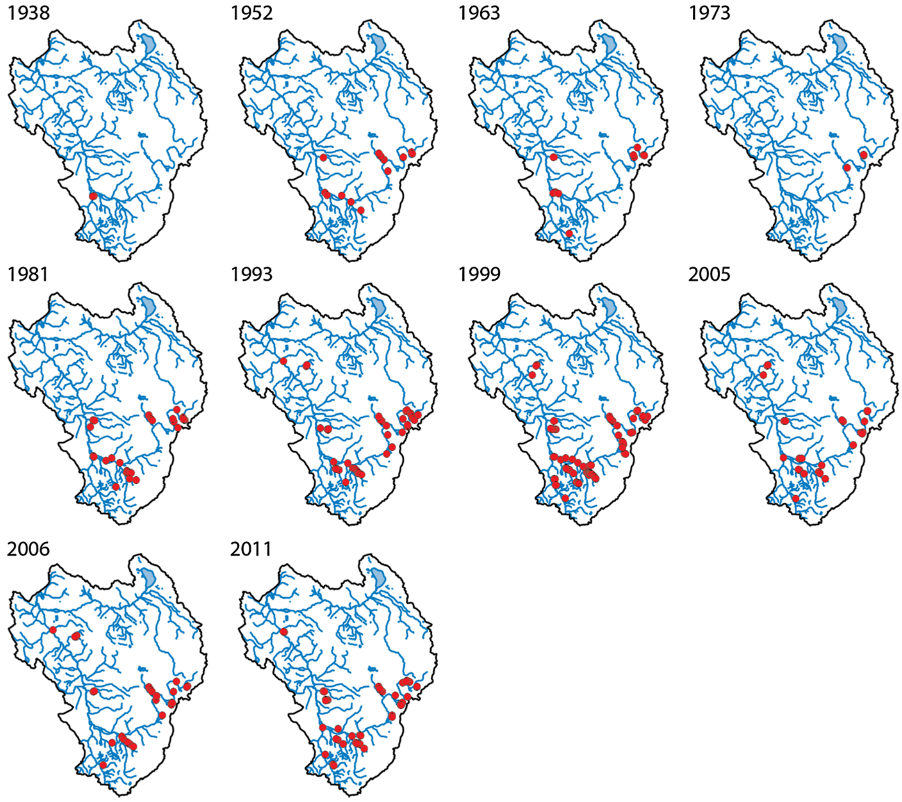
Studies have noted the importance of considering successive beaver dam sequences along a channel, such as the sequences we mapped, when predicting sedimentation rates within watersheds. For example, de Visscher et al. (2013) found that sediment tended to thicken downstream in successive dam sequences, and used detailed sedimentation measurements to analyze rates and thicknesses of sedimentation across these sequences. However, for this analysis we assume that sedimentation rates in individual dam ponds are not affected by upstream or downstream dams.

Results and discussion

Aerial dam identification and temporal dynamics

Our analysis of dams in the Jordan River Watershed (JRW) indicates that the number of dams is generally increasing over the past 75 years, consistent with the rebound of a post-trapping population (Martell et al. 2006). In total, 142 dam sites were identified, representing 271 dam incidences (Fig. 4). The dams are located mainly along and around the upper Jordan River, with a few scattered dams along the tributaries of the lower Jordan River. No dams were found on the main lower Jordan channel, since any beaver dam attempts along this part of the river are removed to ensure recreational boating navigability. The number of beaver dams increased from 2 to 49 between 1938 and 2011, with a few spikes and dips in the dam count (Fig. 5). Most notably, the number of dams increased 7-fold between 1973 and 1998–1999. Johnston and Naiman (1990) found a North American average of 3.2 beaver dams per colony, and 5.2 beavers per colony.

Fig. 4 Spatial distribution of beaver dams from 1938 to 2011



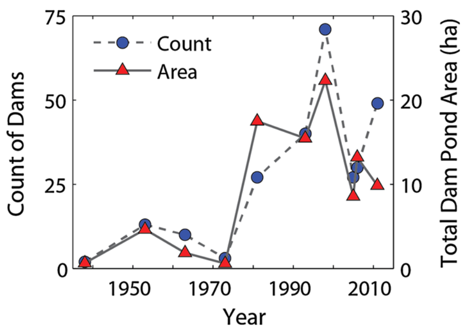


Fig. 5 Time series of dam count and impoundment area from 1938 to 2011

Applying these averages to our dam count, we estimate that the beaver population in the JRW has increased from 3 beaver in 1938 to 80 beaver in 2011. At its peak in 1998–1999, we estimate the population was approximately 115 beaver.

The density of dams per kilometer of river length increased from 0.02 to 0.45 dams/km between 1938 and 2011, with an average density of 0.22 dams/km. This is comparable to Robel and Fox (1993), who found beaver dam densities along 12 riverine habitats in Kansas ranging from 0.08 to 1.40 dams/km.

The total impounded area behind beaver dams largely followed the trend in dams, with the total area covered by beaver dam impoundments increasing from 0.65 to 9.86 ha between 1938 and 2011 (Fig. 5). Individual impoundments were approximately 0.35 ha, with few larger than 1 ha. Typical beaver impoundments in the Jordan range between 0.01 and 0.5 ha. This is on the low end of impoundment sizes noted by Cunningham et al. (2006), who found that impoundments in Acadia National Park, ME, ranged from about 0.37–2.16 ha.

The rate of land area impounded by beaver dams (measured by land area converted to open water) was 0.04 m^2/ha/year for the JRW. This is comparable to rates reported by Snodgrass (1997) of 0.18 m^2/ha/year in the Savannah River watershed in South Carolina, though much lower than the rates of Johnston and Naiman (1990), of 16.73 m^2/ha/year on the Kabetogama peninsula in Voyageurs National Park. The variability is likely due to differences in landscape morphology and characteristics between the three

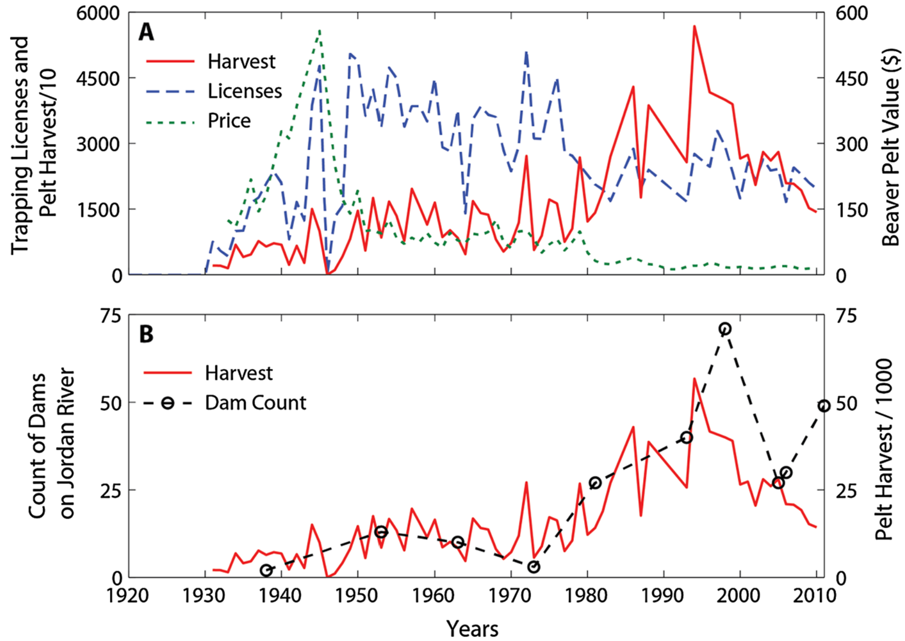


Fig. 6 Time series of human and economic factors that influence the number of beaver dams. **a** Beaver pelt harvest, trapping licenses, and beaver pelt prices from datasets across Michigan; **b** **s**tatewide pelt harvest plotted against dam counts from the Jordan River Watershed (Pearson $r = 0.88$)

study locations as well as how the sites are managed. The Kabetogama peninsula is dominated by lakes and wetlands, and varies in elevation from 340 to 415 m. The Savannah River has a similar relief (ranging from 60 to 128 m) (Lanier 1997), while elevations along the Jordan River range from 177 to 415 m, indicating that pond area may be restricted by valley slope. Additionally, the Jordan River and Savannah River watersheds are characterized by higher human settlement and are subject to beaver trapping, unlike the relatively protected Kabetogama peninsula which lies within Voyageurs National Park.

The comparable impoundment rates of the Jordan River and the Savannah River watersheds, and the much larger impoundment rate of the Kabetogama, suggest that site geomorphology and human influence factor strongly into the impoundment rate of rebounding beaver populations. In areas relatively undisturbed by humans, such as National Parks, resource competition for willow and other food sources by large herbivores such as elk can also limit recovery or in some cases cause a decline in beaver population (Polvi and Wohl 2011). However, in landscapes more affected by human activity, the population dynamics are more likely to experience strong variations that are directly related to changes in human activities and management (Snodgrass 1997; Hyvönen and Nummi 2008).

Management and economic influences

We compared the number of Michigan trapping licenses issued per year against annual beaver harvest and pelt value (Fig. 6a). We found that at the decadal level from the 1930s to the 1990s, harvest was correlated to licenses (Pearson $r = 0.6$ to 0.9), but show only a weak association over the 75-year period of our data (Pearson $r < 0.2$). Trapping licenses increased from less than 1,000 in the early 1930s to about 5,000 in the 1940s, likely in response to a spike in pelt prices, and then began to slowly decline in the 1950s after pelt prices dropped. Harvest substantially increased around the early to mid-80 s, despite the number of trapping licenses remaining relatively steady between 2,000 and 3,000, while the pelt price collapsed. This may be the result of a simultaneous increase in prey abundance which can result in more successful kills per trapping line (Hyvönen and Nummi 2008).

We found that the number of identified dams in the JRW correlates strongly to the twentieth century trend in annual Michigan beaver pelt harvest (Fig. 6b, Pearson $r = 0.88$). This similarity between the Michigan statewide beaver pelt harvest and the Jordan River beaver dam count is remarkable, given their vast spatial differences. The strong correlation of beaver dam count to statewide trapping harvest trends suggests that our aerial identification of dam counts reasonably captures beaver population trends within the Jordan River watershed. The Jordan's history of trapping and logging followed by a short period of marginal agriculture from the 1900s to the 1940s is similar to much of the Upper Great Lakes Region. Therefore, it is likely that the results from the Jordan reflect generalizable patterns of beaver response to human activities (trapping and habitat loss) throughout the state and other regions with similar histories of land use change and human activity.

Other habitat/ecological factors also play a role in beaver population dynamics. Ingle-Sidorowicz (1982), noted that the beaver population in Ontario, Canada, continued to increase along with increasing beaver harvest rates. They suggest that the increasing beaver population was related to a regional expansion in deciduous forest and an increase in favorable beaver habitat caused by human activities. The rebound of beavers in the Jordan River, reflected also by beaver harvest trends, may be controlled by similar habitat/ecological factors, in particular increasing habitat size and suitability resulting from the decline of logging and marginal agriculture. We explore how multiple factors can be combined to model changes in the number of beaver dams below (see "Beaver dam count modeling" section).

Dam re-occurrence patterns

Our digitized dams database was used to identify locations along the Jordan River that have been colonized by beavers multiple times within the study period. Of the 142 dams, 64 were identified as recurring sites (Fig. 7). Most dams were occupied in just two time periods (n = 30), but a few were occupied in as many as 5–7 time periods (n = 9). Fustec and Lode (2001) and Naiman et al. (1988) both noted that beavers tended to rapidly colonize new sites and continued to occupy sites with suitable habitat. Therefore, the recurrence of these sites may indicate that the sites are preferable, offering suitable habitat.

Frequently inhabited sites were along tributaries rather than the main stem Jordan River. These tributaries have lower flow and may fill with sediment more slowly, or dams fail less frequently, providing more suitable long-term habitat. We also observed that the few persisting dams on tributaries to the lower navigable portion of the Jordan River seem to have a

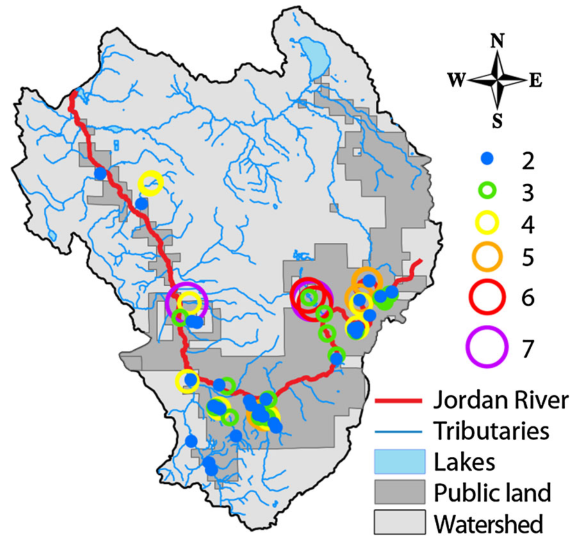


Fig. 7 Number of times each re-colonized beaver dam site was occupied based on the 10 imagery series from 1938 to 2011 (only sites occupied at least twice shown)

high recurrence rate in contrast to their sparse distribution. This may be an effect of higher human density on the lower Jordan, and the resulting restriction of both beaver movement and choice of habitat.

The majority (87 %) of beaver dams identified in our study fall within the typical slope range for beaver habitation (1–4 %) (Fig. 8, Thompson 1988; Beier and Barrett 2013). However, the number of dams in steeper slope areas increased during years with high dam counts. This follows logically—as density increases, beavers are forced to choose less suitable sites and expand into areas with steeper slopes. Eleven dams were located in areas of relatively extreme slopes (>8 %). This may be attributed to the resolution of the DEM used to calculate average slope relative to the nature of the features of interest. In smaller headwater streams in high relief areas, the 50 m buffer zone can span beyond the pond and encompass the higher slopes of the narrow valley walls, yet this area is represented by few DEM cells. Regardless, the occurrence of dams in higher slope areas is coincident with years of high beaver dam counts. These data indicate that slope seems to be a consistent factor in beaver site selection, likely due to increased competition and ability to maximize foraging area with a larger, more stable pond (Beier and Barrett 2013).

The mean distance between dams was approximately 1 km in the 1950s through the late 1960s (Fig. 9a), showing random dispersal (p values 0.50

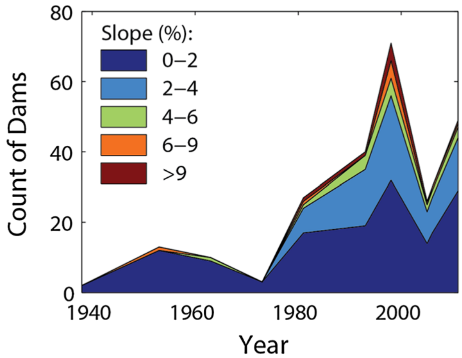


Fig. 8 Number of beaver dams categorized by percent slope. Dams appear in greater number in higher slope areas during years with larger counts

and 0.81, respectively). As the number of dams increased, the distance between dams dropped to a fairly stable value between 250 and 500 m. Indeed, beginning around 1981, dams were significantly clustered (all p values <0.0001), presumably as areas of favorable habitat were found and exploited. John et al. (2010) found that beaver colonies began to cluster after a seemingly chaotic initial dispersal. Due to the territorial nature of beavers, distant sites are often colonized before nearer sites in a rebounding beaver population, with the interconnecting river progressively occupied by dispersers from each site (Fustec and Lode 2001; Bloomquist et al. 2012). Our study supports that when beaver population is low, the distance between sites is longer. The existing beaver dams may also help create suitable surrounding wetland habitat for additional beaver dams nearby, thus promoting later clustering.

As might be expected, across our study period, beaver dams occurred primarily on first order tributaries (Fig. 9b). Other studies have also found that there is a larger proportion of dams on first and second order streams than on higher stream orders (Snodgrass 1997; McCullough et al. 2007). Dams along lower flow tributaries may fill with sediment more slowly and may also have less risk of breach due to lower flows, allowing for a longer period of inhabitance before abandonment.

Our analysis shows that tributary connectivity may be more important than stream order in beaver dam site selection. Specifically, the percentage of dams on 1° tributaries to the Jordan main stem increased from 53.8 to 61.2 % between 1952 and 2011. This increase

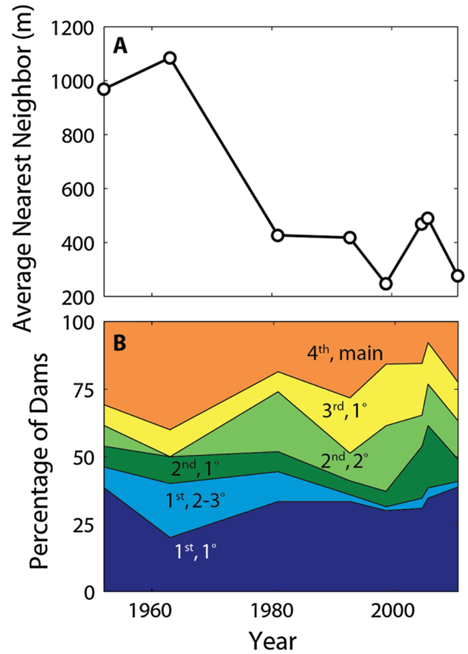


Fig. 9 **a** Observed mean distance between dams through time. **b** Percent distribution of beaver dams in different order tributaries. Each shaded area corresponds to a Strahler stream order (labeled 1st–4th) and degree of separation from the mainstem of the Jordan River (labeled main, 1°–3°). The 1938 and 1973 data sets were excluded because of low sample size

was across 1st, 2nd, and 3rd order streams. The number of dams on tributaries with 2° and 3° connections to the Jordan River remained low, at less than 20 %, throughout the study period. This suggests that tributaries in direct connection to the main stem are more suitable for dams in this system, despite some having higher flow. Indeed, Scrafford (2011) noted that beaver colonies tended to be located near or on tributaries connecting to the main stem, possibly because those locations were more sheltered. Alternatively, this shift into the direct tributaries may be a response to the progression of post-logging forest succession along the main stem Jordan. Aspen population growth surged in post-logging areas along the main stem upper Jordan, offering enhanced habitat and incentivizing dam building along the main river (Thompson 1988). As forest succession proceeded, the young aspen population would have declined and the beavers may have moved off the main river in response.

MDNR records of aspen stands within the Jordan River State Forest show several peaks in number of young stands in the 1930s, 1980s, and late 2000s (Fig. 10a). Both peaks and dips in young aspen stands tend to occur 7 to 12 years prior to similar fluctuations in the number of identified beaver dams (qualitatively visible in Fig. 10a, and quantified in Fig. 10b).

There is a strong relationship between beaver dam counts and the total area of young aspen stands in the watershed (Fig. 10b). Indeed, the time series of beaver dam counts are highly correlated (Pearson $r = 0.74$) with the area of young aspen stands between 0 and 9 years of age with a time lag of 8 years. The beaver dam count can also be related to area of aspen of age 10 to 19, with no lag, although this was a weaker correlation (Pearson $r = 0.55$). The 8 year time lag found in this study is dependent on how stand age is quantified (here defined as maximum stand age). Specifically, the time lag most correlated to dam counts would be different if the average stand age were known. We use an 8-year time lag of young aspen (i.e. 0–9 years of age), representing suitable habitat availability, to further model beaver dam counts as detailed below in "Beaver dam count modeling" section.

Young aspen are thought to be an especially appealing food source for beavers, and therefore may be an important driver of beaver population (Naiman et al. 1988; Thompson 1988; Beier and Barrett 2013). Land clearing and associated aspen regeneration, may act as positive perturbation that is favorable for beaver population expansion (Little et al. 2012). The opposite is true for times with minimal aspen regeneration, presumably as the crop of aspen matures and fewer patches of young growth are available as a food source. Host and Meysembourg (2009) similarly report a time-lagged relationship between aspen age and beaver population in Voyageurs National Park, MN. Our study further suggests that regional aspen dynamics contributes to trends in beaver populations.

Our results show that the majority of dam sites lie in close proximity to aspen stands (53 % of dams were within 50 m of stands, not shown). Other studies have found that beavers often reach their highest densities where natural aspen regeneration occurs along shorelines (Thompson 1988; Martell et al. 2006; Barnes and Mallik 2013). As an early-successional species, aspen stands tend to age and not renew themselves without disturbance or management, which suggests that post-disturbance regeneration may initially be favorable for beavers (Thompson 1988; Little et al. 2012). After logging waned in the 1920s, a surge of aspen growth for two decades would have provided favorable habitat for the regional beaver population to regain a foothold after extirpation: a pattern corroborated by studies conducted in similar post-logging/post-fire habitats (Ingle-Sidorowicz 1982; Naiman et al. 1988; Cunningham et al. 2006; Little et al. 2012). The more modern aspen regeneration in the JRW may be partially related to MDNR forestry management, and stand ages may reflect years of stand harvest cuts. If so, this demonstrates a possible link between current forest management and the beaver population. However, it is also difficult to disentangle the importance of

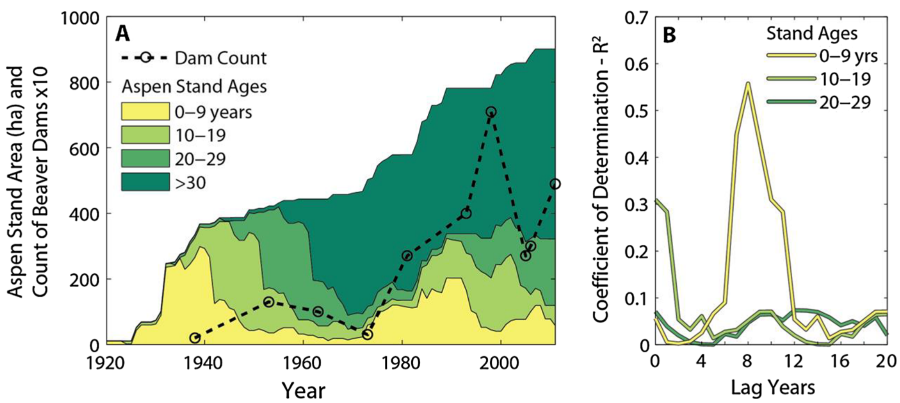


Fig. 10 **a** Age distribution of mapped aspen stands through time, overlain with the beaver dam counts. The cumulative increase in stand age is noted, with peaks and dips in the amount of young regenerating aspen preceding peaks and dips in beaver dam counts. **b** Plot of the coefficient of determination (R^2) as a function of number of years lagged for each of the three younger age bins of Aspen stands

the presence of aspen from other habitat variables that tend to occur simultaneously with aspen. Both beavers and aspen flourish in low-lying, semi-open early successional areas that are close to water, so their co-occurrence could be related to similar habitat needs.

Beaver dam count modeling

We tested three different measurements of human predation pressure (pelt price, beaver harvest, and issued trapping licenses) along with aspen area in a predictive model of the number of beaver dams. We found that time-lagged aspen area along with pelt price provided the best overall model ($R^2 = 0.87$, adjusted $R^2 = 0.83$, p value <0.001, see Fig. 11). This model explained 12 and 22 % more variation than two-parameter models using time-lagged aspen area along with either licenses or harvest (rather than pelt price), respectively. This simple model (which when calibrated such that $N_{dam} \geq 0$ had an $R^2 = 0.86$) described all of the essential shifts in beaver dam counts through time. Early on, when young aspen stands were plentiful (Fig. 10a), beaver populations appear to have had a difficult time recovering from their historic lows, likely due to high trapping pressure as a result of very high pelt prices. Later, as pelt prices, and therefore predation pressure declined, the beaver were able to take advantage of smaller overall increases in habitat availability. More specifically, the highest beaver dam count in our study occurred in 1999, when pelt prices were at their lowest and the area of young aspen 8-years prior was at its 2nd highest. Conversely, in 1952 the beaver dam count was lower than modelled, even though time-lagged young aspen area was high and pelt price was relatively low. This difference could also be due to a natural limitation in population recovery rates from near extirpation during these early years, which is not included in our model.

Sedimentation applications

Beaver dams can also significantly impact the ecosystem of a watershed by altering the sediment regime. We used equations developed by Butler and Malanson (1995) and Pollock et al. (2007) to estimate the total sediment sequestered in the watershed by active beaver dams during our study period to be approximately 2,000 to 100,000 m^3 (Fig. 12). Across all time steps, the two estimates differ by between 24 and 46 %. This analysis provides an example of the role that beaver dams play in the sediment dynamics within a watershed. However, limitations in interpreting the quantitative estimates of sediment retention should be considered. In their analysis, Butler and Malanson (2005) point out that sedimentation rates for beaver ponds appear to be site-specific and note that even within their study area in Glacier National Park, the rates for individual ponds varied by an order of magnitude. While the range of our two estimates is

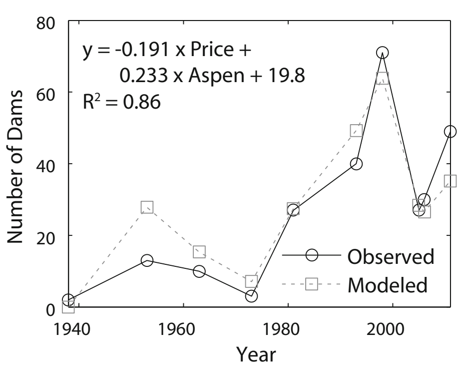


Fig. 11 Plot of model-predicted dam count (*dashed*) in the Jordan River valley along with observed number of dams (*solid*). Note that optimization of model constants was done to constrain the number of dams to be greater than 0. Prices are in 2007 Dollars ($), and Aspen units are hectares (ha) of 0–9 year old stands with an 8 year time-lag

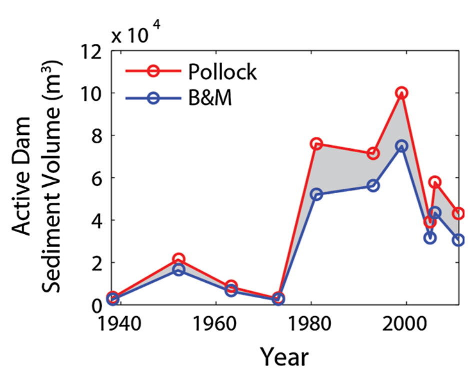


Fig. 12 Plot of total sediment volume retained in active dams, as estimated via equations from Butler and Malanson (1995), labelled B&M, and Pollock et al. (2007). The region between the two estimates is shaded to indicate a likely range of sediment volume retained in this study

less than the variability in the data that produced the equations, they are likely a reasonable predictor of accumulated sediment because we are estimating sediment retention at the watershed scale and thus averaging across the variability among individual dams. It should also be noted that Eqs. 2 and 3 were derived from studies conducted in regions that are in general more climatically and topographically similar to each other than to the JRW.

Future work to more carefully quantify the sediment retention behind JRW beaver dams will help refine estimates of watershed-average retention rates. The two empirical equations used here are both based on cores taken from current and former beaver ponds. Additionally, Kramer et al. (2012) used ground penetrating radar to both identify and quantify volumes of buried beaver dams, as well as to estimate valley aggradation rates. These techniques could be used to refine regional and watershed-specific estimates of sediment storage. Additionally, the spatial connectivity of dam sequences should be considered to better account for sediment supply within storage estimates.

Conclusions

By analyzing aerial and satellite imagery spanning a >70 year period, we identified a general increase in beaver dams, suggesting that the population has been recovering from trapping and habitat loss since at least 1938. Comparison with Michigan's statewide trapping data substantiates our trends and shows linkages between variations in human activity and the beaver dam count, which can be used to estimate beaver-related impacts on the landscape.

Our spatial analyses of the rebounding beaver population show the development of behavioral and habitat-related distributional patterns. Beaver activity has become more spatially clustered over time, which may be attributed to territoriality, the expansion of family colonies, and the self-perpetuating nature of beaver wetland patches. The beavers also seem to preferentially colonize tributaries directly connected to the main stem. This may be related to sedimentation or the progression of post-logging forest succession. Areas of recurring beaver dam colonization were identified, with an observed tendency for directly connected tributaries. A slope analysis revealed that the Jordan beaver population inhabit steeply sloped areas only in years of high beaver dam density.

An analysis of DNR forestry data suggested that the spikes and dips in the number of beaver dams are temporally related to the regeneration of young aspen growth and the intensity of predation by trappers. In particular, a two-parameter linear model including acreage of young aspen stands 8 years prior and current-year beaver pelt price described yearly dam counts with an R^2 of 0.86. Furthermore, sediment retention, an important ecosystem service provided by beaver dams, was estimated through time using empirical equations from two other studies. Mechanistic modeling will likely improve this estimate.

Analysis of aerial and satellite imagery is relatively simple and cost-effective compared to field intensive surveys of beaver population. The striking correlation with trapping harvest records could also be utilized in areas where such records are available to recreate and estimate historical beaver influences on regional stream conditions, specifically sediment retention. As demonstrated here, these methods could be used in appropriate watersheds to estimate regional patterns in beaver populations.

The dynamic spatial and temporal changes of beaver populations are cited by ecological and hydrological modelers as one of the most difficult parameters to characterize (McCullough et al. 2007). By understanding and accurately mapping beaver behavior and the distributional patterns of dams over time, we demonstrate a template by which regional patterns of sedimentation can be quantified, understood, and utilized by natural resource managers. Specifically, records of young aspen populations could likely be used as proxies to anticipate spikes and dips in beaver populations within watersheds, which in turn could be used to predict effects on sediment retention.

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