Reintroduced Beavers Rapidly Influence the Storage and Biogeochemistry of Sediments in Headwater Streams (Methow River, Washington)

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Abstract

North American beavers (*Castor canadensis*) were targeted within North American headwater landscapes by European loggers and fur traders in the 19th century, reducing beaver populations to near extinction by 1900. The extirpation of beavers from river networks has had profound effects on riparian zones, including channel geomorphology, temperature regimes, sediment storage, channel-floodplain connectivity, carbon storage and nutrient dynamics. Consequently, reintroducing beavers has been provisionally implemented as a restoration approach within some watersheds. We characterized how reintroduced beavers influence the short-term dynamics of organic material accumulation within the sediments of 1st and 2nd order streams within the Methow River watershed of Washington State. In collaboration with the Methow Beaver Project, we identified four creeks where they had reintroduced beavers within the past five years, as well as a control non-beaver pond. At each site, we collected shallow sediment cores from upstream, downstream, and within beaver ponds, and then measured organic material via elemental analyses of sediment carbon (%C) and nitrogen (%N) content. We compared those samples to sediments accumulated in local pond areas not created by beaver activity. Our results show greater organic C and N content of sediments in beaver ponds than non-beaver ponds. C/N ratios indicate elevated accumulation of allochthonous organic material in beaver impoundment sediments that would otherwise not be integrated into headwater streams from the terrestrial landscape. These findings suggest that the reintroduction of beavers could be an effective means to promote restoration of whole ecosystem function.

Keywords: beaver reintroduction, river restoration, ecosystem functioning

Introduction

Freshwater systems are some of the most imperiled on the planet (Dudgeon et al. 2006, Abell et al. 2008). Restoring the functionality of these environments will require the persistence of essential species within them, and also the preservation of the biogeochemical heterogeneity that naturally occurs within river networks (Wohl et al. 2005, Palmer et al. 2014). Because beavers (*Castor canadensis*) are known to be significant ecosystem engineers, conservationists and wildlife managers have suggested that the reintroduction of beavers into watersheds that previously supported native beaver populations may benefit those environments at an ecosystem scale (reviewed in Rosell et al. 2005, Burchsted et al. 2010, Pollock et al. 2014). Particularly in river basins experiencing multiple landscape-scale anthropogenic stressors (i.e., agriculture, timber harvest, flow alteration, livestock grazing, fire, and climate change), beaver reintroductions could potentially mitigate the impacts of some human disturbances, buffering systems as they become increasingly modified (e.g., Pollock et al. 2007, Law et al. 2016, Puttock

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et al. 2017). However, little research has focused on the short-term (less than five years) effects that reintroduced beavers have on sediment biogeochemistry in low-order streams, particularly in montane areas of the western United States.

The effects of dam building by beavers on riparian geomorphology, ecology, and ecosystem function has been well documented; a recent literature review by Gibson and Olden (2014) identified several hundred papers published over the past century on these topics in both temperate and dryland ecosystems. Of particular relevance to our study are the sediment biogeochemical impacts of newly established dams in incised, low-order, mountain streams. Basic models can be used to predict how beaver dammed streams develop over time from the initial pond stage to complex riparian systems that include multithread channels and wetland networks (Pollock et al. 2014). Beaver wetlands and meadows often retain sediment, water, nutrients, and carbon in riparian areas that otherwise would not have substantial storage potential (Sutfin et al. 2016, Wegener et al. 2017). Carbon accumulation in headwater streams is often linked to organic-rich debris and sediments impounded behind beaver dam complexes, providing energy to bolster local riparian and aquatic ecosystem diversity and function (Naiman et al. 1994, Johnston 2014).

Within the field of restoration ecology over the past decade, native species reintroduction projects within aquatic ecosystems have become a more common tool used by wildlife managers and conservation organizations, often in tandem with habitat and flow restoration approaches (NOAA Fisheries 2011, US Fish and Wildlife Service 2017). However, species reintroductions often focus on reestablishing a single species' former abundance and distribution within a region, in step with the Endangered Species Act (ESA) guidelines (i.e., humpback chub [*Gila cypha*] in the American Southwest, US Fish and Wildlife Service 2010). While that approach is necessary for many species, modern conservation efforts have additionally concentrated on reestablishing ecosystem processes (i.e., system metabolism, organic matter decomposition, or secondary production within rivers) within degraded environments, using strategic species reintroductions to promote self-sustaining positive outcomes for entire food webs (Marshall et al. 2014, Nummi and Holopainen 2014, Wohl et al. 2015, Law et al. 2016). Beavers are strong candidates for reintroduction because there were approximately 60–400 million beavers within North America prior to European colonization, and by 1900 the species was nearly extinct (Seton 1929, Jenkins and Busher 1979). Despite subsequent population increases in many watersheds in recent decades, opportunities to expand contemporary beaver populations' range and abundance to more closely reflect their historical influence on the landscape are numerous. Beaver bioengineering has the potential to be a useful watershed conservation tool, and the reintroduction of beavers may hasten the beneficial effects of their dam building.

Our aim was to understand the impact of reintroduced beavers on carbon storage in headwater stream segments, which would otherwise store little to no organic-rich sediments, within the first few years after their reintroduction. We used the organic carbon and nitrogen content of stream sediments, and measurements of water properties to characterize the biogeochemical influence of reintroduced beavers on four headwater streams within the Methow River watershed in Washington. Specifically, we explored to what extent recent beaver reintroduction has increased carbon retention in beaver-pond habitat. We also investigated the source (allochthonous vs. autochthonous) of organic material retained in habitats created by beavers. Our study sheds light on the utility of beaver reintroduction as a restoration tool to rapidly restore ecosystem function within complex, multi-use watersheds.

Methods

Study Area

The Methow Valley is a northwest-southeast trending river valley located in Okanogan County in Washington State (Figure 1). This valley lies just east of the North Cascades and west of the Columbia River. The major water body in the Methow Valley is the Methow River, which drains

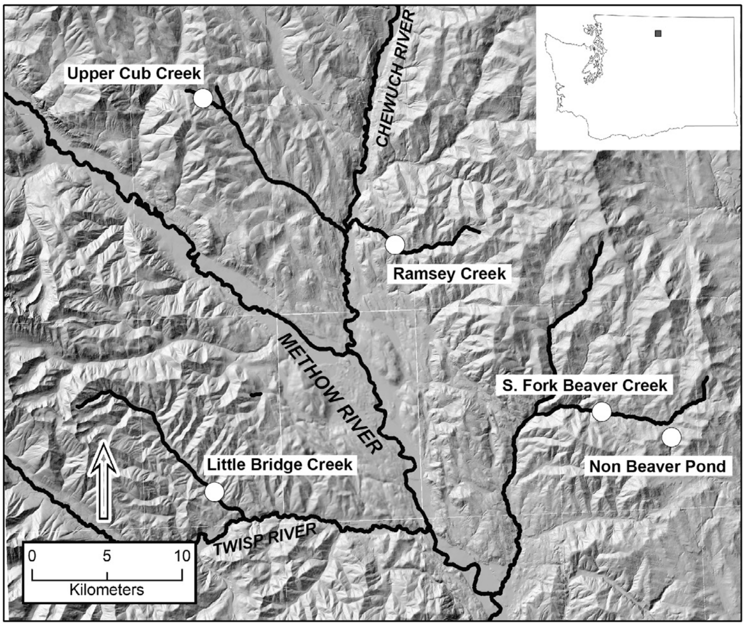

Figure 1. The Methow River watershed in north-central Washington State. Study locations are indicated by white circles. Beaver reintroduction sites are located on Little Bridge Creek, Ramsey Creek, South Fork Beaver Creek, and Upper Cub Creek. The non-beaver pond site is also included.

1,810 square miles from the North Cascades to the west (Konrad et al. 2003). Over 50% of the stream length within the Methow River watershed is comprised of first- and second-order streams. All our sampling locations are within such streams in the Okanogan-Wenatchee National Forest. Land use there is dominated by recreation, timber harvest, and livestock grazing (Woodruff 2015). This study area is also of interest because it contains steelhead and spring Chinook salmon, which are both listed as endangered under the ESA, as well as bull trout, which is listed as threatened. Consequently, restoring ecosystem processes throughout the watershed that promote dynamic and diverse food web structures is important to stakeholders, including US, state, and tribal governments.

Methow Beaver Project

Contemporary river-restoration practices typically characterize baseline stream conditions as continuous and free-flowing with the sporadic integration of woody debris (Burchsted et al. 2010). However, those river characteristics do not account for the historical presence of large beaver populations throughout North America prior to European settlement. The Methow Beaver Project (Twisp, WA) integrates that understanding of the historic hydrologic landscape into the project's modern conservation approach, reintroducing beavers to low-order tributary creeks of the Methow River since 2008 (Woodruff 2015). The particular goals of the Methow Beaver Project are to improve the health of riparian ecosystems, provide instream habitat necessary for historic salmon runs, and examine the effects of beavers on regional aquifers and municipal water budgets in anticipation of climate change impacts throughout the Methow Valley (Woodruff 2015). The project relocates "problem beavers" from downstream areas to upstream creeks; the number of relocations varies annually. For example, in 2014 the project released 38 beavers in 14 release events to 13 sites. The success of the Methow Beaver Project has been monitored by investigating patterns in ecosystem and watershed function. After the first seven years of reintroductions, the project reported positive effects on water storage and riparian ecosystem health from dam building activities (Woodruff 2015). However, the precise impact of these reintroductions on ecosystem processes like carbon flow within stream ecosystems is still poorly understood.

Study Design and Field Sampling

We identified four ponds (areas with water too deep to support emergent plants; Naiman et al. 1994) created by reintroduced beavers over the past two to five years in different stream segments, and one pond of a similar size that was not created by beaver activity. Sampling was conducted in June and July, 2016. We estimated that all ponds ranged in area from approximately 79 to 531 meters^2. At each site, transects were laid out across the pond at its widest point, with the ends of the transects defined by the presence of emergent vegetation on the pond banks. This transect sampling approach was used to account for expected lateral heterogeneity of pond bottom sediment accumulation that might lead to areas of greater deposition in different parts of the ponds. Ten-centimeter (10-cm) sediment cores were then taken along each transect and spaced equidistantly, either one or two meters apart depending on the width of the pond. Sediment cores were extruded from the corer, placed into plastic bags, wet-weighed in the field, and individually frozen for transport. We measured water properties including temperature, pH, conductivity, and dissolved oxygen at each pond using a YSI probe (Yellow Springs Instruments, Yellow Springs, OH).

Upstream and downstream of each beaver pond (within 25 meters linear distance) we also collected water property data, and 10-cm sediment cores (hereafter referred to together as "stream" samples). These stream samples provided reference points to assess whether there was greater carbon content in the pond sediments relative to stream sediments above or below the impoundments. The stream sampling was not done along a channel-spanning transect as the pond sampling was. Instead, stream sediment cores were taken in slack water and point bar areas where deposition of suspended sediment would naturally occur in a headwater stream without the presence of an obstructing structure, like a beaver dam.

To investigate the sediment profile associated with partially submerged (wetland) areas immediately adjacent to a beaver pond, we excavated a pit at edge of the pond on the South Fork Beaver Creek site. Sediment samples were collected at 10-cm depth intervals from the pit sidewall to a depth of 30 cm. Below 30 cm the sediments were completely saturated. We measured bulk density, pH, %C, and %N in these samples. Wetland areas (versus pond or upland) were limited to narrow (few meter) sections adjacent to the ponds at the beaver pond sites.

Lab and Statistical Analyses

Sediment samples were oven- and then freeze-dried. After drying, each sample was weighed again in its entirety for weight percent water calculations. All samples were then sieved through a 2-mm sieve that separated leaf litter, pond vegetation, and other large organics from the sediment. The remaining sample material was homogenized in a ball mill, and 15 mg samples of sediment were weighed into tin boats for analysis of organic carbon and nitrogen content (weight percent). Samples were analyzed using a Costech Instruments 4010 Elemental Analyzer at the University of Puget Sound.

Statistical analyses of sediment %C and %N results were conducted using JMP (version 12.0, SAS Institute Inc.) software and R-Commander. We conducted Welch's *t*-tests between mean pond and stream datasets. To investigate whether the amount (recorded by %C values) and source (interpreted from C/N ratios) of organic material differed among beaver ponds and the non-beaver site, we took two approaches. First, we used Welch's *t*-tests to separately compare %C and C/N between all (pooled) beaver and non-beaver pond samples. We then used a multivariate test (MANOVA with post-hoc Pillai's trace paired comparisons) to explore differences between %C and C/N among beaver ponds and the non-beaver site. A principle components analysis (PCA) helped assess the factors dominating the site-specific environmental variability between beaver ponds.

Results

Reintroduced beavers influenced the amount and source of organic material retained in the sediments of headwater streams in the Methow River watershed. When we compared the stream and beaver pond samples, we found significantly higher organic content (%C) in the pond sediments across all locations (Welch's *t*-test; all locations $P < 0.001$; Figure 2). In fact, the mean %C in beaver pond samples from each site was at least 4X the stream mean %C. Furthermore, we found that mean %C was higher in ponds formed by reintroduced beaver impoundments than in a non-beaver pond within the same watershed (Table 1, Figure 3)

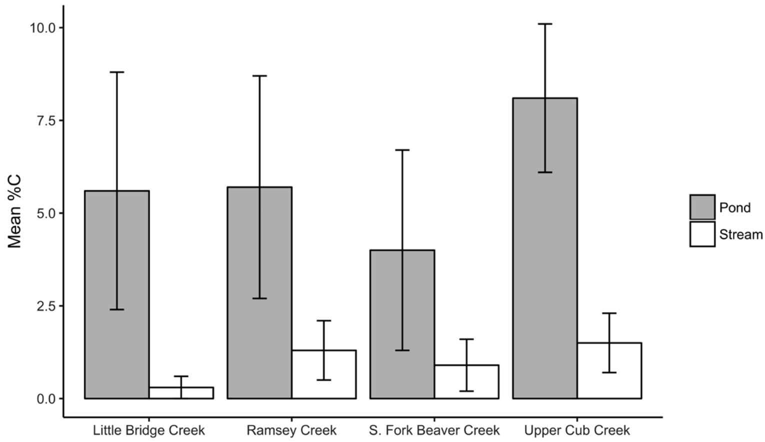

Figure 2. Paired pond and in-stream sediment %C comparisons were significant across all beaver reintroduction locations (Welch's *t*-test; $P < 0.001$).

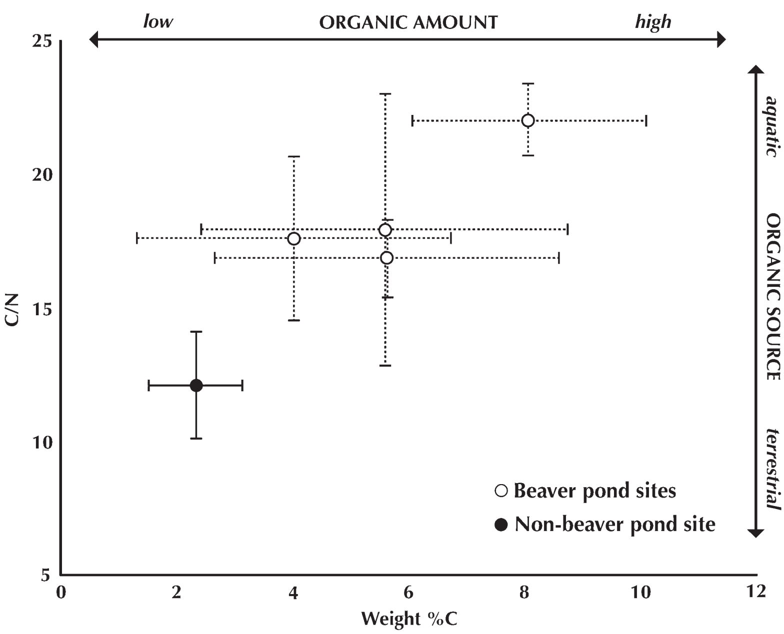

Figure 3. Mean and standard deviation for all %C and C/N ratios of pond sediment samples from each beaver reintroduction pond, and the non-beaver pond.

beaver pond samples were significantly higher than those for the non-beaver pond samples (Table 1, Figure 3) (Welch's *t*-test; $t = 8.491$, df = 30.062, $P < 0.0001$). All pond and stream %C, %N and C/N data are presented in Table S1 (available online).

The C/N ratios and %C values from each beaver pond and the non-beaver pond (Figure 3, Table 1) were significantly different (Whole Model; MANOVA – Pillai's Trace Test; approximate $F_{8,\,112} = 8.603$, $P < 0.0001$). To explore patterns among ponds, when each beaver pond was individually compared to the non-beaver pond using a post-hoc comparison, the mean %C and C/N were significantly higher in all beaver ponds ($P < 0.05$). Post-hoc multivariate pairwise comparisons of %C and C/N among beaver ponds ranged from non-significant to significant, emphasizing that every beaver pond is unique, both hydrologically and geochemically. When all beaver pond samples from all locations were combined, the difference in %C and C/N between the beaver ponds and the non-beaver pond was statistically significant (MANOVA – *F* Test; $F_{2,\,58} = 16.872$, $P < 0.0001$).

(Welch's *t*-test; $t = 6.437$, df = 66.128, $P < 0.0001$). %C was variable within each beaver pond, but the average across all beaver ponds was 2.2 times the mean %C of the non-beaver pond (5.3% versus 2.4%, respectively). The mean C/N ratios of

Within the sediment pit at the South Fork Beaver Creek site, we found that %C and %N decreased with depth, dropping rapidly from 20%

C in the 0–10 cm sample to 3.3% C in the 10–20 cm sample (Table 2). In contrast, pH (overall) and bulk density increased with depth. Within beaver ponds, the PCA identified site-specific environmental variation in water parameters representing a range of temperature, pH, dissolved oxygen, and conductivity (PC1 representing 43% and PC2 representing 31% of variation; Figure 4; Table 3). The beaver and non-beaver ponds were all fairly dispersed in multivariate space indicating that each site was different in water parameter properties. In other words, reintroduced-beaver ponds were not consistently similar to each other when considering all the water parameter data simultaneously.

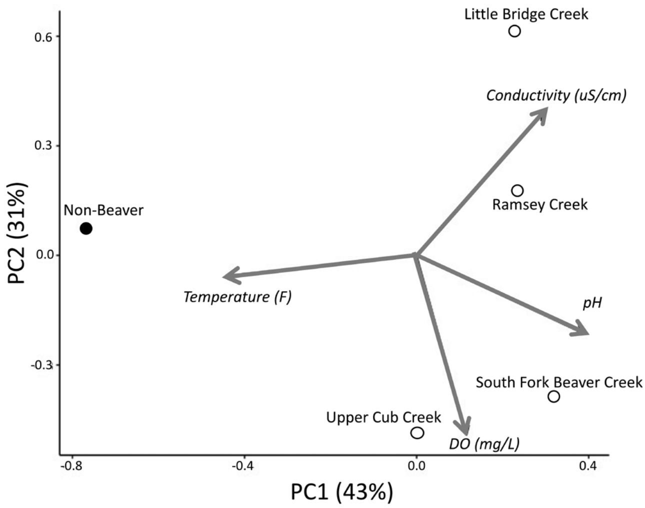

Figure 4. Principle component analysis (PCA) displaying the site-specific environmental variability of reintroduced beaver ponds and the non-beaver pond within the Methow River watershed. Environmental variation represents a range of temperature, pH, dissolved oxygen, conductivity, and pond size with PC1 representing 43% and PC2 representing 31% of variation.

Discussion

The current literature on beaver ecology supports a robust understanding of how beaver dams influence the movement of sediment through watersheds (e.g., Pollock et al. 2014), and the storage of organic carbon in riparian sediments (e.g., Naiman et al. 1994). Sediment records from beaver meadows provide a long-term (decades to centuries) perspective on organic carbon storage (Wohl 2013), whereas samples of suspended stream sediments and sediments from active ponds reflect short-term dynamics (individual flood events to years) (Naiman et al. 1986, Wegener et al. 2017). The magnitude and quantification of the effect of beavers on carbon storage in sediments is generally reported as % organic carbon content, density of organic carbon, or as carbon per area, depending on the spatial and temporal scale of the study. Beaver meadows are particularly well-researched, and studies of beaver sediments have documented everything from local impacts on carbon reservoirs (e.g., the carbon density in beaver meadow soils was nearly two times that in adjacent forest soils after several decades of beaver presence in northern Minnesota [Johnston 2014]), to contributions to landscape scale carbon budgets (for example; active beaver meadow sediments account for nearly a quarter of total organic carbon storage in watersheds of the eastern Rockies [Wohl et al. 2012]). Even without beaver activity, floodplain and wetland sediments in forested riparian systems are substantial reservoirs of organic carbon, so persistent beaver activity enhances storage in a critical riparian area (Sutfin et al. 2016).

In Methow headwater stream sites the sampling and analysis of riparian sediments was constrained by both the recent timing of beaver reintroductions, and the geomorphic settings where reintroductions occurred. Specifically, since the beaver dams had only been active for two to five years—the sites were characterized by active or recently drained ponds, and very small areas of wetland immediately adjacent to the pond banks (no wetland or meadow networks). Additionally, most of the beaver reintroduction sites were in narrow steep-sided valleys with incised stream channels. We aimed to put our results into the context of the substantial literature on carbon storage in beaver sediments, but used caution because records from pond sediments in recently dammed streams may not be directly comparable

TABLE 1. Mean and standard deviation of %C, %N, and C/N ratio for pond samples from the four beaver creek sites, and the non-beaver pond site.

Site	Sample Size (n)	Pond Area (m^2)	%C Mean (SD)	%N Mean (SD)	C/N Mean (SD)
South Fork Beaver Creek	26	531	4.0 (2.7)	0.2 (0.2)	17.6 (3.1)
Little Bridge Creek	9	79	5.6 (3.2)	0.3 (0.2)	17.9 (5.1)
Ramsey Creek	12	113	5.7 (3.0)	0.3 (0.2)	16.8 (1.5)
Upper Cub Creek	10	314	8.1 (2.0)	0.4 (0.1)	22.0 (1.4)
Non-beaver pond	13	531	2.4 (0.8)	0.2 (0.1)	12.1 (2.0)

TABLE 2. South Fork Beaver Creek sediment pit sub-sample properties by depth. %C and %N decreased with depth, while in contrast, pH and bulk density generally increased with depth.

Depth	pH	Bulk Density	%C	%N
0–10	6.14	0.38 g/mL	20.03	0.77
10–20	6.09	1.09 g/mL	3.34	0.20
20–30	6.59	1.30 g/mL	1.61	0.14

to published records derived from wetlands and meadows systems with more complicated depositional and biogeochemical histories.

We found that beavers reintroduced into river segments of the Methow River watershed have had a significant impact on total carbon storage in sediments associated with the beaver impoundments. The Methow in-stream sediment samples (collected both up and down stream of the dam sites) are organic poor, with an average of approximately 1.0% C. The Methow beaver pond sediment average of 5.3% C falls within the range of 3% and 12% for relict, and active beaver meadows, respectively, in Rocky Mountain National Park (Wohl et al. 2012, Wohl 2013), and is comparable to the 6.25% C reported for active beaver ponds in Quebec (Naiman et al. 1986). The Methow pond %C values are much lower than the 23% C reported for pond sediments in Minnesota (Naiman et al. 1994), and generally lower than values reported for shallow (less than 10 cm) beaver meadow sediments from sites in Voyageurs National Park (Johnston 2014). Ultimately, sediment retention and carbon storage is system specific, and the absolute values may only be directly comparable in similar riparian settings in given region. Our study suggests that while it may take decades before the full scope of abiotic and biotic impacts fully emerge, aquatic food webs may be substantially bolstered by increased carbon sequestration within only a few seasons of beaver reintroduction. This finding has restoration implications because little work has examined if impacts on sediment biogeochemistry are similar between transplanted beavers and beavers that independently choose dam locations. Our findings clearly suggest that transplanted beavers do substantially and rapidly influence carbon sequestration within their pond habitats on a similar scale to non-transplanted beavers (Naiman et al. 1986).

The higher average %C and C/N ratio in the beaver ponds compared to the non-beaver pond are likely from the active loading of terrestrial organic material by beavers into the ponds via feeding and dam building practices (Jenkins 1980, Naiman et al. 1986). Concurrently, variable mineralization conditions in response to altered oxidation-reduction reactions within the beaver ponds could be contributing to the higher %C values we observed (Naiman et al. 1994). Consistent with previous beaver studies, the reintroduced Methow beavers added organic carbon sources from the surrounding terrestrial environment into the aquatic food web, which otherwise, would not have been incorporated (e.g., France 2000). Across ecosystems, terrestrial plants tend to have much higher C/N ratios (generally greater than 10) than aquatic primary producers (generally less than 10) such as phytoplankton, macrophytes, algae and periphyton (reviewed in Finlay and Kendall 2007). In our system, the average C/N ratios of the organics that accumulated in the non-beaver and beaver ponds were 12.1 versus 18.2,

TABLE 3. Water property data for beaver and non-beaver pond sites.

Site	Dissolved Oxygen (DO) (mg L^{-1})	Temperature (°C)	pH	Conductivity (uS/cm)
Little Bridge Creek	4.82	11.4	7.52	708
S. Fork Beaver Creek	9.41	9.5	7.84	677
Upper Cub Creek	8.63	16.9	8.00	663
Ramsey Creek	6.85	10.6	7.57	693
Non-Beaver Pond	6.20	23.6	6.53	661

respectively. The non-beaver sediment organics were likely primarily derived from a mixture of aquatic materials, and terrestrial leaf litterfall. In contrast, the bioengineering and feeding activity of reintroduced beavers in the beaver ponds resulted in a higher amount of terrestrial organic material (i.e., wood, foliage, feces) being introduced and retained in headwater stream sediments. Based on observations by Kent Woodruff, the main tree and shrub species available to the reintroduced beavers are aspen (*Populus tremuloides* Michx.), willow (*Salix* spp.), alder (*Alnus* spp.), black cottonwood (*Populus trichocarpa* Torr. & A. Gray ex Hook), and red-osier dogwood (*Cornus sericea* L.*)*, which together constitute over 70% of the deciduous trees found around our beaver pond sites.

Intriguingly, recruitment and retention of terrestrially-derived, organic carbon in riparian zones can produce both desired and undesired conservation outcomes on stream traits like alteration of riparian vegetation composition, stream temperature shifts, and native-fish-habitat modification (Rosell et al. 2005, Kemp et al. 2011). Nonetheless, the terrestrial carbon subsidies, in tandem with increased nutrient loads from runoff and beaver fecal matter, are known to augment algal production (Coleman and Dahm 1990), and aquatic invertebrate diversity (Naiman et al. 1988). For example, lentic invertebrates like oligochaetes, pelycopods, and odonates are known to increase in abundance in soft bottom sediments within beaver ponds (McDowell and Naiman 1986, Hagglund and Sjöberg 1999). Such changes in stream community composition undoubtedly have bottom-up impacts on the structure and functioning of aquatic food webs (Malison et al. 2015).

Beavers facilitate the recruitment and storage of carbon in stream ecosystems in the form of terrestrial organic material because their dams increase the deposition of coarse wood and other debris. The sediment pit (0–30 cm depth) data from the South Fork Beaver Creek site (a site that would otherwise store little to no organic material), suggested that pond formation has influenced carbon accumulation in sediments adjacent to the ponds in the two years since beavers were reintroduced. (Table 2). Beaver-driven landscape modification adds habitat heterogeneity (i.e., lentic habitat) while also creating stepping-stone habitats for future wetland meadow formation (see successional model in Pollock et al. 2014). Presumably, even if the dams are not maintained within the landscape, legacy effects in terms of sediment and carbon accumulation could persist with wetland or meadow habitat for decades (Naiman et al. 1994, Burchsted et al. 2010).

Conclusions

This study adds to a growing body of literature suggesting that beavers can be used as an innovative tool for whole ecosystem restoration (Pollock et al. 2007, Gibson and Olden 2014, Petro et al. 2015, Law et al. 2017). More specifically, our findings suggest that a substantial increase in organic matter retention can occur within a few seasons, much faster than the well-established decadal timeline previously observed. Organic sediment retention in fluvial ecosystems is consequential because increased organic matter in beaver dam sediments provides energy to local pond, riparian and emergent wetland areas. Within our study region, the large-scale benefit of beaver reintroductions appears to have also increased overbank flow thus contributing greater volumes of water to the valley's aquifers. Continued beaver reintroduction and its accompanying slackwater habitat creation, riparian area emergence, and carbon retention also improve salmon spawning and rearing habitat. The successful efforts of the Methow Beaver Project highlight the viability of reintroduced beavers as a conservation tool, and have resulted in a positive effect on ecosystem recovery via allochthonous carbon storage that will have lasting effects in the Methow Valley watershed. Our findings cautiously support the conclusion that whole ecosystem restoration may be augmented and accelerated by reintroducing beaver to areas of historically high abundance.

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