

Beavers Buffering Blazes: The Potential Role of *Castor canadensis* in Mitigating Wildfire Impacts on Stream Ecosystems

Erin Stewart

Summary

1. Beavers (*Castor canadensis*) are considered ecosystem engineers due to the influence of their dam-building activities on abiotic and biotic characteristics of stream ecosystems. After near extirpation, beaver populations remain far below historical levels.
2. Beaver reintroduction has been used as a restoration tool to reverse stream incision, store groundwater, restore riparian vegetation, and create wildlife habitat. Beaver reintroduction could also help mitigate the effects of wildfire on stream ecosystems. Studies examining this interaction between beavers and wildfires are lacking.
3. In this study, we examined the impact of wildfire on stream ecosystems with and without beavers using benthic macroinvertebrates as indicators of water quality. We collected macroinvertebrates and recorded abiotic stream characteristics above and below beaver dams in burned and unburned areas in the Methow Valley, Washington.
4. Macroinvertebrate community composition varied across sites types, with higher numbers of sensitive taxa (Ephemeroptera, Plecoptera, and Trichoptera) generally found in unburned areas, and below dams in burned areas. Above-dam burned areas tended to have higher amounts of fine sediments, and overall showed greater variability in stream characteristics reflecting the heterogeneity among sites.
5. These findings provide preliminary backing for the hypothesis that beaver dams mitigate the impacts of wildfire on downstream ecosystems. Therefore, this work supports the assertion that beaver reintroduction presents a viable method of climate change adaptation.

Introduction

Beavers as Ecosystem Engineers

When the term “ecosystem engineer” was coined by Jones and colleagues in 1994, beavers (*Castor canadensis*) were one of the primary examples described due to the way in which they reshape the physical environment. Historically, these herbivorous rodents were widespread across North America, numbering between 60 and 400 million and ranging from northern Mexico to the arctic tundra (Seton 1929, Naiman et al. 1988). However, by 1900 the fur trade had nearly extirpated beaver populations, leaving only an approximated 100,000 individuals (Naiman et al. 1988, Miller 2009, Gibson and Olden 2014). Following the decline of the fur trade and trapping beavers have exhibited a partial recovery, but the total population, estimated at 12 million, remains far below historical levels (Naiman et al. 1988, Gibson and Olden 2014, Wohl 2019).

Where they have recolonized, beavers exert a strong influence on stream ecosystems. In terms of geomorphology and hydrology, beaver dams expand wetland habitat, increase groundwater storage, promote deposition of sediment and organic material, and sequester nutrients (Gibson and Olden 2014, Hood and Larson 2015, Majerova et al. 2015, McCreesh et al. 2019). While studies have documented both increases and decreases in water temperatures below dams, in general beaver complexes serve to buffer summer temperature extremes and create cool-temperature refuges (Gibson and Olden 2014, Majerova et al. 2015, Weber et al. 2017). There is also evidence that beaver dams maintain water flow year-round in otherwise ephemeral streams and reduce stream velocity during peak floods (Gibson and Olden 2014).

The biotic impacts of beavers are also substantial. Compared to riparian ecosystems with no history of beaver occupation, beaver-modified habitats exhibit higher abundances of riparian vegetation and differences in species composition (Wright et al. 2002, Gibson and Olden 2014). Although cottonwood abundance tends to decrease due to beaver herbivory, willow appears to benefit, showing robust regrowth following foraging (Gibson and Olden 2014). Beaver activities also benefit a range of animal taxa; researchers have documented increased abundance and altered composition of small mammals, increased abundance and species richness of birds (particularly riparian species), and expanded refuge habitat for fish and amphibian species in beaver-occupied riparian areas compared to unoccupied areas (Gibson and Olden 2014). At the landscape scale, beaver activities enhance habitat heterogeneity, increase riparian vegetation species richness, maintain fish biodiversity, and aid wetland habitat connectivity (Wright et al. 2002, Smith and Mather 2013, Gibson and Olden 2014, Hood and Larson 2015). The impacts of beavers therefore extend beyond their immediate range.

Because of their important role in stream ecosystems, a growing number of restoration projects relocate “nuisance” beavers from places where their activities threaten infrastructure and property to remote or less-developed areas. While the primary goal of many of these projects is to present a non-lethal alternative to dealing with nuisance beavers, secondary goals include the enhancement of water storage, restoration of riparian vegetation, control of sediments, and improvement of habitat for wildlife (Pilliod et al. 2018). Studies also indicate that beaver relocation could be used as a tool to reverse the process of stream channel incision as dams raise streambed elevation by trapping sediment (Pollock et al. 2007, Levine and Meyer 2014). This reversal can be fairly rapid, with significant accumulation of allochthonous organic materials behind dams within 5 years of beaver reintroduction (McCreesh et al. 2019). Looking to the future, beaver activities could help mitigate the effects of climate change at higher elevations as the creation of ponds and dams can attenuate larger spring and winter floods, and expanded groundwater storage can augment severe low flows due to drought in the summer months (Baldwin 2015).

Beaver restoration may also help mitigate the impacts of wildfire on stream ecosystems (Baldwin 2015). Wildfires are a growing ecological and human threat: in the western United States the frequency of large wildfires and the total area burned in such fires has been increasing since the 1980s (Dennison et al. 2014). Concurrently, the annual fire season and time from discovery to control of individual fires has lengthened (Westerling et al. 2006). These trends are related to a number of factors including decreased precipitation during the fire season as a result of anthropogenic climate change, fuel load accumulation due to historical fire suppression practices, and the temporal and spatial expansion of wildfire impact due to human-ignited wildfires (Westerling et al. 2006, Bladon et al. 2014, Dennison et al. 2014, Balch et al. 2017, Holden et al. 2018). In the future, wildfire risk is projected to increase in the western United States, specifically in the Southwest, Pacific coast, and Rocky Mountains regions (Liu et al. 2013).

Wildfires can significantly alter aquatic ecosystems, driving transient or long-term changes in water quality (Bladon et al. 2014). While the effects of wildfire on stream temperatures are highly variable, studies have documented elevated temperatures during and immediately following burns (Hitt 2003, Koontz et al. 2018). Streams show a higher frequency of warmer temperatures in the year following a wildfire, and maximum temperatures may remain elevated more than a decade after the initial impact (Dunham et al. 2007, Mahlum et al. 2011, Koontz et al. 2018). These elevated temperatures are associated with the burning of riparian vegetation and loss of canopy cover (Cooper et al. 2015).

Wildfires also promote rapid runoff and flood events by increasing the water repellency of soil through creation or exposure of a hydrophobic layer (Bladon et al. 2014). This runoff carries ash, charcoal, and unstable soil into streams and raises flow levels (Smith et al. 2011, Bladon et al. 2014, Dahm et al. 2015). In flood events following wildfires, resultant “slurry flows” are characterized by high concentrations of suspended solids and nutrients, extremely low levels of dissolved oxygen, and drops in pH (Cooper et al. 2015, Dahm et al. 2015). These effects persist, with elevated levels of suspended sediments, nitrogen, phosphorus, particulate metals, and major ion flux documented up to five years following wildfire (Smith et al. 2011, Silins et al. 2014, Rust et al. 2018). Of particular relevance to humans, this degradation in water quality following wildfires threatens drinking water resources (Smith et al. 2011, Bladon et al. 2014, Dahm et al. 2015).

Alterations in abiotic stream conditions also impact aquatic biota (Bladon et al. 2014). In the five years after wildfire, algal abundance increases dramatically, likely due to the high levels of nitrogen and phosphorus (Silins et al. 2014, Cooper et al. 2015). Macroinvertebrate communities show sharp reductions in density and taxon richness immediately following post-fire floods, and while density generally recovers or even exceeds pre-fire levels within one year, taxon richness remains low for longer (Vieira et al. 2004, Mellon et al. 2008, Silins et al. 2014, Verkaik et al. 2015, Musetta-Lambert et al. 2019). These new communities are characterized by

disturbance-oriented families including Chironomidae, Simuliidae, and Baetidae, and much lower proportions of sensitive orders including Ephemeroptera, Plecoptera, Trichoptera (Mellon et al. 2008, Silins et al. 2014, Verkaik et al. 2015, Musetta-Lambert et al. 2019).

Macroinvertebrate community composition exhibits high variability up to a decade following wildfire, and this variability is associated with changes in sediment, organic debris, large woody debris, and riparian cover (Minshall et al. 2001, Arkle et al. 2009). In particular, higher levels of sediment and organic debris tend to favor fine-sediment tolerant groups (Arkle et al. 2009).

Further up the food chain, fish and amphibians are also impacted by wildfire. Salmonid populations, for instance, show moderate to severe declines immediately following wildfires (Sestrich et al. 2011, Cooper et al. 2015). While populations can recover relatively quickly, individuals often exhibit faster growth rates—a common response to variability in environmental conditions or food resources—as well as lower lipid content and earlier maturity, all of which may result in decreased fitness (Sestrich et al. 2011, Silins et al. 2014, Rosenberger et al. 2015). The effect of wildfire on salmonid populations is also dependent on life stage, with the delivery of woody debris enhancing overwintering habitat for juveniles and adults, while the delivery of fine sediment degrades habitat for eggs and fry (Flitcroft et al. 2016). The responses of amphibians to wildfire are highly species- and context-specific (Hossack and Pilliod 2011). For some, wildfire appears to aid connectivity and colonization and enhance breeding habitat, while for others post-fire sedimentation eliminates breeding habitat (Hossack and Pilliod 2011). The effects of wildfire may take years to manifest, with occupancy of certain species not showing declines until over 5 years after initial impact (Hossack et al. 2013). Wildfire presents a particular threat to populations of low-fecundity, cold water breeders that are already fragmented and facing other environmental stressors (Hossack and Pilliod 2011).

Beaver Restoration and Wildfire

Beaver relocation presents a potential tool for mitigating the adverse effects of wildfires on stream ecosystems. By expanding the wetted perimeter of streams, beaver dams could act as natural firebreaks, checking the initial spread of wildfire in riparian areas. In addition, beaver-enhanced groundwater storage could help maintain cooler stream temperatures following fires, while dam presence could trap sediment mobilized by postfire runoff, thereby preserving downstream water quality (Baldwin 2015). These possibilities are supported by preliminary data showing that the aquatic macroinvertebrate community in a burned area downstream of a dam was more similar to communities in unburned areas than those in burned areas without dams (Shampain 2019). Furthermore, streams in overgrazed areas – analogous to burned areas in that they exhibit elevated stream temperatures, higher sedimentation rates, and lower salmon and trout abundance – show signs of recovery following beaver introduction (Kauffman and Krueger 1984, Quinn et al. 1992, Law et al. 2017).

In this study I ask whether beaver dams help buffer the effects of wildfire on freshwater ecosystems, using benthic macroinvertebrates as bioindicators of stream health.

Macroinvertebrates are commonly used to assess the status of freshwater ecosystems due to their sensitivity to water quality, disturbance, and fine sediment cover (Kerans and Karr 1994, Wallace and Webster 1996, Relyea et al. 2000, Wagenhoff 2012). As living organisms, macroinvertebrates integrate environmental conditions over time, providing a more holistic measure of water quality than single measurements of physical stream parameters. In addition, benthic macroinvertebrates are central to stream ecosystem function, controlling algal abundance, serving as a food source for salmonids and other fish species, and facilitating decomposition and nutrient cycling (Wallace and Webster 1996). To assess the hypothesis that beaver dams mitigate the effect of wildfire on stream ecosystems, I examined the macroinvertebrate communities and physical characteristics above and below dams in burned and unburned streams. Compared to burned areas above dams, I predicted that burned areas below dams would show (1) higher macroinvertebrate community characteristics indicating good water quality, (2) lower macroinvertebrate community characteristics indicating poor water quality, and (3) lower levels of fine sediment. Furthermore, I predicted that burned areas below dams would be similar to unburned areas. A better understanding of the interactions between burns, beaver dams, and stream ecosystem health is necessary to provide guidance for future restoration projects and fire management practices.

Methods

Study Area

The Methow River, a tributary to the Columbia River, is located in north-central Washington and drains an area of 4700 km². The Methow River Watershed has been impacted by frequent, large wildfires, such as the Carlton Complex fire in 2014 and the Okanogan Complex Fires in 2015 (Whipple 2019). In addition, the area is home to the Methow Beaver Project, a long-term program that relocates “problem” beavers to Methow River tributaries in an effort to increase stream complexity, aid salmon recovery, store water, and benefit overall ecosystem health (Bondi 2009). Over the past 11 years, the program has overseen the release of ~400 beavers in the area (Methow Salmon Recovery Foundation 2018).

Sampling was conducted from June 11-20, 2019 in a number of headwater streams throughout the valley. Twelve sites, 11 of which were identified and used by Whipple (2019) to assess the impact of beaver reintroduction on dissolved nutrients and riparian vegetation, were sampled (Figure 1). These sites were grouped into three blocks based on geomorphological characteristics. Each block contained (1) an unburned beaver site, (2) a burned beaver site, (3) an unburned control site, and (4) a burned control site, resulting in a sample size of three for each geomorphological type. Beaver sites were defined as those containing or having significant remnants of hydrologically significant beaver dams (i.e. those holding water and sediment), while control sites had no documented beaver presence. Burned sites were burned by 2014 and 2015 wildfires, while unburned had no recent (< 10 years ago) wildfire impact. Data were

collected in three riffles (regions of fast-flowing water) at each control site, and in three riffles above the dam and three riffles below the dam at each beaver sites. Riffle samples were spaced at least 3 meters apart and were sited far enough above and below dams to avoid features of the pond and impoundment.

Macroinvertebrate Sampling

In each riffle, macroinvertebrates were collected using a Surber sampler. The Surber sampler was placed on the streambed and any large cobbles and boulders within the sampling frame were removed to a separate container and cleaned to dislodge macroinvertebrates. The remaining substrate was then disturbed to a depth of approximately 5 cm for about 1 minute to dislodge macroinvertebrates. The flow carried the macroinvertebrates into the filter, after which they were combined with the previously captured macroinvertebrates, rinsed several times, and stored in 70% ethanol.

In lab, macroinvertebrate samples were poured into a large 10x10 gridded petri dish, and the macroinvertebrate nearest to each intersection was removed for a total of 100 individuals. Each selected macroinvertebrate was identified to family or genus and grouped into morphospecies. The remainder of the sample was poured into another large petri dish divided into quadrants, and all macroinvertebrates in one randomly selected quadrant were counted. This number was multiplied by 4 and added to 100 to obtain an estimate of abundance.

Based on the 100 macroinvertebrates identified from each sample, the following community characteristics were calculated: species richness, Ephemeroptera richness, Plecoptera richness, Trichoptera richness, cumulative EPT (Ephemeroptera-Plecoptera-Trichoptera) richness, percent EPT, percent Diptera, percent dominance. Based on these seven characteristics, plus percent EPT, a modified B-IBI (Benthic Index of Biotic Integrity) score was computed for each sample. Shannon diversity index (H) was used to quantify diversity. The mean of each characteristic was calculated for each set of triplicate samples.

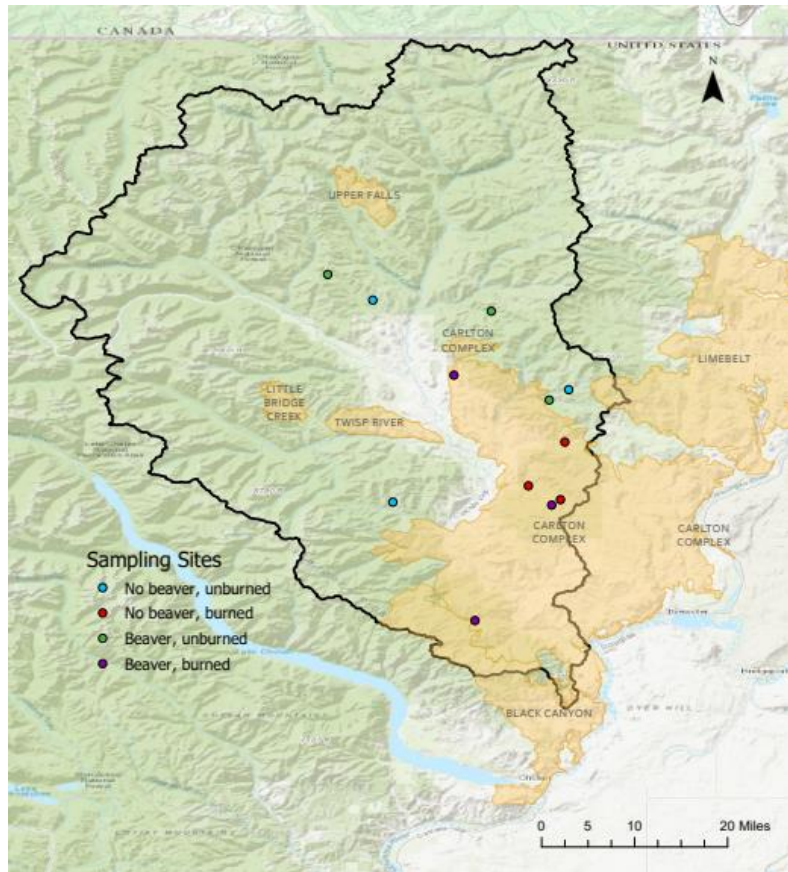


Figure 1. Sampling sites within the Methow Valley. Shaded orange regions indicate the extent of 2014-15 wildfires; the Methow River watershed is outlined in black.

Physical Parameter Characterization

At each riffle, water temperature was measured using a thermometer. Stream width was measured from bank to bank, and depth was measured $\frac{1}{4}$, $\frac{1}{2}$, and $\frac{3}{4}$ of the way across the stream. These values were used to calculate channel area. Velocity was determined by timing how long it took a bobber to move 1 m, and was taken as the average of 4 such trials. Canopy cover was estimated using a densiometer.

Within the Surber sampler frame, the percent coverage of algae was visually estimated prior to macroinvertebrate sampling. Separately, the percent coverage of bedrock, boulders, cobble, gravel, sand, silt, and clay within the sampling frame was visually estimated. Because no bedrock or clay was observed, these categories were excluded from further analyses.

To determine percent organic carbon, sediment was collected adjacent to the Surber sampler frame. To minimize the loss of fine sediments, a stilling well, or baffle, was used to slow down the current while sediment was collected using a shovel (8 $\frac{1}{2}$ " x 11") (Hames et al. 1996). Sediment was transferred to a 1 or 2-gallon plastic bag and later air-dried. Samples were sieved through 2 mm mesh to isolate the fine sediments. These sediments were homogenized using a mortar and pestle, and 15 mg were weighed into tin boats. Samples were analyzed with a Costech Instruments 4010 Elemental Analyzer to determine the percent organic carbon of the sediment.

Statistical Analysis

All statistical analyses were conducted in R using an α value of 0.05 to determine significance and 0.10 to identify marginal significance (R Core Team 2017). Two-way ANOVAs were used to analyze the relationship between site type and macroinvertebrate community characteristics. For these analyses, community characteristic values were calculated as the residual of each site from the block mean. This adjustment centered values from all blocks around zero while maintaining the variation between sites within each block. Control sites were excluded from the analysis due to substantial habitat heterogeneity and to simplify analysis, but were included in figures to show general trends. Data were checked using the Shapiro-Wilk test and Levene's test to ensure normality and homogeneity of variance. If the interaction term of the two-way ANOVA was significant, two-sample t-tests were used to determine pairwise significance.

Principal component analysis was used to assess how stream characteristics varied among the four different site types. In the initial analysis, boulder and cobble were highly associated, as were sand and silt. The percent coverage of each pair was therefore summed, resulting in a total of eight physical parameters for analysis (Table 1). Packages ggplot2, ggfortify, and factoextra were used to compute and visualize PCA results.

Table 1. Physical parameters used in Principal Component Analysis

Characteristic	Description
temperature	Water temperature
channel area	Cross-sectional area of stream
velocity	Stream velocity
canopy cover	Percent canopy cover above sampling frame
boulder/cobble	>60 mm
gravel	2-60 mm
sand/silt	<2 mm
organic carbon	Percent organic carbon in sediment

Results

Macroinvertebrate Community Structure

A total of 54 macroinvertebrate samples were collected at the 12 sites. Taxa identified included Ephemeroptera, Plecoptera, Trichoptera, Diptera, Coleoptera, Hemiptera, Collembola, Arachnida, Crustacea, Platyhelminthes, Annelida, Mollusca, and Nematoda. Across all samples, an average of 21.7 species per sample were identified, and B-IBI averaged 33 out of 40, indicating good water quality (Table 2). Among the general community characteristics of abundance, species richness, diversity, and B-IBI, only species richness varied significantly among site types (Figure 2, Table 3). Species richness depended on whether samples were collected above or below dams as well as burn status, which showed a marginally significant interaction. Compared to above-dam burned areas, an average of 5.2 more species were found in below-dam burned areas, and an average of 5.6 more species were found in above-dam unburned areas.

EPT characteristics varied substantially among site types (Figure 3, Table 3). The effect of burn status on Ephemeroptera, Plecoptera, and overall EPT richness, but not Trichoptera richness, depended on whether samples were collected above or below the dam. Above dams, an average 4.3 more Ephemeroptera species, 3.3 more Plecoptera species, and 6.7 more EPT species overall were collected in unburned areas compared to burned areas. Focusing on burned areas, 4.3 more Ephemeroptera species, 1.2 more Plecoptera species, and 6.6 more EPT species overall were collected below dams compared to above dams. Across burned and unburned areas, Trichoptera richness averaged 1.8 more species below dams compared to above dams. Indicators of poor water quality, namely dominance and Diptera, were not significantly affected by site type (Figure 4, Table 3).

Table 2. Summary statistics for 10 macroinvertebrate community characteristics measured across all twelve sites.

Characteristic	Mean \pm SE
Abundance	370 \pm 32
Species richness	21.7 \pm 0.7
Shannon diversity	2.25 \pm 0.05
B-IBI	33 \pm 1
EPT richness	13.6 \pm 0.8
Ephemeroptera richness	7.5 \pm 0.6
Plecoptera richness	2.4 \pm 0.3
Trichoptera richness	3.7 \pm 0.4
Dominance (%)	29 \pm 2
Diptera (%)	27 \pm 4

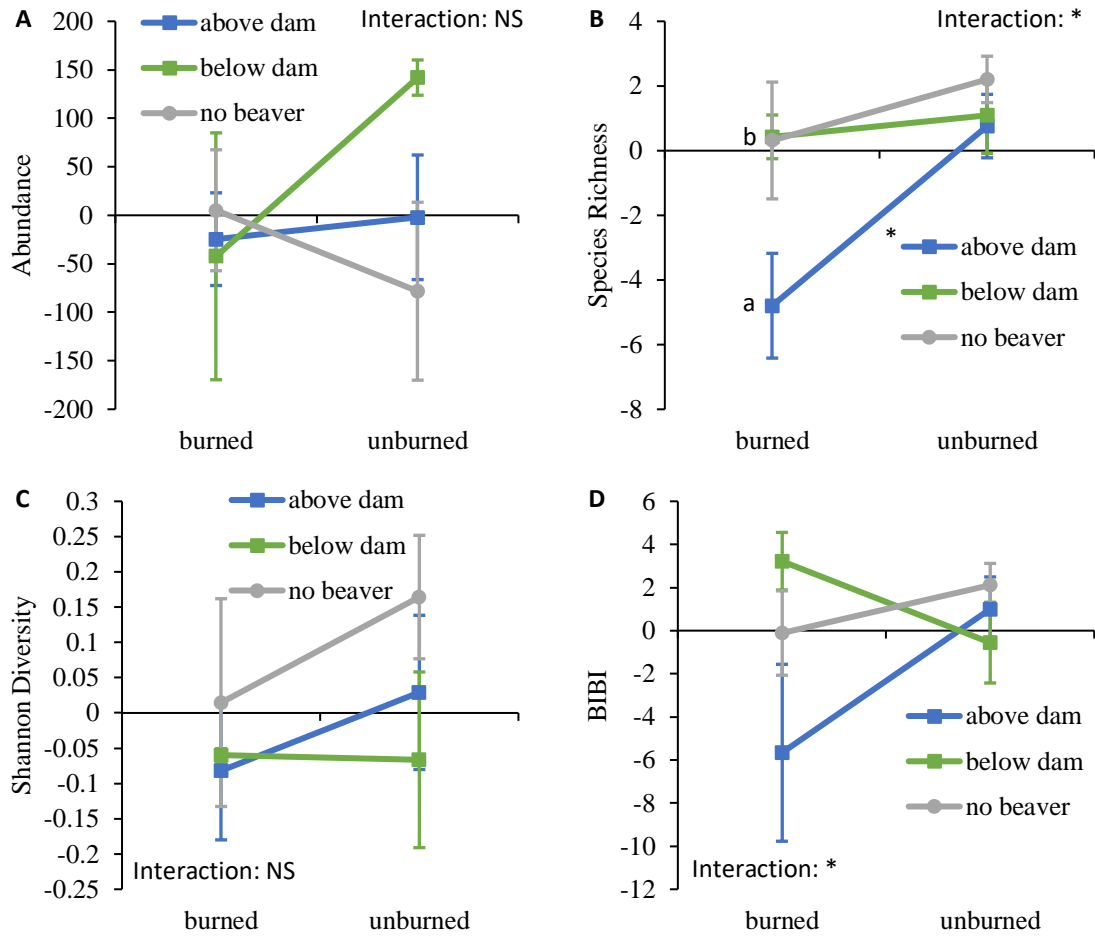


Figure 2. Effect of burns and beaver dams on mean (± 1 SE) (A) abundance, (B) species richness, (C) diversity, and (D) B-IBI. Y-axis shows units of difference. A significant interaction term is indicated by a * (NS = not significant). An (a) and (b) indicate that above-dam and below-dam sites differ significantly from one another (depending on burn status, if interaction is significant); * indicates significant differences between burned and unburned sites (depending on whether samples were collected above or below the dam, if interaction is significant). Control (no beaver) sites are included to show general trends. N = 3 sites for each point.

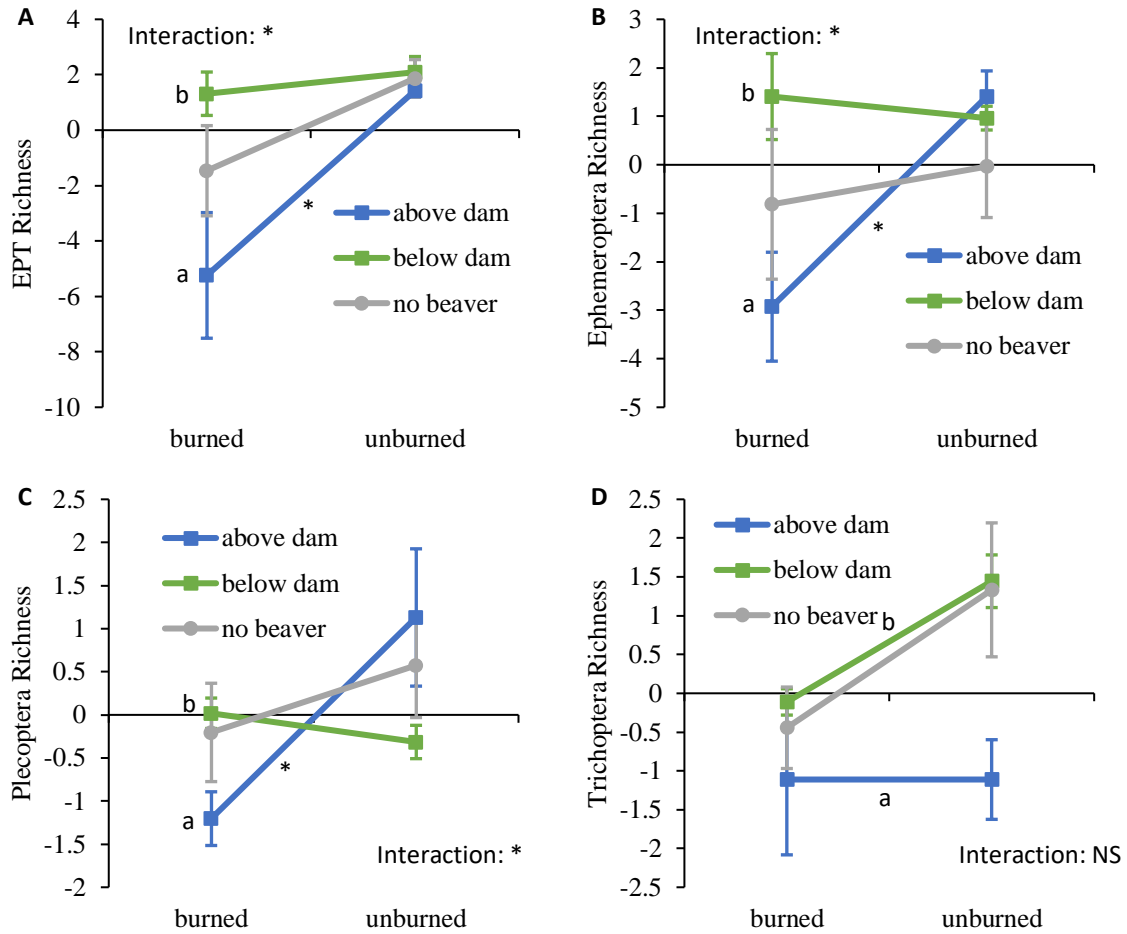


Figure 3. Effect of burns and beaver dams on mean (± 1 SE) (A) EPT richness, (B) Ephemeroptera richness, (C) Plecoptera richness, and (D) Trichoptera richness. Y-axis shows units of difference. A significant interaction term is indicated by a * (NS = not significant). An (a) and (b) indicate that above-dam and below-dam sites differ significantly from one another (depending on burn status, if interaction is significant); * indicates significant differences between burned and unburned sites (depending on whether samples were collected above or below the dam, if interaction is significant). Control (no beaver) sites are included to show general trends. N = 3 sites for each point.

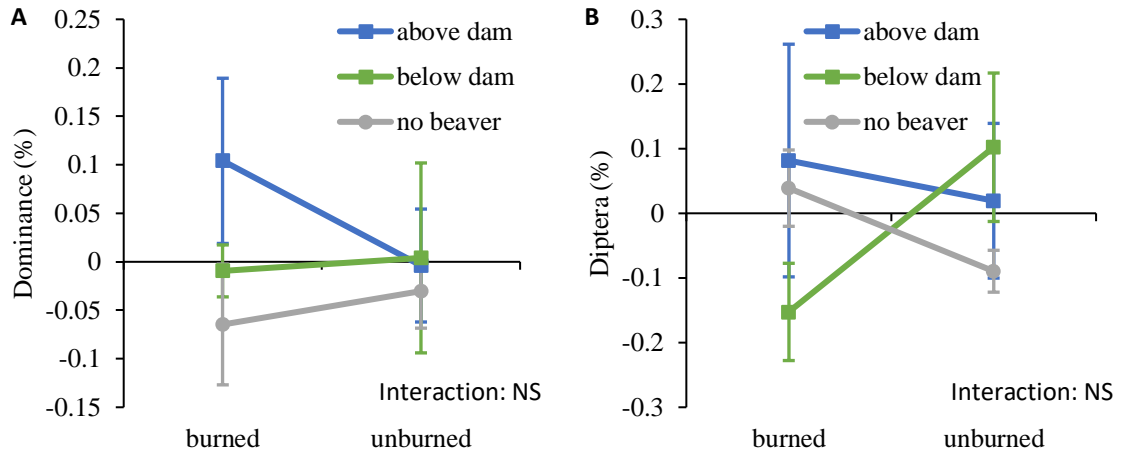


Figure 4. Effect of burns and beaver dams on mean (± 1 SE) (A) percent dominance and (B) percent Diptera. Y-axis shows units of difference. NS indicates that the interaction term is not significant. Control (no beaver) sites are included to show general trends. N = 3 sites for each point.

Table 3. Statistical results for two-way ANOVA tests of the effect of burns and beaver dams on macroinvertebrate community characteristics. Values represent F-values (two-way ANOVA) or t-values (post-hoc two-sample t-test). P-values are shown in parenthesis. Significant results are bolded.

Characteristic	Interaction	Burned vs. unburned		Above vs. below	
Abundance	1.14 (0.317)	1.86 (0.209)		0.70 (0.428)	
Shannon diversity	0.37 (0.559)	0.29 (0.603)		0.15 (0.713)	
Trichoptera richness	1.79 (0.217)	1.79 (0.217)		9.37 (0.016)	
Percent Dominance	0.70 (0.426)	0.43 (0.532)		0.53 (0.486)	
Percent Diptera	1.53 (0.251)	0.57 (0.474)		0.35 (0.571)	
Characteristic	Interaction	Above dam: burned vs. unburned	Below dam: burned vs. unburned	Burned: above vs. below dam	Unburned: above vs. below dam
Species richness	4.39 (0.069)	-2.93 (0.043)	-0.49 (0.650)	-2.97 (0.041)	-0.22 (0.839)
B-IBI	4.48 (0.067)	-1.53 (0.202)	1.64 (0.176)	-2.06 (0.109)	0.65 (0.551)
EPT richness	5.66 (0.045)	-2.93 (0.043)	-0.81 (0.466)	-2.73 (0.052)	-1.09 (0.336)
Ephemeroptera richness	9.56 (0.015)	-3.49 (0.025)	0.48 (0.654)	-3.03 (0.039)	0.76 (0.488)
Plecoptera richness	8.89 (0.016)	-2.73 (0.053)	1.27 (0.272)	-3.41 (0.027)	1.76 (0.153)

Physical Parameters

The first two principal components derived by the PCA analysis explained 37.58% and 21.95% of the variation in stream characteristics respectively (Figure 5). Silt and sand, gravel, and organic carbon showed a strong positive correlation with PC1, while boulders and cobble, channel area, velocity, and algae showed a strong negative correlation. As a result, the axis appears to represent a stream energy gradient, with higher PC1 values indicating lower stream energy and vice versa. Meanwhile, temperature, gravel, and organic carbon were positively correlated with PC2, while silt and sand were negatively correlated with PC2. Above-dam sites showed a slight upward shift along PC1 compared to their respective below-dam sites. Furthermore, burned above-dam sites showed much more variation along PC2 than any of the other site types.

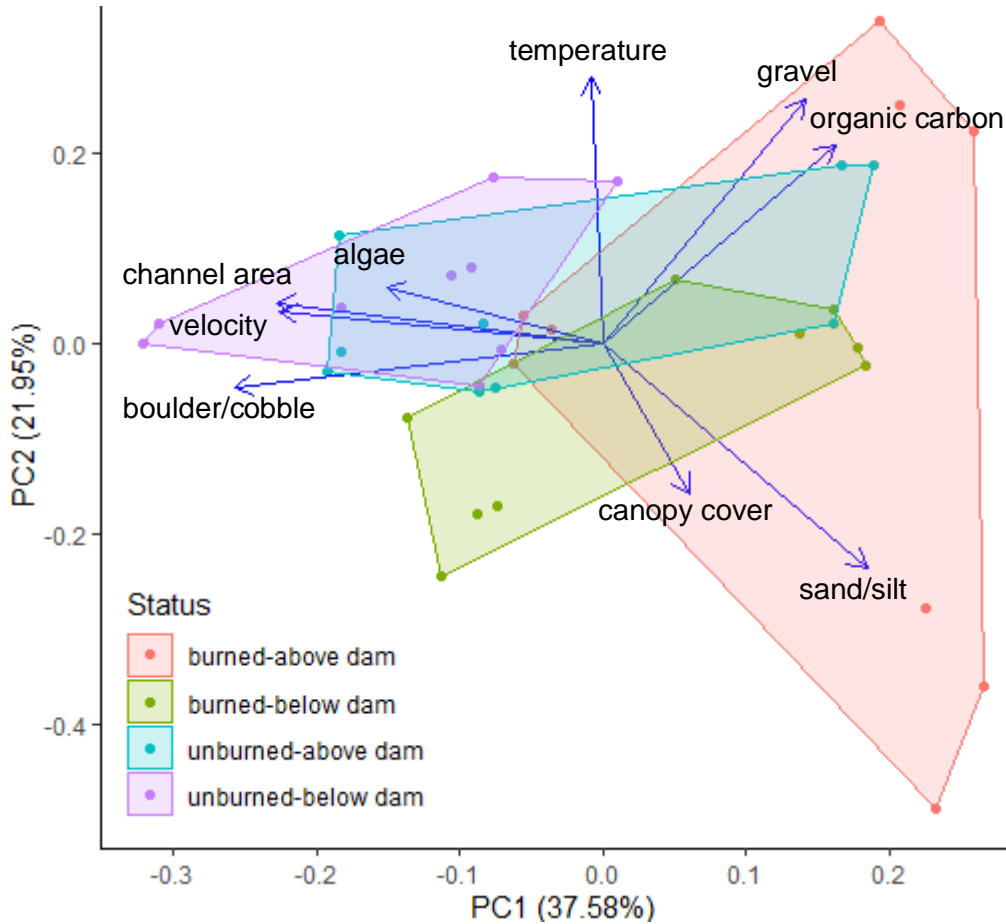


Figure 5. Principal component analysis of stream characteristics displaying variation stream, sediment, and canopy features across beaver sites sampled. PC1 explains 37.58% and PC2 explains 21.95% of the variability in the data. Boulders and cobble, gravel, sand and silt, organic carbon, channel area, velocity, and algae were strongly correlated with PC1, while temperature, gravel, sand and silt, and organic carbon were strongly correlated with PC2.

Table 4. Variable loadings for each principal component.

Variable	PC1	PC2
boulders + cobble	-0.90	-0.12
channel area	-0.80	0.11
velocity	-0.79	0.09
algae	-0.53	0.16
temperature	-0.03	0.75
canopy cover	0.21	-0.42
gravel	0.49	0.69
organic carbon	0.57	0.56
sand + silt	0.65	-0.63

Discussion

As climate change progresses, wildfires will pose an increasingly significant threat to the health of stream ecosystems (Baldwin 2015). To counter this threat, low-cost, ecosystem-based solutions are much needed. In this study I examined how beaver dams and wildfire interact to influence abiotic and biotic characteristics of headwater streams in north-central Washington. Specifically, I analyzed how macroinvertebrate assemblages and stream characteristics varied around beaver dams in areas with and without recent wildfire impacts. My general hypothesis was that beaver dams would buffer the impacts of wildfire, thus reducing its downstream effects.

Macroinvertebrate Assemblages

My first prediction was that macroinvertebrate community characteristics indicating good water quality would be similar between unburned areas and below-dam burned areas, but would be lower in above-dam burned areas. Multiple metrics bore this prediction out. Ephemeroptera, Plecoptera, EPT, and overall species richness were all higher at burned below-dam sites and unburned above-dam sites when compared to burned above-dam sites. Meanwhile, across burned and unburned sites Trichoptera richness was higher below dams compared to above dams. While not significant, Shannon diversity and B-IBI showed trends similar to trends in richness. From unburned to burned areas, Shannon diversity declined above dams but not below dams, while in burned areas B-IBI was substantially higher below dams compared to above dams. Other studies have also found declines in various metrics associated with good water quality in response to wildfire: Mellon et al. (2008) documented reduced diversity, Silins et al. (2014) documented reduced EPT percent composition, and Verkaik et al. (2015) documented reduced taxonomic richness. In this study, the lack of such responses to wildfire in below-dam communities support the hypothesis that dams are buffering wildfire impacts.

To assess the prediction that indicators of poor water quality would be higher in above-dam burned areas, we quantified overall macroinvertebrate abundance, percent Diptera, and percent dominance in each sample. We did not find significant differences among site types for these metrics, which runs counter to the findings of other studies that document an association between wildfire and elevated densities of macroinvertebrates (Mellon et al. 2008, Silins et al. 2014, Verkaik et al. 2015, Musetta-Lambert et al. 2019) and higher dominance of Chironomidae and Simuliidae (Mellon et al. 2008, Verkaik et al. 2015). This discrepancy could be related to the timeline of the respective studies or the severity of the wildfires in question. Regarding timeline, Mellon et al. (2008) found higher densities of macroinvertebrates in burned areas in the two years immediately following a wildfire. This study is highly comparable to our study because it was conducted in the Kettle Mountain Range of eastern Washington and researchers captured macroinvertebrates using a Surber sampler. However, we sampled 4-5 years following wildfire impact, at which point community density may have returned to original levels even as community composition remained perturbed. Because headwater streams in the Methow Valley

generally exhibit cool temperatures and high water quality, streams that rebounded would be expected to show relatively low levels of Diptera overall. In terms of wildfire severity, Malison and Baxter (2010) compared benthic macroinvertebrate communities across streams subjected to low- and high-intensity burns. They found that the total density of primary consumers, Chironomidae, and Simuliidae in low-severity burns was less than that of high-severity burns and was similar to unburned areas (Malison and Baxter 2010). While the severity of the fires at the burned sites in the Methow Valley was not assessed, if they were of low severity it would explain the lack of a response of abundance, percent Diptera, and percent dominance to wildfire. Effects of high-intensity fires could also be diluted if burns are patchy, resulting in a minimal response from macroinvertebrate communities.

Stream Characteristics

Though not all metrics were significant, it is clear that macroinvertebrate community composition differed among the different site types. These differences were likely driven in part by differences in the physical environment. The principal component analysis revealed substantial variation in physical parameters including sediment composition and stream characteristics. The variables associated with PC1 suggest that it reflects a stream energy gradient, with lower values on the axis representing large, fast streams dominated by cobbles and boulders, and higher values on the axis representing small, slow streams with finer sediments and more organic carbon. However, the axis may also reflect wildfire impact to some extent, as post-fire runoff tends to carry fine sediments into streams, while low-intensity fires might be expected to channel more organic carbon into streams. This notion is supported by the fact that the burned sites, and above-dam burned sites in particular, tended towards the higher end of PC1. Below-dam burned sites were shifted slightly lower on the PC1 axis than the above-dam burned sites, likely because the dam and associated pond served to catch fine sediments carried into the system in post-fire runoff.

PC2 was strongly associated with temperature. Although stream temperatures fluctuate considerably throughout the seasons, the fact that all of our measurements were taken within two weeks of one another allows for comparison of relative temperatures among sites. Above-dam burned sites showed substantially greater variation along PC2, extending both above and below the other site types. This could be related to the initial removal of shading vegetation in some streams impacted by fire and increased shading by post-fire successional species in others. The greater thermal variability documented above dams in burned areas compared to below dams supports the idea that dams could play a role in buffering downstream temperatures, as suggested by Baldwin (2015). Previous work showing that beaver dams are associated with lower daily maximum and higher daily minimum temperatures downstream also supports the notion that dams act as thermal buffers (Weber et al. 2017). Overall, the greater variation in physical parameters at the burned above-dam sites compared to all other site types suggests that wildfires increase ecosystem variability, but that the presence of a dam can stabilize downstream habitat.

Ephemerality and Heterogeneity

Stream ephemerality is a potential complicating factor in this study. When sites were revisited in late August, the site above the Benson Creek dam was damp but had no flowing water, while the site above the Bear Creek dam was completely dry. It is unknown whether the lack of water was anomalous and due to unusually dry conditions, or if these sections of the streams dry annually. In the latter case, annual drying could play a significant role in structuring macroinvertebrate communities in those stream sections. The impacts of drying on macroinvertebrate communities is highly variable: one study found a 50% decline in taxa richness and a 96% decline in macroinvertebrate density following a two-month dry period, while another study documented 88% of original taxa less than four days after resumption of flow following a dry period of almost four months (Miller and Golladay 1996, Fritz and Dodds 2004). Even with drastic declines in richness and abundance, communities generally recover within one month of the disturbance (Miller and Golladay 1996, Boulton 2003). Periodic disturbance, however, may select for specific community assemblages that are more resistant or resilient to disturbance (Miller and Golladay 1996, Boulton 2003). In particular, seasonal drying appears to favor organisms that either possess desiccation-resistant life stages or are capable of rapid recolonization (Miller and Golladay 1996). Multiple studies have identified certain Diptera families possessing these traits, particularly Simuliidae and Chironomidae, as early colonizers (Miller and Golladay 1996, Boulton 2003, Churchel and Batzer 2006). Such colonization patterns may explain the community structure observed in the samples taken above the dam at Bear Creek, in which Simuliidae comprised 61% of the sample.

Another complicating factor is the high degree of habitat heterogeneity among streams. While burned and unburned sites were matched for geomorphological characteristics including watershed size, elevation, and gradient, they still varied substantially in terms of how intact the dams were and, among burned sites, the severity of the burn. Vegetative community composition and woody vegetation density also differed considerably between streams (Whipple 2019). There was even notable variation above and below the dam for some sites; Bear Creek, for example, passed through open pine forest above the dam and closed deciduous forest below the dam. The fact that systematic differences between and within burned and unburned streams are evident despite this tremendous variability suggests that the interaction between dams and wildfire is fairly robust.

Conclusions and Future Directions

The broader-scale interactions between beavers and wildfire remain relatively unexplored. Thus far, the only other study examining this interaction explicitly analyzed dissolved nutrients and riparian vegetation in burned and unburned streams with and without hydrologically significant beaver dams (Whipple 2019). This study found that phosphorus concentrations and pH were lower in burned streams below dams compared to burned streams without beavers, and were

similar between unburned streams and burned streams with beavers (Whipple 2019). Beaver presence also seemed to reduce the density of introduced plant species in burned areas relative to areas without beavers (Whipple 2019). In combination with this study, our study provides support for the hypothesis that beaver dams reduce the negative impacts of wildfire on stream habitats and communities. In future studies, it would be valuable to conduct macroinvertebrate sampling around beaver dams within a year of wildfires in order to identify the more immediate and transient impacts of burns on habitat quality and macroinvertebrate community structure. Furthermore, examination of the interactions between beavers and wildfires in other environments would provide insight into the broader applicability of these findings. Overall, the urgency of climate change and the feasibility of beaver reintroduction as a method of climate change adaptation make further research in this area critical.

Acknowledgements

I would like to thank Peter Wimberger for acting as my thesis advisor and for providing support and guidance throughout the research project, as well as Kena Fox-Dobbs, my thesis reader, who supplied valuable insights and suggestions. I am grateful to Amanda Foster, Hayley Rettig, and Will Brooks for providing assistance and good company in the field. Alexa Whipple helped make this research a possibility by sharing sampling sites and data. Employees of the Methow Beaver Project Julie Nelson, Alec Spencer, and Torre Stockard graciously shared their knowledge, office space, and wi-fi, and allowed us to assist with a beaver relocation. Kent Woodruff helped us locate study sites and gave valuable feedback in the initial stages of the project. Michal Morrison-Kerr kept us supplied and up-to-code. Summer research funding was provided by the McCormick Scholar Award.

References

- Arkle, R. S., D. S. Pilliod, and K. Strickler. 2010. Fire, flow and dynamic equilibrium in stream macroinvertebrate communities. *Freshwater Biology* 55:299–314.
- Balch, J. K., B. A. Bradley, J. T. Abatzoglou, R. C. Nagy, E. J. Fusco, and A. L. Mahood. 2017. Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Sciences* 114:2946–2951.
- Baldwin, J. 2015. Potential mitigation of and adaptation to climate-driven changes in California’s highlands through increased beaver populations. *California Fish and Game* 101:218–240.
- Bladon, K. D., M. B. Emelko, U. Silins, and M. Stone. 2014. Wildfire and the future of water supply. *Environmental Science & Technology* 48:8936–8943.
- Bondi, S. 2009. EcoTrust whole watershed restoration project completion report [project update]. Winthrop, WA: Methow Conservancy. 22 p.
- Boulton, A. J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology* 48:1173–1185.
- Churchel, M. A., and D. P. Batzer. 2006. Recovery of aquatic macroinvertebrate communities from drought in Georgia Piedmont headwater streams. *The American Midland Naturalist* 156:259–272.

- Cooper, S. D., H. M. Page, S. W. Wiseman, K. Klose, D. Bennett, T. Even, S. Sadro, C. E. Nelson, and T. L. Dudley. 2015. Physicochemical and biological responses of streams to wildfire severity in riparian zones. *Freshwater Biology* 60:2600–2619.
- Dahm, C. N., R. I. Candelaria - Ley, C. S. Reale, J. K. Reale, and D. J. V. Horn. 2015. Extreme water quality degradation following a catastrophic forest fire. *Freshwater Biology* 60:2584–2599.
- Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz. 2014. Large wildfire trends in the western United States, 1984–2011. *Geophysical Research Letters* 41:2928–2933.
- Dunham, J. B., A. E. Rosenberger, C. H. Luce, and B. E. Rieman. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. *Ecosystems* 10:335–346.
- Flitcroft, R. L., J. A. Falke, G. H. Reeves, P. F. Hessburg, K. M. McNyset, and L. E. Benda. 2016. Wildfire may increase habitat quality for spring Chinook salmon in the Wenatchee River subbasin, WA, USA. *Forest Ecology and Management* 359:126–140.
- Fritz, K. M., and W. K. Dodds. 2004. Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system. *Hydrobiologia* 527:99–112.
- Gibson, P. P., and J. D. Olden. 2014. Ecology, management, and conservation implications of North American beaver (*Castor canadensis*) in dryland streams. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24:391–409.
- Hames, D. S., B. Conrad, A. Pleus, and D. Smith. 1996. Field comparison of the McNeil sampler with three shovel-based methods used to sample spawning substrate composition in small streams. Olympia, WA: Northwest Indian Fisheries Commission. 39 p.
- Hitt, N. P. 2003. Immediate effects of wildfire on stream temperature. *Journal of Freshwater Ecology* 18:171–173.
- Holden, Z. A., A. Swanson, C. H. Luce, W. M. Jolly, M. Maneta, J. W. Oyler, D. A. Warren, R. Parsons, and D. Affleck. 2018. Decreasing fire season precipitation increased recent western US forest wildfire activity. *Proceedings of the National Academy of Sciences* 115:E8349–E8357.
- Hood, G. A., and D. G. Larson. 2015. Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. *Freshwater Biology* 60:198–208.
- Hossack, B. R., W. H. Lowe, and P. S. Corn. 2013. Rapid increases and time-lagged declines in amphibian occupancy after wildfire. *Conservation Biology* 27:219–228.
- Hossack, B. R., and D. S. Pilliod. 2011. Amphibian responses to wildfire in the Western United States: emerging patterns from short-term studies. *Fire Ecology* 7:129–144.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1996. Organisms as ecosystem engineers. Pages 130–147 in F. B. Samson and F. L. Knopf, editors. *Ecosystem Management: Selected Readings*. Springer, New York, NY.
- Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications: A review. *Journal of Range Management* 37:430–438.

- Kerans, B. L., and J. R. Karr. 1994. A benthic index of biotic integrity (B-IBI) for rivers of the Tennessee Valley. *Ecological Applications* 4:768–785.
- Koontz, E. D., E. A. Steel, and J. D. Olden. 2018. Stream thermal responses to wildfire in the Pacific Northwest. *Freshwater Science* 37:731–746.
- Law, A., M. J. Gaywood, K. C. Jones, P. Ramsay, and N. J. Willby. 2017. Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. *Science of The Total Environment* 605–606:1021–1030.
- Levine, R., and G. A. Meyer. 2014. Beaver dams and channel sediment dynamics on Odell Creek, Centennial Valley, Montana, USA. *Geomorphology* 205:51–64.
- Liu, Y., S. L. Goodrick, and J. A. Stanturf. 2013. Future U.S. wildfire potential trends projected using a dynamically downscaled climate change scenario. *Forest Ecology and Management* 294:120–135.
- Lyon, J. P., and J. P. O’connor. 2008. Smoke on the water: can riverine fish populations recover following a catastrophic fire-related sediment slug? *Austral Ecology* 33:794–806.
- Mahlum, S. K., L. A. Eby, M. K. Young, C. G. Clancy, and M. Jakober. 2011. Effects of wildfire on stream temperatures in the Bitterroot River Basin, Montana. *International Journal of Wildland Fire* 20:240–247.
- Majerova, M., B. T. Neilson, N. M. Schmadel, J. M. Wheaton, and C. J. Snow. 2015. Impacts of beaver dams on hydrologic and temperature regimes in a mountain stream. *Hydrology and Earth System Sciences* 19:3541–3556.
- Malison, R. L., and C. V. Baxter. 2010. Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. *Journal of the North American Benthological Society* 29:1324–1338.
- McCreech, R. K., K. Fox-Dobbs, P. Wimberger, K. Woodruff, G. Holtgrieve, and T. K. Pool. 2019. Reintroduced beavers rapidly influence the storage and biogeochemistry of sediments in headwater streams (Methow River, Washington). *Northwest Science* 93:112–121.
- Mellon, C. D., M. S. Wipfli, and J. L. Li. 2008. Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A. *Freshwater Biology* 53:2331–2343.
- Methow Salmon Recovery Foundation. 2018. Methow beaver project: status report 2016-2017. 31 p.
- Miller, A. M., and S. W. Golladay. 1996. Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. *Journal of the North American Benthological Society* 15:670–689.
- Miller, P. 2009. Before New York, rediscovering the wilderness. *National Geographic Magazine* 126: 122–137.
- Minshall, G. W., T. V. Royer, and C. T. Robinson. 2001. Response of the Cache Creek macroinvertebrates during the first 10 years following disturbance by the 1988 Yellowstone wildfires. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1077–1088.

- Musetta-Lambert, J., D. Kreutzweiser, and P. Sibley. 2019. Influence of wildfire and harvesting on aquatic and terrestrial invertebrate drift patterns in boreal headwater streams. *Hydrobiologia* 834:27–45.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. *BioScience* 38:753–762.
- Pilliod, D. S., A. T. Rohde, S. Charnley, R. R. Davee, J. B. Dunham, H. Gosnell, G. E. Grant, M. B. Hausner, J. L. Huntington, and C. Nash. 2018. Survey of beaver-related restoration practices in rangeland streams of the Western USA. *Environmental Management* 61:58–68.
- Pollock, M. M., T. J. Beechie, and C. E. Jordan. 2007. Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. *Earth Surface Processes and Landforms* 32:1174–1185.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Relyea, C. D., G. W. Minshall, and R. J. Danehy. 2000. Stream insects as bioindicators of fine sediment. *Water Environmental Federation* 24:663–686.
- Rosenberger, A. E., J. B. Dunham, J. R. Neuswanger, and S. F. Railsback. 2015. Legacy effects of wildfire on stream thermal regimes and rainbow trout ecology: an integrated analysis of observation and individual-based models. *Freshwater Science* 34:1571–1584.
- Rust, A. J., T. S. Hogue, S. Saxe, and J. McCray. 2018. Post-fire water-quality response in the western United States. *International Journal of Wildland Fire* 27:203–216.
- Sestrich, C. M., T. E. McMahon, and M. K. Young. 2011. Influence of fire on native and nonnative salmonid populations and habitat in a Western Montana Basin. *Transactions of the American Fisheries Society* 140:136–146.
- Seton, J. R. 1929. *Lives of game animals. Vol. 4, Part 2, Rodents, etc.* Doubleday, Doran, Garden City, NY.
- Silins, U., K. D. Bladon, E. N. Kelly, E. Esch, J. R. Spence, M. Stone, M. B. Emelko, S. Boon, M. J. Wagner, C. H. S. Williams, and I. Tichkowsky. 2014. Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. *Ecohydrology* 7:1508–1523.
- Smith, H. G., G. J. Sheridan, P. N. J. Lane, P. Nyman, and S. Haydon. 2011. Wildfire effects on water quality in forest catchments: A review with implications for water supply. *Journal of Hydrology* 396:170–192.
- Smith, J. M., and M. E. Mather. 2013. Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshwater Biology* 58:1523–1538.
- Verkaik, I., M. Vila-Escalé, M. Rieradevall, C. V. Baxter, P. S. Lake, G. W. Minshall, P. Reich, and N. Prat. 2015. Stream macroinvertebrate community responses to fire: are they the same in different fire-prone biogeographic regions? *Freshwater Science* 34:1527–1541.

- Vieira, N. K. M., W. H. Clements, L. S. Guevara, and B. F. Jacobs. 2004. Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshwater Biology* 49:1243–1259.
- Wagenhoff, A., C. R. Townsend, and C. D. Matthaei. 2012. Macroinvertebrate responses along broad stressor gradients of deposited fine sediment and dissolved nutrients: a stream mesocosm experiment. *Journal of Applied Ecology* 49:892–902.
- Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology* 41:115–139.
- Weber, N., N. Bouwes, M. M. Pollock, C. Volk, J. M. Wheaton, G. Wathen, J. Wirtz, and C. E. Jordan. 2017. Alteration of stream temperature by natural and artificial beaver dams. *PLOS ONE* 12:e0176313.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase Western U.S. forest wildfire activity. *Science* 313:940–943.
- Whipple, A. 2019. Riparian resilience in the face of interacting disturbances: understanding complex interactions between wildfire, erosion, and beaver (*Castor canadensis*) in grazed dryland riparian systems of low order streams in north central Washington State, USA [dissertation]. Cheney: Eastern Washington University.
- Wohl, E. 2019. *Saving the dammed: why we need beaver-modified ecosystems*. Oxford University Press, New York, NY.
- Wright, J. P., C. G. Jones, and A. S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101.