

**Restoration potential of beaver for hydrological resilience  
in a changing climate**

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**Abstract**

**Restoration potential of beaver for hydrological resilience  
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Beavers have long been recognized for their ability to increase the ecological function of riparian and aquatic ecosystems. Beaver pond complexes increase geomorphic complexity, surface and groundwater storage, and moderate stream temperature, leading to higher levels of biological and ecosystem diversity. Recently, it has been proposed that beaver may be able to reduce the ecological impacts associated with climate change. In the Pacific Northwest (USA), climate models suggest that temperatures will continue to rise through the next century. Elevated winter temperatures will cause a greater portion of precipitation to fall as rain instead of snow and will lead to earlier snowmelt at higher elevations. With less snowpack, summer low flows are likely to be reduced, potentially threatening aquatic species that rely on cool stream temperatures supplemented by snowmelt. Here, I evaluated whether increasing current beaver populations could reduce these hydrologic impacts of climate change at a variety of spatial and temporal

scales. I first developed a predictive beaver habitat model – the beaver intrinsic potential habitat model – as a tool to identify where beaver could exist in a given watershed and to assist in translocation prioritization. Using results from this model, I trapped 91 beaver from lowland areas and relocated them into the Skykomish River watershed, in Washington State, and evaluated how relocated beaver affect stream temperature and surface and groundwater storage. Using these results, I then developed a regional model for western Washington and Oregon that explored the degree to which beaver reintroductions could offset reductions in water availability under various climate scenarios and time frames. The intrinsic potential habitat model identified and ranked potential beaver habitat with a 92 percent accuracy. Population surveys during field validation found beaver to be present in 43 percent of habitable reaches. Through my reintroduction experiment, I found that successful beaver relocations created 243 m<sup>3</sup> of surface water storage per 100 m stream reach in the first year following relocation and stored approximately 2.4 times as much groundwater as surface water per relocation reach. On average, stream reaches downstream of newly created beaver dams exhibited a 2.3°C cooling effect in stream temperature during summer base flow conditions. Finally, the regional storage model indicated that despite substantial storage potential from dams, their contribution will likely be small relative to the large amount of snowpack projected to be lost by the end of this century. In snow-dominated basins, beaver may be able to offset small amounts of lost snowpack due to climate change. In basins of the Pacific Northwest that are historically rain dominated, however, beavers have the potential to increase summer water availability by up to 20%. Supporting re-colonization of beavers in areas in which they have not reached carrying capacity could increase hydrologic and thermal resilience to climate change in many basins of the Pacific Northwest.

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## Chapter 1. Introduction

Recent observations and current climate models suggest that the Pacific Northwest (USA) will continue to experience considerable climatic and hydrologic alterations over the next century (Dalton et al. 2013, Mote and Salathé 2010, IPCC 2013). Temperatures will continue to increase and these increases will be most pronounced in mountainous areas. Changes in precipitation will vary regionally, but in many places summer precipitation and stream flow will likely decrease, as will snowpack. Snow melt is projected to come earlier in the year, and winter precipitation, storm intensity, and stream temperatures will likely increase (Littell et al. 2009, Dalton et al. 2013).

These changes will likely disrupt physical, hydrologic, and ecosystem processes, which could have adverse impacts on riparian habitats and species (Mauger et al. 2015). For example, increased winter storm quantity and intensity have the potential to cause salmonid redd scour, bed and bank erosion, and floodplain disconnection from channel down-cutting (Pollock et al. 2014). Summer stream flow is also expected to be adversely affected by lower base flow and higher peak temperatures (Stewart et al. 2005, Littell et al. 2013). The reduction of surface water and soil moisture may result in increased stress and disturbances such as wildfire (Mauger et al. 2015, Gergel et al. 2017). Both hydrologic stability and ecosystem resilience will be substantially reduced by these changes. ESA-listed fish and wildlife, such as salmon (*Oncorhynchus*) and steelhead (*O. mykiss*), may have limited habitat if these projections are realized.

Continued impacts from anthropogenic disturbances, such as development, are likely to further exacerbate the impacts of climate change on aquatic systems and the ecosystem services that they provide. The loss of up to 50% of historical wetlands in many areas, straightening of stream and river systems, and encroachment into floodplains have increased the magnitude and

duration of both peak and low flows. As summer precipitation and base flow decrease, there will be increased need to identify and use remaining areas of high quality habitat. Likewise, there will be a greater human demand for water. This is already apparent where competing human and ecological interests have sparked a debate on the use of water rights for agriculture or for preserving minimum base flows for fish and other aquatic species.

Beavers (*Castor canadensis*) have long been recognized for their ability to increase the ecological function of riparian and aquatic ecosystems. Beavers alter the landscape by building dams to create pond and wetland complexes. They increase surface and groundwater storage (Johnston and Naiman 1987, Majerova et al. 2015) and geomorphic complexity (Gurnell 1998, Meentemeyer and Butler 1999). Their dams have been shown to attenuate peak flows (Parker 1986, Nyssen et al. 2011) and regulate stream temperature and base flow. They also promote and improve water quality and nutrient cycling (Smith et al. 1991, Correll et al. 2000), and they regulate sediment transport and retention (Meentemeyer and Butler 1999), leading to channel aggradation and floodplain reconnection (Pollock et al. 2014). By removing riparian vegetation and raising groundwater tables adjacent to ponds, beavers alter plant community structure, composition, and successional patterns (Pastor et al. 1984, Johnston and Naiman 1990). This increase in heterogeneity (Naiman et al. 2000) leads to increased biological diversity (Jones et al. 1994, Pollock et al. 1995, McMaster and McMaster 2000) and ecosystem resilience (Naiman et al. 1986).

The types of impoundments that beavers create may offset hydrologic and temperature changes anticipated to occur in a changing climate. The use of beaver specifically as a climate-change adaptation strategy, however, has not been well tested. The ecological implications resulting from observed and predicted changes have placed an increased emphasis on identifying

approaches that reduce impacts to ecological communities, and the processes that maintain them. Thus, further study of the role of beavers as ecosystem engineers is needed to enhance ecological resilience in aquatic systems.

### **1.1. Objectives and dissertation chapters**

This dissertation fills key gaps in our understanding of how beaver affect processes that regulate water storage and water temperature at multiple spatial scales. The collection of chapters in this dissertation provide ecological and hydrological context for how local-scale processes are affected by beaver relocation and new dam-building, and how beavers might reduce some climate impacts if at sufficient numbers. My objectives were the following:

- (1) Develop a predictive tool to identify potential beaver habitat that could be used for relocation, prioritization for restoration, characterization of meta-populations, and for subsequent modeling purposes (Chapter 2);
- (2) Quantify the effects of beaver relocation on surface and groundwater storage, stream temperature, and geomorphology (Chapter 3);
- (3) Model the water storage potential of beaver activity at basin and regional scales to assess the degree to which beaver complexes may supplement summer water availability and offset late-season snowpack loss under future climate scenarios (Chapter 4);
- (4) Provide an overview of my research results and discussion of future research needs, including evaluation of how beaver influence scale-dependent ecosystem processes (Chapter 5).

## 1.2. References

- Correll, D. L., T. E. Jordan, and D. E. Weller. 2000. Beaver pond biogeochemical effects in the Maryland Coastal Plain. *Biogeochemistry* 49:217–239.
- Dalton, M. M., P. W. Mote, A. K. Snover, and A. k. S. Dalton, M.M., P.W. Mote. 2013. *Climate Change in the Northwest: Implications for Our Landscapes, Waters, and Communities*. Island Press, Washington Dc.
- Gergel, D. R., B. Nijssen, J. T. Abatzoglou, D. P. Lettenmaier, and M. R. Stumbaugh. 2017. Effects of climate change on snowpack and fire potential in the western USA. *Climatic Change* 141:287–299.
- Gurnell, A. M. 1998. The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography* 22:167–189.
- Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. *Landscape Ecology* 1:47–57.
- Johnston, C. A., and R. J. Naiman. 1990. Aquatic patch creation in relation to beaver population trends. *Ecology* 71:1617–1621.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.
- Littell, J. S., M. Elsner, L. C. W. Binder, and A. Snover. 2009. *The Washington climate change impacts assessment: Evaluating Washington’s future in a changing climate*. Climate Impacts Group, Seattle, Washington.
- Littell, J. S., G. S. Mauger, E. P. Salathé, A. F. Hamlet, S. Y. Lee, M. R. Stumbaugh, M. Elsner, R. Norheim, E. R. Lutz, and J. Nathan. 2013. *Uncertainty and extreme events in future climate and hydrologic projections for the Pacific Northwest: Providing a basis for vulnerability and core/corridor assessments*. Climate Impacts Group, Seattle, WA, USA.
- 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.
- Mauger, G. S., J. H. Casola, H. A. Morgan, R. L. Strauch, B. Jones, B. Curry, T. M. B. Isaksen, L. W. Binder, M. B. Krosby, and A. K. Snover. 2015. *State of Knowledge: Climate Change in Puget Sound*. Climate Impacts Group, Seattle, WA, USA.
- McMaster, R. T., and N. D. McMaster. 2000. Vascular flora of beaver wetlands in western

- Massachusetts. *Rhodora*:175–197.
- Meentemeyer, R. K., and D. R. Butler. 1999. Hydrogeomorphic effects of beaver dams in glacier national park, Montana. *Physical Geography* 20:436–446.
- Mote, P. W., and E. P. Salathé. 2010. Future climate in the Pacific Northwest. *Climatic Change* 102:29–50.
- Naiman, J. R., J. M. Melillo, J. E. Hobbie, R. J. Naiman, J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67:1254–1269.
- Naiman, R. J., S. R. Elliott, J. M. Helfield, and T. C. O’Keefe. 2000. Biophysical interactions and the structure and dynamics of riverine ecosystems: The importance of biotic feedbacks. *Hydrobiologia* 410:79–86.
- Nyssen, J., J. Pontzele, and P. Billi. 2011. Effect of beaver dams on the hydrology of small mountain streams: Example from the Chevral in the Ourthe Orientale basin, Ardennes, Belgium. *Journal of Hydrology* 402:92–102.
- Parker, M. 1986. Beaver, water quality, and riparian systems. Pages 28–30 Wyoming Water 1986 and Streamside Zone Conference. The Center, Casper, Wyoming, USA.
- Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes. 1984. Moose, microbes, and boreal forest 38:770–777.
- Pollock, M. M., T. J. Beechie, J. M. Wheaton, C. E. Jordan, N. Bouwes, N. Weber, and C. Volk. 2014. Using beaver dams to restore incised stream ecosystems. *BioScience* 64:279–290.
- Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1995. Beaver as engineers: Influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 in C. G. Lawton and J. J. H., editors. *Linking species to ecosystems*. Chapman & Hall, New York, NY, USA.
- Smith, M. E., C. T. Driscoll, B. J. Wysłowski, C. M. Brooks, and C. C. Cosentini. 1991. Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Canadian Journal of Zoology* 69:55–61.
- Stewart, I. T., D. R. Cayan, and M. D. Dettinger. 2005. Changes toward earlier streamflow timing across western. *North American Journal of Climatology*. 18:10.

## Chapter 2. **Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation**

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### **2.1. Abstract**

Through their dam-building activities and subsequent water storage, beaver have the potential to restore riparian ecosystems and offset some of the predicted effects of climate change by modulating streamflow. Thus, it is not surprising that reintroducing beaver to watersheds from which they have been extirpated is an often-used restoration and climate-adaptation strategy. Identifying sites for reintroduction, however, requires detailed information about habitat factors – information that is not often available at broad spatial scales. Here we explore the potential for beaver reintroductions throughout the Snohomish River Basin in Washington, USA with a model that identifies some of the basic building blocks of beaver habitat suitability and does so by relying solely on remotely sensed data. More specifically, we developed a generalized intrinsic potential model that draws on remotely sensed measures of stream gradient, stream width, and valley width to identify where beaver could become established if suitable vegetation were to be present. Thus, the model serves as a preliminary screening tool that can be applied over relatively large extents. We applied the model to 5,019 stream km and assessed the ability of the model to correctly predict beaver habitat by surveying for beavers in 352 stream reaches. To further assess the potential for reintroduction, we assessed land ownership, use, and land cover in the landscape surrounding stream reaches with varying levels of intrinsic potential. Model results

showed that 33% of streams had moderate or high intrinsic potential for beaver habitat. No site that was classified as having low intrinsic potential had any sign of beavers and that beaver were absent from at nearly three quarters of potentially suitable sites, indicating that there are factors preventing the local population from occupying these areas. Of the riparian areas around streams with high intrinsic potential for beaver, only 38% are on public lands and only 17% are on large tracts of privately-owned timber land. Thus, although there are a large number of areas that could benefit from relocation and restoration using beavers, current land use patterns may substantially limit feasibility in these areas.

## 2.2. Introduction

North American beaver (*Castor canadensis*) have long been recognized as ecosystem engineers, creating diverse and resilient wetland and riverine systems (Pollock et al. 1995, Wright et al. 2002). Prior to near extirpation in the early 1900's due to over-trapping and habitat conversion (Mackie 1997), beavers and beaver-created wetland complexes were a ubiquitous component of riparian systems (Johnston and Naiman 1986). Many species depend upon these systems due to the high geomorphic complexity, aquatic thermal variability, and habitat diversity that they afford. For example, the decline in populations of some aquatic species, including Pacific Coho salmon (*Oncorhynchus kisutch*), have been partially attributed to the loss of beaver ponds (Pollock et al. 2004), a feature that salmonids have evolved with since at least the Pleistocene (Robinson et al. 2007).

Because of their abilities to modify streams and floodplains, beavers have the potential to play a critical role in shaping how riparian and stream ecosystems respond to climate change. The Pacific Northwest of the United States is experiencing increases in annual air temperature and decreases in snow pack and summer precipitation (Elsner et al. 2010, Raymond et al. 2014), resulting in lower base flows, particularly in streams that rely on late season snowmelt. Climate shifts have altered stream-temperature regimes to the detriment of cold-water fishes, including Pacific salmon (Elsner et al. 2010). Recent increases in winter precipitation and storm magnitude have increased the potential for stream scour, channel incision, and floodplain disconnection, thereby promoting the drying of adjacent riparian areas (Stavros et al. 2014, Pollock et al. 2014). By damming streams, beavers create pond and wetland complexes that increase spatial heterogeneity and geomorphic complexity, species and habitat diversity, and therefore ecosystem resilience to climate-induced environmental change (Naiman et al. 2000, Janzen and Westbrook 2011, Gibson and Olden 2014). Beaver impoundments slow stream velocity allowing sediment

suspended in the water column to precipitate, aggrading incised stream systems, and reconnecting streams with their floodplains (Pollock et al. 2014). The increase in surface water promotes groundwater recharge, storage, and supplementation during base flows (Janzen and Westbrook 2011). The increased geomorphic complexity also promotes higher thermal variability and cold-water refugia in deeper waters and in areas of downstream upwelling. In recent years, beaver populations have begun to rebound in many areas of their historical range, and recolonized formerly occupied areas (Johnston and Naiman 1990, Snodgrass 1997, Whitfield et al. 2015). As they have done so, there have been responses in riparian ecosystem resilience and functionality (Kemp et al. 2012).

Understanding and predicting where suitable beaver habitat exists within their geographic range can help inform recovery efforts, restoration planning, and conflict avoidance in populated areas. Beavers are generalist species (Jenkins 1975) and can be found in most biomes of North America (Jenkins and Busher 1979). Regional habitat suitability index (HSI) models have been developed throughout North America to map suitable beaver habitat characteristics (Table 2.1). These models predict currently suitable beaver habitat, but have less utility for predicting where beaver could be if they modify the landscape, or appropriate restoration actions or land-use management actions were taken. Because vegetation often does not meet criteria that a traditional HSI model would identify as suitable, many potentially suitable areas are not considered for restoration planning or relocation actions. Additionally, and perhaps more importantly, vegetation data are not currently mapped at fine enough spatial resolutions to allow for landscape-scale HSI models to be applied over larger spatial extents.

Intrinsic potential models provide an alternative to HSI models (which generally use both intrinsic and extrinsic predictors) by using geomorphic variables that are less prone to change

through time. Intrinsic potential models have been previously used to inform fish habitat restoration work (Burnett et al. 2003), and some have proposed using intrinsic potential for non-fish species, including beaver (Benda et al. 2007). To date, however, beaver intrinsic potential (BIP) models have not been developed and field-verified. BIP models may be more appropriate than HSI models for predicting where beavers can likely exist within a watershed given the ability of beavers to modify variable habitat characteristics such as vegetation density and type. Intrinsic variables appropriate for use in BIP models are those that cannot be readily altered by beaver colonization. These include site features such as regional climate, precipitation regime, stream gradient, stream width, and valley width. The variables used in previous HSI models (Table 2.1) are often good predictors of current or historical beaver presence. However, they fail to identify areas that may become suitable if transformed by beavers into high quality habitat through restoration actions or management changes, and are therefore less useful in areas below carrying capacity or areas altered by anthropogenic impacts.

Here, we develop and apply a beaver intrinsic potential model that can both predict where high quality beaver habitat currently exists as well as areas likely to be colonized as population levels increase or if management changes are made (e.g. expansion of a riparian buffer or greater implementation of non-lethal beaver management options). We developed our BIP model within the Snohomish River Basin, Washington State, and validated it within the Skykomish River sub-basin. Our study had four primary objectives. The first was to develop a BIP model parameterized with readily available, remotely sensed, public data, thus facilitating the transferability of the approach to other regions. The second was to evaluate the effectiveness of our BIP model within a large basin that has high levels of hydrogeomorphic complexity and highly variable beaver population densities. The third objective was to assess the potential for

continued population expansion by assessing the degree to which beaver occupied areas with high intrinsic potential. Finally, we aimed to explore the potential constraints or barriers to colonization and occupancy of areas with high intrinsic potential by assessing land use in riparian areas with high intrinsic potential.

## **2.3. Materials and methods**

### ***2.3.1. Site description***

The Snohomish River Basin (4,807 km<sup>2</sup>), located on the west slope of the Cascade Range in Washington State, was selected for BIP model development, and the Skykomish River sub-basin (2,160 km<sup>2</sup>) was used for model validation (Figure 2.1). The Snohomish basin was chosen because this area provides an excellent test case as the region's hydrology is both highly spatially and temporally variable; abundant precipitation in the winter and sporadic precipitation in the summer adds complexity to model development. Channel gradient and morphology varies greatly throughout the basin. Mountainous areas contain narrow, glacially carved valleys and high-gradient streams, which transition to low-gradient streams across a wide, hilly plateau, and a large river floodplain with extensive side channels and tributary junctions. This varying geomorphic context allows for a more thorough assessment of geomorphic conditions (e.g. gradient and valley width) as suitability predictors. Additionally, the Snohomish Basin is a priority area for regional salmonid recovery work as well as a focus area for regional climate-change research, environmental monitoring, and intensive beaver population surveys (Snohomish Basin Salmon Recovery Forum 2005, Raymond et al. 2013, 2014). The basin is representative of other watersheds in the region in terms of habitat conditions, importance for

regional aquatic species, and potential climate refugia for wildlife (Snohomish Basin Salmon Recovery Forum 2005, Scheuerell et al. 2006, Bartz et al. 2015).

### ***2.3.2. Data collection and model development***

In preparation for BIP model development, we evaluated previously proposed beaver habitat suitability models documented in the literature (Table 2.1). The environmental variables most commonly cited as the best predictors of habitat suitability were vegetation composition, stream gradient, stream bankfull width, and stream valley width.

Stream gradient is frequently correlated with beaver presence and is an ideal indicator of intrinsic potential due to its low likelihood to change over time. Beavers will most often colonize streams with gradients from 0 to 6% (Allen 1982), although those below 3% are preferred (Retzer 1956). Stream gradient is associated with a number of related site characteristics that make it a good predictor of suitable beaver habitat. Low gradient reaches have slower moving water with finer substrates, which allows beavers to anchor dams to the stream-bed and provides mud for dam and lodge construction. Low gradient reaches also allow constructed dams to spread water across a larger area, increasing surface area to dam ratio and decreasing costs and risks of dam-building (e.g. effort required for tree cutting and increased predation while on land) (Pollock et al. 2014).

Stream bankfull width and associated environmental variables such as upstream contributing basin size and stream power have been identified as primary characteristics of potentially suitable habitat. Suzuki and McComb (Suzuki and McComb 1998) reported that beavers in preferred streams between 3-4 m wide for damming with an outside range of 2-10 m Oregon's Coast Range, USA. Barnes and Mallik (Barnes and Mallik 1997) found that the upstream watershed area was most useful for differentiating active and previously colonized sites

from sites with no dams, in Ontario, Canada. Pollock et al. (Pollock et al. 2004) analyzed the effect of stream power, a measure of stream force incorporating discharge and channel slope, and found that beaver dams were limited to sites with a stream power of less than  $2,000 \text{ J*s}^{-1}\text{m}^{-1}$  in streams of Washington State, USA. Streams of a larger size or power have the likelihood of breaching dams during yearly high flow periods so beaver preference for lower power flows would be a successful adaptation strategy.

Valley width is a measure of stream confinement commonly used in HSI models and is often correlated with stream order and gradient. Earlier studies of habitat suitability did not use this metric as it requires more advanced spatial analysis software to generate basin-wide quantitative measures. More recent studies have found valley width to be a strong predictor of habitat suitability, and potentially for intrinsic potential (Cox and Nelson 2009). This metric may be more important in mountainous and topographically diverse areas where stream confinement more frequently occurs. Reaches with valley widths greater than 46 m were found to be optimal (Allen 1982, Perkins 2000). This measure, however, is likely regionally variable and requires further characterization.

We did not include extrinsic or modifiable factors such as vegetative cover in our model because those variables may change over time and are more difficult to assess remotely. Thus, the BIP model is intended to identify sites where the hydrogeomorphic, or underlying intrinsic physical conditions, are suitable for beaver dams. Unlike most habitat suitability models, the BIP model does not classify sites as unsuitable if habitat restoration, management changes, or beaver modification could allow beaver to thrive there.

We compiled and derived remotely sensed spatial, hydrogeomorphic, and other physical data for the Snohomish River Basin. We processed all spatial data layers and compiled them in a

Geographic Information System (GIS) using ArcGIS. We obtained hydrography data layers consisting of a combination of field-verified and Digital Elevation Model (DEM)-derived stream segments from King and Snohomish Counties, Washington. We derived stream slope, bankfull width, discharge, and stream segment breaks using the methodology outlined by Davies et al. (Davies et al. 2007). The valley width for each stream segment was then calculated using the methodology described in Beechie and Imaki (Beechie and Imaki 2014). Valley width was defined as the average width of the area adjacent to a stream segment that was within 2 m vertical elevation of the channel elevation. We obtained soil type and permeability layers within the study watershed from U.S. Forest Service soil inventories (Snyder and Wade 1970). Soil types (e.g. sandy-loam) were converted to percent silt, clay, and sand so that these data could be treated as continuous variables instead of factors for multivariate analysis during validation.

To assist in identifying the range of intrinsic potential habitat within our study basin, we selected 501 stream segments showing signs of current or recently abandoned beaver ponding using Google Earth and NAIP orthographic imagery. These segments were sampled from the Snohomish watershed, but excluded the Skykomish sub-basin where model validation occurred. We described stream slope, stream width, and valley width within each segment to identify the range of conditions present at sites that beavers colonized (Figure 2.2).

Based on the range of conditions present at potentially suitable sites, we assigned a ranked value from 0-4 to each of these variables, commensurate with their level of intrinsic potential according to the criteria in Table 2.2. Ranking values for each variable were based on a combination of expert opinion and analysis of habitat preference at locations identified in Figure 2.1. Higher weight (value 4) was given to metrics with high intrinsic habitat potential (e.g. slope  $\leq$  1%). We assigned a final BIP

score for each segment by summing the ranked scores of stream slope, stream width, and valley width (analogous to the IP model of Burnett et al. (Burnett et al. 2003). We assigned intrinsic potential scores to all stream segments within the Snohomish River Basin to produce the BIP model. The model possesses four predictive categories of beaver intrinsic potential: No BIP, Low, Moderate, and High BIP, numbered 0-3, respectively.

Following completion of model development, we compared the spatial distribution of modeled intrinsic potential to land use in the Snohomish Basin to identify how habitat was distributed across the landscape and where it might be at odds with existing human use. Land use was identified within 30-m buffers of all modeled streams using Snohomish County zoning GIS data.

### ***2.3.3. Field validation of remote sensing based BIP***

We field verified the BIP model in the Skykomish River sub-basin, testing how well the modeled intrinsic potential predicted field-assessed intrinsic potential at surveyed sites. We limited survey locations to those that were within stream segments that had a relatively homogenous gradient and stream width within the mapped stream segment. Using a quasi-random approach, we selected 100 stream segments from each of the four BIP classes (0-3) for a total of 400 survey sites, which were reduced to 352 due to access limitations in some cases. We conducted a blind assessment of conditions at each field location. The same metrics used to construct model scores within mapped stream segment, stream slope, width, and valley width, were evaluated in the field. A field score for each segment was found using the same methods used in the model ( Table 2.2). Together, these surveys evaluated 32.1 stream kms.

Prior to validating model scores with field conditions, we established an intrinsic potential threshold, or a cutoff, separating high IP model scores from those thought to be less

suitable using methods in (Hirzel et al. 2006). We established a threshold between values 1 and 2, thereby grouping model values 0 and 1 as no BIP, and values 2 and 3 as high BIP. We arrived at this threshold by comparing stepwise combinations of model scores.

We performed a validation test for the BIP model's ability to predict the site's intrinsic habitat potential. Validation was conducted by comparing modeled suitability with observed BIP at 352 stream segments using a contingency table. Overall model accuracy, sensitivity, and specificity were assessed.

#### ***2.3.4. Predicting beaver occupancy***

In addition to comparing our model predictions to BIP assessed in the field, we determined the degree to which BIP based on remotely sensed data predicted beaver occupancy. We surveyed the same 352 sites used in our validation effort for signs of both current and historical occupation. Site occupancy was determined by the presence of recent beaver sign, such as freshly chewed sticks, cut logs, fresh scent mounds, or presence of actively maintained dam or lodge structures (following Snodgrass and Meffe (Snodgrass and Meffe 1998)). In areas with questionable occupancy we confirmed presence with multiple revisits, use of wildlife cameras, and by placing small notches in the crest of dams and monitored them through the summer for repair. A number of sites appeared to be recently vacated, yet retained high intrinsic habitat potential; these sites lacked new sign or recently maintained structures, but still had dams that impounded water to near the crest, supporting a large wetland complex.

## **2.4. Results**

### ***2.4.1. Data & model development***

The BIP model assigned one of four BIP values (*High, Moderate, Low, or No BIP*) to 48,397 stream segments comprising 5,019 stream km within the Snohomish River Basin (Figure 2.3 and Table 2.3). Most reaches with high BIP were concentrated in lower gradient areas outside of the Cascade Mountains. Approximately 23% of all streams were categorized as high BIP, 10% as moderate, and 8% as low BIP. The remainder of the streams (ca. 59%) in the basin were classified as having no intrinsic potential for beaver colonization. Most of these were high gradient headwaters. The majority of high BIP reaches were located in low gradient streams (i.e.  $\leq 3\%$ ) with wide floodplains or on side channels of large rivers. Smaller pockets of high BIP reaches were also identified in more mountainous areas.

### ***2.4.2. Field validation and beaver occupancy***

Within 352 randomly selected field points, we rated 91 segments modeled as high BIP, 82 segments modeled as medium BIP, 83 low BIP segments, and 96 modeled as no BIP (Figure 2.4). Comparison of modeled (expected) site scores with field-observed site conditions reveal that overall map accuracy was 91%, model specificity (rate of low BIP prediction accuracy) was 86%, and sensitivity (rate of high BIP prediction accuracy) was 99% (Table 2.4). Error in stream alignment in the original stream data layer was likely the greatest source of model error, and when present, likely precipitated other environmental variable error.

Of the 352 stream segments that were field verified, 39 sites were actively colonized and 85 had evidence of active or historic dam-building (Table 2.3). Fifty nine percent of all sites classified as having moderate or high intrinsic potential had signs of current or past beaver

occupancy. No site that was classified as having low intrinsic potential had any sign of beavers (Table 2.4).

### **2.4.3. Land use**

Although 60% of all 30-m riparian buffers are located within open space and on public timber lands in the Snohomish Basin – areas likely to experience the lowest conflict from beaver colonization due to fewer competing human interests – 79% of these areas are classified as having no intrinsic potential for beavers. Over half of areas with high BIP (59%) are located in human-dominated landscapes (Figure 2.5A). Furthermore, higher intensity, human dominated land uses, such as agriculture and residential development have much greater proportions of higher quality BIP habitat than natural lands, demonstrating why human-beaver conflicts are so common (Figure 2.5B).

## **2.5. Discussion**

Beaver reintroductions hold much potential for habitat restoration and for addressing the impacts of climate change (Pollock et al. 2015). Identifying where to perform those introductions over large areas, however, remains a conservation challenge. Here, we demonstrate how models of remotely sensed intrinsic habitat potential identify potential habitat with high confidence. This approach offers a straightforward method for developing accurate estimates of the potential for beaver habitat using readily available data. The accuracy of this model makes it particularly useful for identifying sites that are suitable for beaver reintroduction and beaver-assisted restoration.

Beavers present a unique challenge and opportunity for accurate habitat model development, especially in areas where populations are below carrying capacity or where a large

amount of unimproved vacant habitat exists. The use of BIP models has the advantage over traditional habitat suitability models of detecting potential habitat, regardless of the current vegetative cover or land use. In areas such as the Snohomish basin, where our model found population levels to be at less than half of carrying capacity, the effects of beaver colonization (i.e. dam building, pond formation, and subsequent aggradation of stream channels: (Pollock et al. 2014)) – have the potential to increase the suitability of surrounding habitat.

Our study demonstrates that there is a large amount of potential habitat within the Snohomish watershed that remains unoccupied by beavers, much of which is in fragmented landscapes and in ownership patterns to which it is not easy to apply beaver restoration (Figure 2.5). Although there appear to be many opportunities to use beaver as a restoration tool and to mitigate the effects of climate change throughout the Snohomish basin, many of these opportunities exist in areas where ownership patterns are diverse. Watersheds such as the Skykomish sub-basin, however, which are dominated by public ownership, provide ample opportunities to test how beavers can be reintroduced into landscapes where they are absent or at low population levels.

In the Skykomish sub-basin, site assessments showed no sign or evidence of past beaver presence in many stream segments categorized as geomorphologically suitable beaver habitat by the BIP model and site surveys. Field surveys indicate that close to three-quarters of geomorphologically suitable sites in the basin are vacant, raising the question: why are there no colonies in these areas? A recent study of the European beaver (*Castor fibre*) demonstrates that in areas where beaver populations are depressed, but unexploited, they will increase rapidly towards carrying capacity (Parker and Rosell 2014). It is possible that a combination of top-down, bottom-up, and abiotic controls are preventing colonization or suppressing population

growth rates. Top-down and abiotic constraints on recovery rates could include high predation levels, environmental stressors (e.g. harsh winter conditions at higher elevations), limited dispersal corridors due to fragmented habitat and constrained topography, or undocumented recreational trapping. Bottom-up pressures may include previously unexplored interactions such as conifer encroachment into historical beaver meadows and a shift in vegetative composition to include less palatable species. Given these pressures, uncolonized areas meeting minimal habitat requirements may experience a very gradual expansion as beavers go through the initial steps of transforming each site's morphology and vegetative composition. In the meantime, areas surrounding currently occupied sites may experience occasional, temporary colonization, but will not be continuously occupied. It is within these sites that there are opportunities for restoration and reintroductions.

It is also possible that such reaches were inhabited by beavers prior to their extirpation by European trappers in the early to mid-1800s, but that the length of time passed since extirpation, land-use activities, and the humid climate has removed more obvious signs of their existence. Unfortunately, we could find no historical records characterizing pre-European beaver abundance in our study basin, so we have no such data to which we can compare our model results.

Like many watersheds, the Snohomish is projected to experience substantial hydrologic change over the next 100 years due to changing climatic conditions (Mote et al. 2008). Summer precipitation is projected to decrease and winter precipitation to increase. This may convert some perennial streams to seasonal streams and in winter months may result in an increase in stream power. Beavers may be able to mitigate some of these hydrologic changes by reducing stream power, allowing reaches to aggrade (Pollock et al. 2014) and converting higher gradient streams

into stepped pools that disperse energy. These pools also impound surface water, allowing it to recharge groundwater (Westbrook et al. 2011) and supplement streams during low-flow periods (Pollock et al. 2003).

The recolonization of large areas and the subsequent landscape-level changes that may ensue could result in changes to the hydrogeomorphic variables that BIP models use. Over time, effective stream gradient may change as beavers create series of step pools, and stream power may decrease as water is spread over larger areas. Additionally, as flow regimes change, so will some of the physical and hydrologic characteristics of streams, including stream size and power. Areas experiencing hydrologic and hydrogeomorphic changes due to either climate change or rapid population growth, respectively, may require the model to be re-run periodically.

Like any model, the intrinsic potential model described here has its limitations. For example, our BIP model captured most riverine wetlands, but missed adjacent palustrine wetlands (*sensu* (Cowardin et al. 1979)). During field surveys, crews often discovered depressional wetland habitat located adjacent to, but separate from streams. Where depressional wetlands share the subsurface hydrology of the adjacent stream, there is potential for beavers to expand this habitat substantially creating stream-wetland matrices. These areas can enhance surface and groundwater storage, provide periodic surface connections to backwater rearing areas for juvenile fish, and provide unique habitat for amphibians and other riparian species (Stevens et al. 2007, Law et al. 2016). Other limitations are related to the quality of the remotely sensed data, such as misaligned stream layers.

Despite these limitations, using a BIP model such as the one described here can allow practitioners to identify candidate sites for beaver reintroduction without extensive field surveys or complex modeling. Although this type of model is one of many tools available to

practitioners, it has the potential to speed the reintroduction and restoration process and reduce the financial cost of finding suitable sites.

## **2.6. Acknowledgments**

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## 2.7. References

- Allen, A. W. 1982. Habitat suitability index models: Beaver, FWS/OBS-82. U.S. Fish and Wildlife Service, Washington, DC.
- Anderson, J., and J. Bonner. 2014. Modeling Habitat Suitability for Beaver (*Castor canadensis*) Using Geographic Information Systems. International Conference on Future Environment and Energy 61:12–23.
- Barnes, D. M., and A. U. Mallik. 1997. Habitat factors influencing beaver dam establishment in a northern Ontario watershed. The Journal of Wildlife Management 61:1371–1377.
- Bartz, K. K., M. J. Ford, T. J. Beechie, K. L. Fresh, G. R. Pess, R. E. Kennedy, M. L. Rowse, and M. Sheer. 2015. Trends in developed land cover adjacent to habitat for threatened salmon in Puget Sound, Washington, U.S.A. PLoS ONE 10:1–22.
- Beechie, T., and H. Imaki. 2014. Predicting natural channel patterns based on landscape and geomorphic controls in the Columbia River basin, USA. Water Resources Research 50:39–57.
- Benda, L., D. Miller, K. Andras, P. Bigelow, G. Reeves, and D. Michael. 2007. NetMap: A new tool in support of watershed science and resource management. Forest Science 53:206–219.
- Burnett, K., G. Reeves, D. Miller, S. Clarke, and K. Christiansen. 2003. A First Step Toward Broad-Scale Identification of Freshwater Protected Areas for Pacific Salmon and Trout in Oregon, USA. Pages 144–154 in J. Beumer, A. Grant, and D. Smith, editors. Aquatic Protected Areas: what works best and how do we know? Proceedings of the World Congress on Aquatic Protected Areas, Cairns, Australia, August 2002. North Beach, WA, Australia.
- Castro, J., M. Pollock, C. Jordan, G. Lewallen, K. Woodruff, and O. Lewallen, G., Pollock M., Woodruff K. 2015. The Beaver Restoration Guidebook. Page Working with Beaver to Restore Streams, Wetlands, and Floodplains. Portland, OR.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. Laroe. 1979. Classification of wetlands and deepwater habitats of the United States. Washington DC.
- Cox, D. R., and T. A. Nelson. 2009. Beaver Habitat Models for Use in Illinois Streams. Transactions of the Illinois State Academy of Science 102:55–64.
- Davies, J. R., K. M. Lagueux, B. Sanderson, and T. J. Beechie. 2007. Modeling stream channel characteristics from drainage-enforced DEMs in Puget Sound, Washington, USA. Journal of

- the American Water Resources Association 43:414–426.
- Elsner, M. M., L. Cuo, N. Voisin, J. S. Deems, A. F. Hamlet, J. A. Vano, K. E. B. Mickelson, S. Y. Lee, and D. P. Lettenmaier. 2010. Implications of 21st century climate change for the hydrology of Washington State. *Climatic Change* 102:225–260.
- 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.
- Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199:142–152.
- Howard, R. J., and J. S. Larson. 1985. A Stream Habitat Classification System for Beaver. *The Journal of Wildlife Management* 49:19–25.
- Janzen, K., and C. J. Westbrook. 2011. Hyporheic Flows Along a Channelled Peatland: Influence of Beaver Dams. *Canadian Water Resources Journal* 36:331–347.
- Jenkins, S. H. 1975. food selection by beavers. *Oecologia* 21:157–173.
- Jenkins, S. H., and P. E. Busher. 1979. *Castor canadensis*. *Mammalian species* 120:1–8.
- Johnston, C. A., and R. J. Naiman. 1986. Boundary dynamics at the aquatic-terrestrial interface : The influence of beaver and geomorphology 57:47–57.
- Johnston, C. A., and R. J. Naiman. 1990. Aquatic patch creation in relation to beaver population trends. *Ecology* 71:1617–1621.
- Kemp, P. S., T. A. Worthington, T. E. L. Langford, A. R. J. Tree, and M. J. Gaywood. 2012. Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries* 13:158–181.
- Law, A., F. McLean, and N. J. Willby. 2016. Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshwater Biology* 61:486–499.
- Macfarlane, W. W., J. M. Wheaton, N. Bouwes, M. L. Jensen, J. T. Gilbert, N. Hough-Snee, and J. A. Shivik. 2015. Modeling the capacity of riverscapes to support beaver dams. *Geomorphology*.
- Mackie, R. S. 1997. *Trading Beyond the Mountains: The British Fur Trade on the Pacific, 1793-1843*. UBC Press, Vancouver, BC.
- McComb, W. C., J. R. Sedell, and T. D. Buchholz. 1990. Dam-site selection by beavers in an

- eastern Oregon basin. *The Great Basin Naturalist* 50:273–281.
- Mote, P., A. Hamlet, and E. Salathé. 2008. Has spring snowpack declined in the Washington Cascades? *Hydrology and Earth System Sciences* 12:193–206.
- Naiman, R. J., S. R. Elliott, J. M. Helfield, and T. C. O’Keefe. 2000. Biophysical interactions and the structure and dynamics of riverine ecosystems: The importance of biotic feedbacks. *Hydrobiologia* 410:79–86.
- Parker, H., and F. Rosell. 2014. Rapid rebound in colony number of an over-hunted population of Eurasian beaver *Castor fiber*. *Wildlife Biology* 20:267–269.
- Perkins, T. E. 2000. The spatial distribution of beaver (*Castor canadensis*) impoundments and effects on plant community structure in the lower Alsea drainage of the Oregon Coast Range, Thesis. Oregon State University, Corvallis, OR.
- Pollock, M. M., T. J. Beechie, J. M. Wheaton, C. E. Jordan, N. Bouwes, N. Weber, and C. Volk. 2014. Using beaver dams to restore incised stream ecosystems. *BioScience* 64:279–290.
- Pollock, M. M. M. M., M. Heim, and D. Werner. 2003. Hydrologic and Geomorphic Effects of Beaver Dams and Their Influence on Fishes. *American Fisheries Society Symposium* 37:20.
- Pollock, M. M. M. M., G. R. G. G. R. Pess, T. J. Beechie, and D. R. Montgomery. 2004. The Importance of Beaver Ponds to Coho Salmon Production in the Stillaguamish River Basin, Washington, USA. *North American Journal of Fisheries Management* 24:749–760.
- Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1994. Beaver as engineers: Influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 in C. G. Lawton and J. J. H., editors. *Linking species to ecosystems*. Chapman & Hall, New York, NY, USA.
- Raymond, C. L., D. L. Peterson, and R. M. Rochefort. 2013. The North Cascadia adaptation partnership: A science-management collaboration for responding to climate change. *Sustainability (Switzerland)* 5:136–159.
- Raymond, C. L., D. L. Peterson, and R. M. Rochefort, editors. 2014. Climate change vulnerability and adaptation in the North Cascades region, Washington. General Technical Report, PNW-GTR-892, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Retzer, J. L. 1956. Suitability of physical factors for beaver management in the Rocky Mountains of Colorado. (Technical Bulletin 2).

- Robinson, S., A. B. Beaudoin, D. G. Froese, J. Doubt, and J. J. Clague. 2007. Plant macrofossils associated with an early Holocene beaver dam in interior Alaska. *Arctic* 60:430–438.
- Scheuerell, M. D., R. Hilborn, M. H. Ruckelshaus, K. K. Bartz, K. M. Lagueux, A. D. Haas, and K. Rawson. 2006. The Shiraz model: a tool for incorporating anthropogenic effects and fish-habitat relationships in conservation planning. *Canadian Journal of Fisheries and Aquatic Sciences* 63:1596–1607.
- Snodgrass, J. W. 1997. Temporal and spatial dynamics of beaver-created patches as influenced by management practices in a south-eastern North American landscape. *Journal of Applied Ecology* 34:1043–1056.
- Snodgrass, J. W., and G. K. Meffe. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. *Ecology* 79:928–942.
- Snohomish Basin Salmon Recovery Forum. 2005. Snohomish River basin salmon conservation plan. Snohomish Basin Salmon Recovery Forum, Everett, WA, USA.
- Snyder, R. V., and J. M. Wade. 1970. Mt. Baker National Forest soil resource inventory. U.S. Forest Service, Washington DC.
- Stavros, E. N., J. T. Abatzoglou, N. K. Larkin, D. McKenzie, and E. A. Steel. 2014. Climate and very large wildland fires in the contiguous Western USA. *International Journal of Wildland Fire* 23:899–914.
- Stevens, C. E., C. A. Paszkowski, and A. L. Foote. 2007. Beaver (*Castor canadensis*) as a surrogate species for conserving anuran amphibians on boreal streams in Alberta, Canada. *Biological Conservation* 134:1–13.
- Suzuki, N., and W. C. McComb. 1998. Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon Coast Range. *Northwest Science* 72:102–110.
- Westbrook, C. J., D. J. Cooper, and B. W. Baker. 2011. Beaver Assisted River Valley Formation. *River Research and Applications* 27:247–256.
- Whitfield, C. J., H. M. Baulch, K. P. Chun, and C. J. Westbrook. 2015. Beaver-mediated methane emission: The effects of population growth in Eurasia and the Americas. *AMBIO* 44:7–15.
- Wright, J., C. Jones, and A. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101.

## 2.8. Tables

Table 2.1. Summary of select general and regional beaver habitat suitability models, identifying the most commonly important environmental variables for predicting historical or present-day beaver occupation. Note that some studies focused on specific variable categories for the purpose of their study objectives (e.g. vegetation).

Habitat Quality Variables	Allen (1982)	Retzer (1956)	Howard and Larson (1985)	Barnes and Mallik (1997)	Suzuki and McComb (1998)	McComb et al. (1990)	Pollock et al. (2004)	Cox and Nelson (2009)	Anderson and Bonner (2014)	Macfarlane et al. (2015)	All Studies
	USA	Rocky Mts	MA	ON	OR	OR	WA	IL	WV	UT	10
Intrinsic											27
Valley width		X			X		X	X			4
Stream length	X										1
Stream gradient	X		X		X	X	X	X	X	X	8
Stream depth & width			X		X	X	X			X	5
Stream bank steepness		X									1
Stream substrate						X					1
Stream power/flood risk		X		X			X			X	4
Basin size, perennial flow			X				X			X	3
Extrinsic											17
Vegetation comp.	X		X			X			X	X	5
Vegetation density		X			X			X			3
Canopy cover	X			X	X	X					4
Canopy height	X										1
Stem diameter	X										1
Habitat & veg. area	X									X	2
Shoreline devel. ratio	X										1

Table 2.2. Additive scoring criteria for environmental variables in each stream segment used to categorize the beaver intrinsic potential (BIP) of all 5,182 km of stream segments in the Snohomish River Basin. Total BIP Score was found by adding the variable scores, Stream Slope + Stream Width + Valley Width (max=12, min =0), and adjusted to categories 0-3 for ease of display and analysis.

Stream slope & score	Stream width & score	Valley width & score	Cumulative score	Adjusted score	BIP categories
< 1 %    4	< 7 m    4	> 30 m    4	11 - 12	3	High
< 2 %    3	< 10 m    3	< 30 m    2	10 - 11	2	Med
< 4 %    2	< 18 m    2	< 20 m    0	8 - 10	1	Low
< 6 %    1	< 24 m    1		< 8	0	No BIP
< 10 %   0.5	> 24 m    0				
> 10%    0					

Table 2.3. BIP model predictions for beaver habitat intrinsic potential in the Snohomish River Basin, showing number and total length of streams segments by category. Observed conditions, number of validation sites visited within each modeled BIP class, and beaver presence is described for field-validated sites, which occurred within the Skykomish River subbasin.

Modeled Conditions				Observed Conditions			
BIP	Stream segments	Length (km)	% of stream segments	Validation sites	High BIP sites	Current or historical occupancy	Occupied
High	11,768	1,171	23%	91	87	26	34
Moderate	4,987	481	10%	82	57	59	5
Low	5,058	389	8%	83	1	0	0
No BIP	26,584	2,978	59%	96	0	0	0
Total	48,397	5,019	100%	352	145	85	39

Table 2.4. Model validation contingency table and supporting test statistics, comparing field-observed BIP with modeled BIP (left), and evaluation of model prediction at sites currently or historically occupied by beavers (center), and actively occupied sites (right).

BIP model prediction	Field-observed BIP		Evidence of beaver	
	Low	High	Current or historically occupied	Currently occupied
No & low	177	1	0	0
Med & high	30	144	85	39
Accuracy	0.92		1	1
95% CI	(0.88, 0.94)		(0.96, 1.00)	(0.96, 1.00)
Sensitivity	0.99		1	1
Specificity	0.86		1	1
Observations	352		85	39

## 2.9. Figures

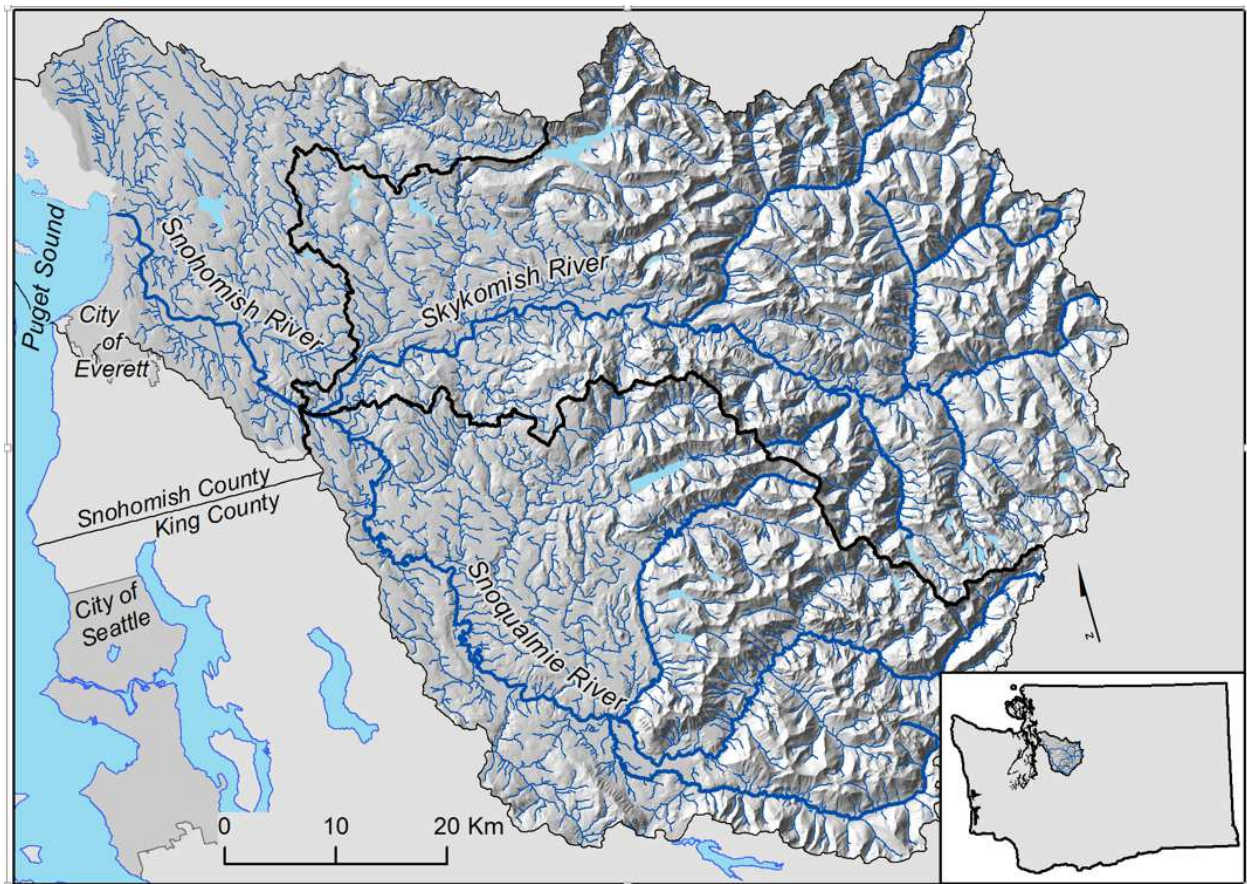


Figure 2.1. The Snohomish River Basin (4,807 km<sup>2</sup>), Washington State, showing the Skykomish River sub-basin (2,160 km<sup>2</sup>), with major and minor river bodies. BIP was modeled in the entire Snohomish Basin and validated using survey data from the Skykomish sub-basin. Input data to inform model variables was derived from stream segments in the Snohomish watershed, but excluded the Skykomish sub-basin where model validation occurred.

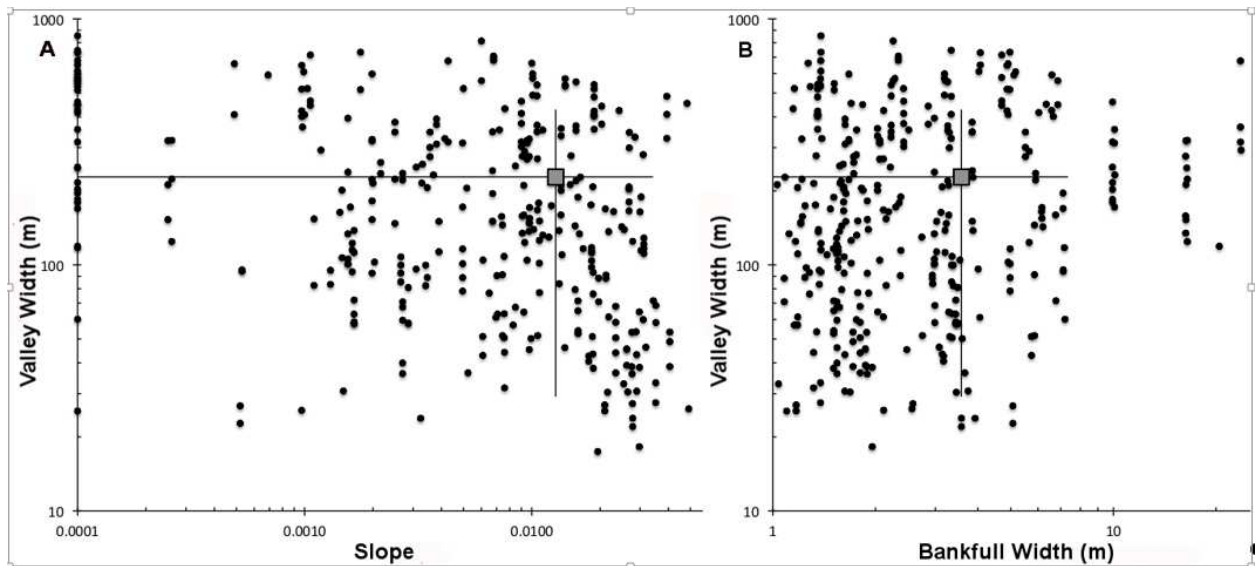


Figure 2.2. Geomorphic characteristics of stream segments in the Snohomish River Basin occupied by beaver. (A) valley widths v. slope, (B) valley width v. bankfull width. Crosshair lines represent the standard deviations, and square symbols are the means. Note that the scale is logarithmic. The data show that dam-building beaver generally prefer streams with slope  $< 0.04$ , bankfull width  $< 8$  m, and valley width  $> 30$  m.

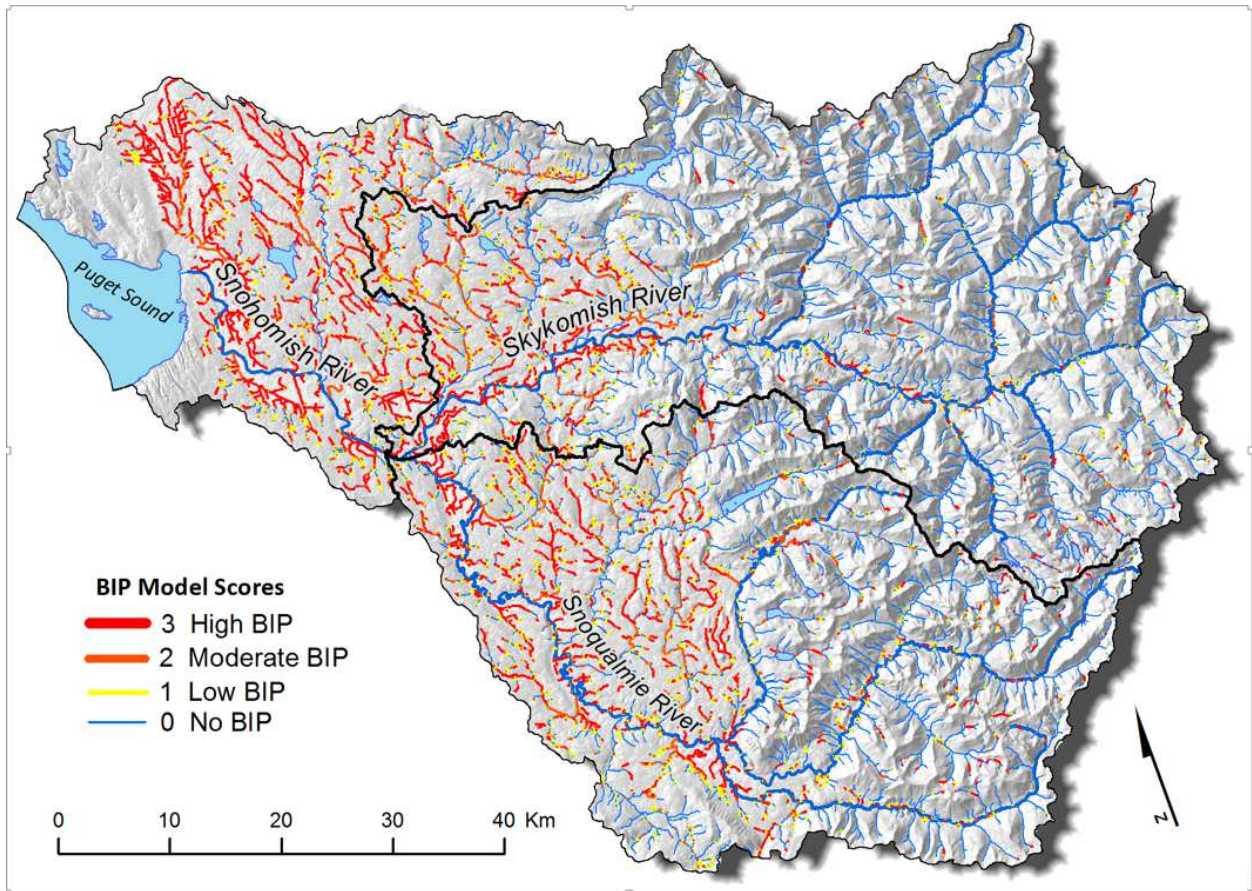


Figure 2.3. BIP model in the Snohomish Basin. Large, low-gradient rivers and small, high-gradient streams are grouped as not suitable, while small to medium sized low-gradient streams have higher suitability values.

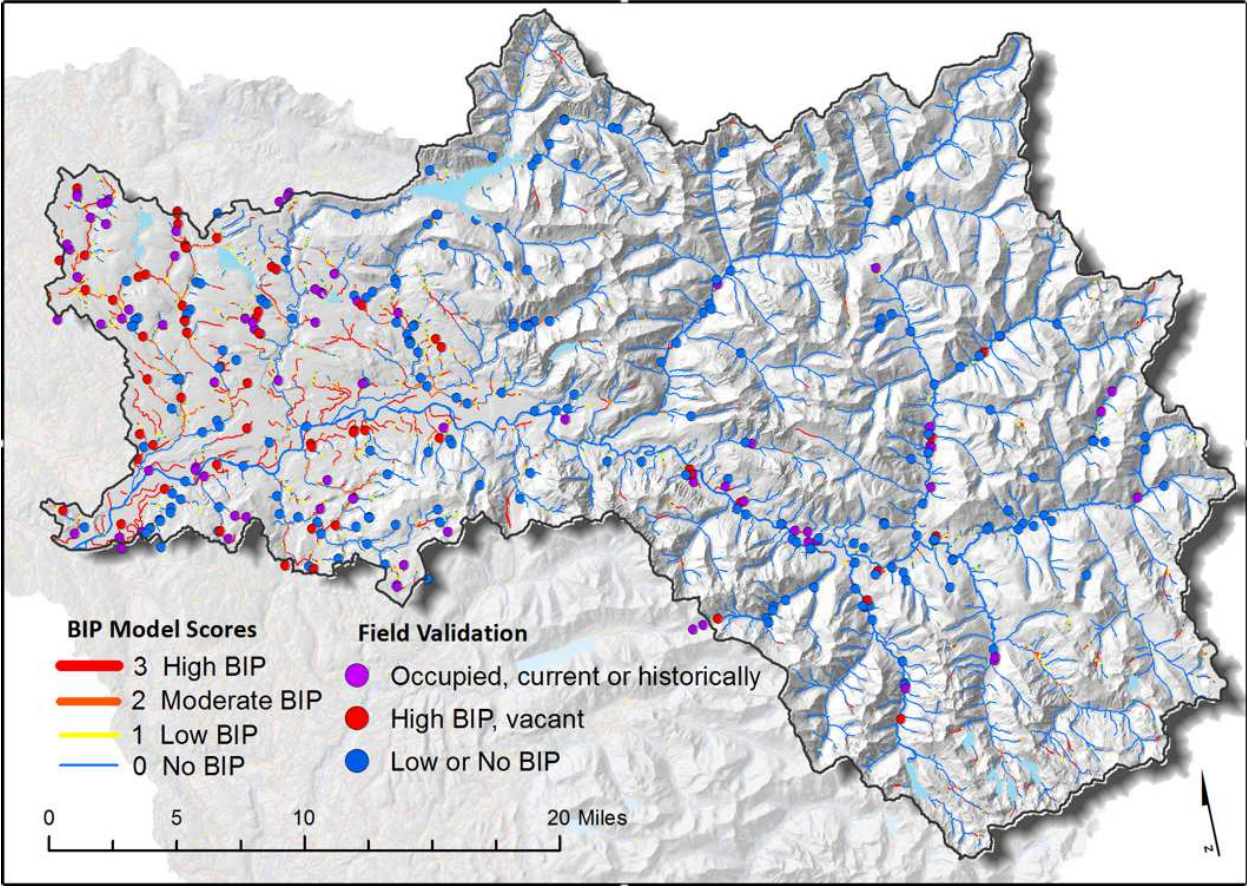


Figure 2.4 Field validation sites in the Skykomish subbasin.

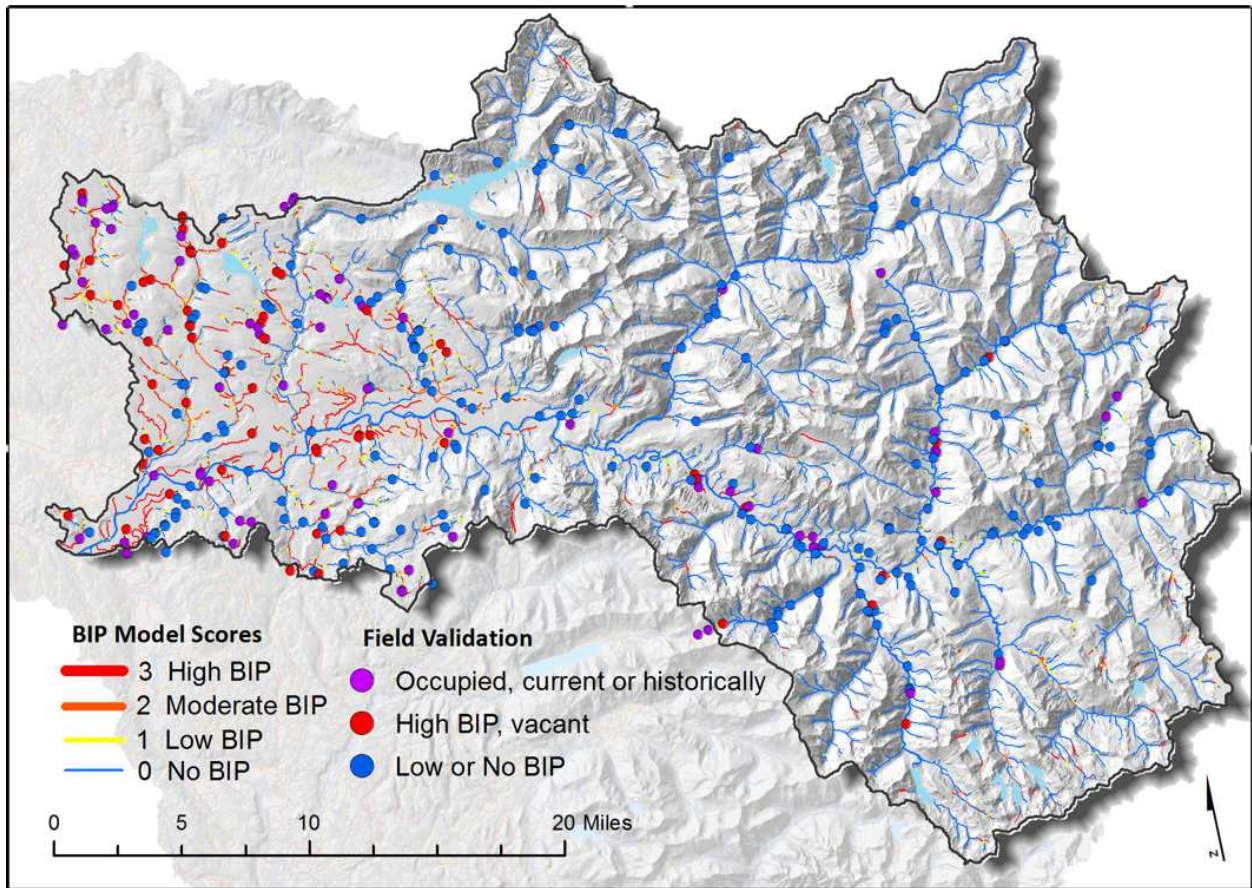


Figure 2.5. (A) Distribution of 30-m riparian buffers and high quality BIP segments in the Snohomish Basin by land use type. (B) Proportion of high, medium, low and no BIP by land use type.

## Chapter 3. Evaluating the hydrologic effects of beaver in headwater streams

### 3.1. Abstract

Consistent with modern climate change, many areas are experiencing increasing stream temperatures and some are experiencing reduced summer stream flows and water availability. Because their dam building and pond formation can increase water storage, stream cooling, and riparian ecosystem resilience, beavers have been proposed as a potential climate adaption tool. Despite the large number of studies that have evaluated how beaver activity may affect these responses, there are few experimental studies that have quantified changes in temperature or water storage following beaver relocation. We address this gap in knowledge by evaluating the temperature and storage response following the relocation of 71 beavers into headwater stream reaches of the Skykomish River watershed within the Snohomish River basin, Washington, USA. We evaluated how beaver dams affected surface and groundwater storage and stream temperature. Successful relocations created 243 m<sup>3</sup> of surface water storage per 100 m stream reach in the first year following relocation. Dams raised water table elevations by up to 0.33 m and stored approximately 2.4 times as much groundwater as surface water per relocation reach. Stream reaches downstream of dams exhibited, on average, a 2.3°C decrease in stream temperature during summer base flow conditions. We also assessed how dam age, condition, and pond morphology influenced stream temperature at wetland complexes constructed by naturally-colonized beavers. Small, abandoned dams produced more warming than all other dam morphologies, including those created by relocated beavers. Our findings demonstrate that dam-building can increase water storage and reduce stream temperatures in the first year following successful beaver relocation. When deciding where to relocate beavers, however, initial

morphology in candidate reaches may determine the type and magnitude of response. Relocation to reaches with existing small, abandoned ponds may address cooling goals by converting them from warming to cooling reaches, whereas relocation within large, abandoned complexes or vacant habitat may result in greater water storage. Although beaver relocation can be an effective climate adaptation strategy to retain more stable hydrologic regimes and water quality in our study area, there appear to be regionally specific environmental and geomorphic factors that influence how beavers affect water storage and temperature. More research is needed to investigate how and why these regional differences affect water storage and stream temperature response in beaver-influenced systems.

### 3.2. Introduction

The Pacific Northwest region of the United States is undergoing considerable hydrologic change and will continue to do so over the next century (CIG 2009, Littell et al. 2013, Huss et al. 2017). Summer precipitation, stream flow, and snowpack are all decreasing (Mauger et al. 2015). Snow melt is projected to occur earlier in the year and winter precipitation, storm intensity, and stream temperatures will likely continue to increase (Das et al. 2011). These changes have the potential to disrupt physical, hydrologic, and ecosystem processes, which may threaten sensitive species and habitats and impact farmlands and human communities through increased flooding and decreased summer water availability (Van Vliet et al. 2013).

North American beavers (*Castor canadensis*) have long been recognized for their ability to create pond and wetland complexes, thereby altering hydrologic processes and conditions in aquatic ecosystems. The impoundment of surface water in beaver ponds allows for increased groundwater recharge and thermal variability. These effects, coupled with the increased habitat complexity found within beaver complexes (Burchsted et al. 2010, Polvi and Wohl 2013, Consolati-Machen 2016), can lead to greater biodiversity (Pollock et al. 1995, Naiman et al. 2000, Wright et al. 2002) and ecosystem resilience (Johnston and Naiman 1986, Naiman et al. 2000). Increasing water storage and potentially reducing in-stream temperatures through beaver reintroduction may be an effective climate change adaptation strategy (Rosemond and Anderson 2003, Lawler 2009, Beechie et al. 2012, Dittbrenner et al. 2018).

Beaver complexes have been shown to substantially increase surface and groundwater storage potential. It is estimated that, worldwide, beaver complexes store up to 11 km<sup>3</sup> of surface water (Karran et al. 2016) with up to 30% of a stream's surface water stored in beaver ponds (Duncan 1984). Some have found that beavers increased the width of riparian areas along streams from 11 to 34 m in their study area McKinstry et al. (2001), and in reaches downstream

of dams pool volume also increased (Stack and Beschta 1989). Dammed stream reaches have been found to extend the lateral extent of the hyporheic zone by up to 8 m beyond control reaches (Shaw 2009), while larger ponds extended groundwater extent by over 50 m (Lowry 1993). Due to the complexity and high variability of local geology, landform, soil type, and other morphological features, however, estimates of total storage are difficult to quantify. Furthermore, most of these studies have documented storage at well-established beaver complexes, whereas the effects of relocated beaver on surface and groundwater storage remains unclear.

The effect of beaver dams on stream temperature is also highly variable among studies depending on location and methodology. Past research has found evidence of warming (Patterson 1951, Avery 2002), cooling (White 1990), warming and cooling depending upon season (Avery 1983), or no relationship between dam presence and temperature (McRae and Edwards 1994). In higher elevation headwater systems, where stream temperature is very cold, some have found a temperature increase of 6 to 9°C downstream of beaver ponds (Margolis et al. 2001). More recent studies have evaluated stream temperatures at larger scales and found that beaver ponds can also have a net cooling effect (White and Rahel 2008, Weber et al. 2017) due to groundwater recharge and upwelling (Pollock et al. 2007). Like many storage studies, however, few studies have documented how relocated beavers affect downstream temperature.

Beaver relocation has been proposed for habitat restoration and climate adaptation, yet there is still limited experimental evidence on whether, and if so how, newly introduced beavers affect water storage and temperature, especially in headwater riparian systems where climate-change impacts are predicted to be most pronounced (CIG 2009, Huss et al. 2017). This study sought to address this knowledge gap by evaluating how newly established beaver colonies affect the hydrology and temperature of stream systems in headwater riparian areas. Specific

objectives were to: (1) quantify the surface and subsurface storage and influence of beaver complexes during summer low-flow conditions; (2) identify how beaver complexes affect stream temperature; and (3) evaluate the restoration potential of beaver reintroduction as a tool to increase ecosystem resilience to climate impacts.

### **3.3. Methods**

#### ***3.3.1. Study area and site selection***

The Skykomish River watershed (2,160 km<sup>2</sup>) is located on the west slope of the Cascade Mountain range in Washington State, USA (Figure 3.1). This area is representative of upland basins in the west-slope Cascades. The hydrology in the region is highly variable spatially and temporally due in part to abundant precipitation in the winter and sporadic precipitation in the summer. Mountainous areas contain narrow, glacially carved valleys and high-gradient streams, which transition to low-gradient streams across a wide, hilly plateau, and a large river floodplain. The basin is representative of other watersheds in the region in terms of habitat conditions, importance for threatened and endangered salmonid species, and potential climate refugia for wildlife (Snohomish Basin Salmon Recovery Forum 2005, Scheuerell et al. 2006, Bartz et al. 2015).

In 2013 and 2014, we conducted a survey of potential beaver habitat within the Skykomish River watershed and developed a beaver intrinsic potential (BIP) habitat model to predict where beaver habitat could exist based on extrinsic landscape variables (i.e., stream gradient and width, and valley width) (Dittbrenner et al. 2018). Within the Skykomish basin, we found that of the 1,652 km of streams with high and moderate quality beaver habitat, 73% of the reaches were vacant and could be used as potential relocation sites.

We narrowed this initial set of potential relocation reaches to 30 sites using criteria such as ease of relocation (e.g., proximity to a road), proximity to other known beaver populations, and size of vacant reaches predicted by the BIP model to contain high or moderate quality habitat. We then conducted detailed site surveys at proposed relocation sites. Prior to relocation, proposed sites were monitored for beaver occupation using a combination of wildlife cameras (Bushnell model 119875C) and repeated site visits to evaluate whether there was sign present, such as dam building, herbivory, or scent mounds (following Snodgrass and Meffe 1998). In proposed relocation reaches that contained evidence of historical beaver activity, such as unmaintained dams or lodges, we notched dam structures and noted whether rebuilding took place. In all cases, no active beaver sightings or sign was evident in proposed relocation reaches for at least a year prior to relocation.

### ***3.3.2. Experimental design***

We designed this experiment using a before, after, control, impact (BACI) experimental design (Stewart-Oaten et al. 1992, Stewart-oaten and Bence 2001, Downes et al. 2002; Figure 3.2) to measure how beavers affect stream temperature and surface and groundwater impoundment. This approach was modified, however, after it was found to be impractical due to the high variability that we observed in relocation success between years and periodic gaps in temperature data. Thirty sites were instrumented with continuous water temperature loggers at the upstream and downstream extent of the site. Paired upstream and downstream groundwater monitoring well arrays were installed in a subset of sites. The lower array was located at the planned relocation site, and the upper array was located upstream of anticipated ponds as a control.

### **3.3.3. *Beaver relocation***

Between 2014 and 2016, 91 beavers were trapped from lowland areas of King and Snohomish counties in the study basin. We attempted to trap and relocate all members of a colony to increase site relocation fidelity (Pollock et al. 2018). After capture, colony members were held at a husbandry facility until all members of a family were trapped from a site. In cases where only one beaver was captured, we grouped singly trapped beavers into mating pairs. Prior to relocation, sites were prepared by constructing a temporary relocation lodge of logs and supplementing the site with cuttings if necessary. Following relocation, the site was monitored using a combination of wildlife cameras and surveys to track occupancy and dam building. Beavers were relocated to new sites in a stepwise fashion until half of the sites contained established colonies. Sites were initially designated as controls until a relocated colony was ostensibly established according to two criteria: (1) colony persistence for at least one season following relocation, and (2) dam construction sufficient to create a pond or wetland complex that expanded the stream width to at least twice that prior to beaver relocation.

Over three years, we relocated 23 beavers in 7 colony groups at 6 sites (2014), 24 beavers in 8 groups to 6 sites (2015), and 22 beavers in 7 groups to 6 sites (2016). In cases where an initial relocation failed (i.e., beavers emigrated from the site or were depredated), we relocated another colony to the same site either later in the season or in the following year. Of the 22 colonies relocated to 13 unique sites, 11 relocations were considered successful in that beavers remained onsite for a year or longer (Table 3.1). During the period of this study, 5 out of 11 established relocations had dam-building activity that resulted in enough impounded stream water to form a pond or wetland complex for a year or longer. In some cases, beavers persisted onsite following relocation but initiated dam construction only after we had completed our study (i.e., during or after 2017). These cases are not reported as part of this study.

In addition to the five successfully established relocation sites, we monitored conditions at 20 other sites included in the initial pool of 30 sites (Table 3.2). Of these, eight consisted of control sites, which were free-flowing streams containing no historical dams or active sign of beaver activity during the study period. Six sites were categorized as relict reaches, containing a single, small historical dam with no sign of an active colony, recent beaver occupancy, or dam maintenance. Four sites were categorized as relict complexes. These sites contained either one large historical pond or a large pond-wetland complex with no sign of recent activity. Finally, two sites were well established complexes with large dams, ponds, or wetland habitat that had been colonized for many years.

#### ***3.3.4. Surface and groundwater estimation***

We monitored surface-water storage at all relocation sites using a combination of survey-based and remote sensing techniques. At each site, all surface waters were mapped and digitized through surveys (Topcon QS Total Station), GPS (Topcon GR3 GPS, Trimble TNJ31), and unmanned aerial vehicle (UAV)-derived imagery. Georeferenced and digitized UAV imagery was collected again in subsequent years after relocation and dam building to track changes in surface water area. Pond area was also measured at each site during each yearly site assessment by walking the pond perimeter or measuring using a range finder (TruPulse Laser Rangefinder model 360), and pond heights were collected at the dam and at the location of maximum depth. We estimated pond volume using methods identified in Karran et al. (2016).

Groundwater elevations were characterized at established relocation sites using mini-piezometers (Baxter et al. 2003). We installed arrays of approximately 30-40 wells at relocation sites prior to beaver relocation throughout the area expected to be affected by dam construction (Figure 3.2). We installed a control array in the same reach above the zone of influence of the

beaver colony. Three pairs of arrays were installed and each was related to an arbitrary datum. Groundwater levels were monitored monthly during low flow periods using a Solinst 101P7 water-level meter.

Groundwater depth was recorded at control and relocation wells at least monthly to identify changes in groundwater height and storage following established relocation. Interannual variation in groundwater elevation at each site was normalized by subtracting mean groundwater elevation at the treatment site from the mean elevation of the upstream control array. We assessed elevation change during low flow conditions, generally from July 15 through September 15 of 2014 – 2016 (Dunham et al. 2005). Total storage change following established relocation was calculated by multiplying the mean normalized groundwater elevation change by the area affected by damming and the soil porosity of the soil at each site (Woo and Waddington 1990).

### ***3.3.5. Stream temperature***

Stream temperature was measured using continuous temperature probes, recording every 30 minutes, placed at all 25 sites at the upstream and downstream extent of each sample reach (Figure 3.2). Following established relocation at the five treatment sites, additional stream temperature probes were installed along colonized areas to detect small-scale temperature fluctuations. We calculated the net warming or cooling effect ( $\Delta T$ ) within each reach by subtracting the mean daily stream temperature at the upstream probe location from the downstream location. Negative values indicated that stream temperature was cooling over that reach, and positive values indicated warming. A test of independence (e.g., Durbin-Watson test) was performed to ensure that serial correlation of errors was minimized and did not overinflate significance (McDowall et al. 1980).

The effect of dam building and pond formation on stream temperature before and after relocation ( $\Delta T_{after} - \Delta T_{before} = \Delta T_{after-before}$ ) was evaluated at the five established relocation sites with linear mixed effects models. We focused our analysis within an annual window of July 27 through August 28, 2014 – 2016 to avoid confounding effects of heavy precipitation events on stream temperature that often occurred later in the summer each year. The use of a linear mixed-effect modeling approach reduces serial autocorrelation in time series and allows for separation among means between fixed and random explanatory variables (Seltman 2014). We fit the models to the response data using the R-package ‘nlme’ (Pinheiro et al. 2018).

### ***3.3.6. Spatial and climate data***

We acquired site-level environmental data from public datasets and analyzed them in GIS (ESRI 2014). Stream gradient was calculated from 10 m digital elevation models (DEM) (USGS 2014a). Hydrogeomorphic data (e.g., stream lines, stream size, contributing area) were obtained from online datasets (USGS 2014b). We used publicly available remotely sensed color IR orthoimagery from 2013 and 2015 (USDA 2014a). Higher-resolution imagery was collected annually using UAVs (SZ DJI Technology Co.; 3DR, Inc.) and imagery was post-processed using Hugin (D’Angelo 2014) for photo mosaicking. We used GIS for georeferencing and Pix4D Mapper (Pix4D SA, Inc.) for mapping and image creation. Daily precipitation and hourly air temperature were obtained from National Weather Service weather stations closest to each site below 1,500 m elevation (i.e., stations SKKW1, TINDEX; NOAA 2014). Hourly air temperature for sites above 1,500 m was collected with a Hobo Pendant temperature probe (Onset Computer Corp.) deployed at site OLN02. Total daily solar irradiance data were obtained from a weather station KWAGOLDB6 (WU 2016) located near the center of study sites. We used spatially

explicit data on climate (yearly precipitation and air temperature) (PRISM 2004) and soils (USDA 2014b).

### **3.4. Results**

#### ***3.4.1. Surface and groundwater storage***

Within the first year following relocation, beavers constructed 19 dams at five successful relocation sites. These five sites stored roughly 22 times as much water as control sites. At these relocation sites, dam-building led to the retention and impoundment of 243 m<sup>3</sup> of water per 100 m stream reach in 2014 – 2016 (Figure 3.3) with a mean pond volume of 983 m<sup>3</sup>. During this period, control reaches remained relatively constant with a mean volume of 11 m<sup>3</sup>/100 m (SD = 8).

Relocation sites with established ponds stored 2.4 times more ground water than surface water in ponds. At relocation sites fitted with groundwater well arrays (sites SFS02 and FOS02) mean normalized groundwater elevations increased 0.18 and 0.26 m, respectively, following pond formation (Figure 3.4). Additionally, one naturally colonized and well-established complex site (SFS08) had a 0.33 m mean normalized groundwater elevation increase after transitioning from having limited beaver activity in 2015 to having very active dam construction in 2016. This increase in groundwater elevation at established relocation sites equated to an increase in groundwater volume of 581 m<sup>3</sup> per 100 m in the first year following relocation.

#### ***3.4.2. Stream temperature***

Prior pond creation, four of the five relocation sites showed downstream warming (i.e., higher temperatures downstream compared to upstream temperature probes, Figure 3.5a) over the entire summer base-flow period (i.e., July 15 – September 15). Following beaver relocation, dam

building, and pond formation, this trend reversed (i.e., streams tended to be cooler downstream) (Figure 3.5b). One established relocation site (FOS02) differed from this trend in that water temperatures were cooler downstream prior to relocation (Figure 3.5c). Although the cooling trend continued after dam construction, the magnitude of the cooling decreased (Figure 3.5d). Additionally, the amplitude of diel stream temperature was substantially dampened after established relocation within this reach.

Frequent and periodic heavy precipitation events occurring throughout the summers of 2014-2016 had a substantial effect on stream temperature. Cold weather fronts associated with these events brought cooler air, precipitation, and increased cloud cover, leading to substantial stream cooling. Some of the relocation sites showed shifts in the relationship between stream temperatures at upper and lower probes. For example, prior to beaver relocation at site SFS02 (Figure 3.5a), the warming trend observed throughout most of the summer was temporarily suppressed during heavy precipitation events (e.g., 224 mm between August 29 and September 3, 2014). After dam-building at SFS02 (Figure 3.5b), the downstream cooling trend observed for much of the summer was reversed during large precipitation events (e.g., 538 mm between August 29 and September 4, 2015) when high flows pushed warm surface water in the ponds over the dam and past the downstream temperature probe.

Linear mixed effects model results showed that the differences that we observed in stream temperature at the five established relocation sites were associated with air temperature, 3-day mean precipitation, stream slope, and stream volume (Table 3.4). The most parsimonious model included air temperature and 3-day precipitation, both of which were negatively correlated with differences in upstream and downstream temperature.

We analyzed the effect of relocation on stream temperature during the period from July 27 through August 28 in 2014-2016 to avoid the conflating effect of heavy precipitation events described above. During this focal period, the construction of beaver ponds in streams within the Skykomish watershed resulted in an overall increased cooling effect of  $\Delta T_{after-before} = -2.3^{\circ}\text{C}$  among sites (Figure 3.7). Prior to beaver relocation, stream reaches had a mean cooling effect of  $\Delta T_{before} = -0.1^{\circ}\text{C}$  (SD =  $1.9^{\circ}\text{C}$ ). Following relocation and dam construction, sites showed a mean cooling effect of  $\Delta T_{after} = -2.4^{\circ}\text{C}$  (SD =  $1.9^{\circ}\text{C}$ ). Four of the five established relocation sites had an increase in cooling following dam building Figure 3.7 (see Figure S 3.1, Figure S 3.2 for maximum cooling and warming effect per site). Temperature shifts at these sites ranged from  $\Delta T_{after-before} = -6.0^{\circ}\text{C}$  (site BEC02) to  $\Delta T_{after-before} = -0.3^{\circ}\text{C}$  (BEC04). One site (SFS02) had a  $\Delta T_{after-before} = 1.1^{\circ}\text{C}$  warming shift following relocation, but the site retained an overall cooling effect ( $\Delta T_{SFS02, after} = -1.6^{\circ}\text{C}$ , SD =  $0.9^{\circ}\text{C}$ ).

### ***3.4.3. Temperature effects in multiple beaver pond classes***

When we broadened our investigation beyond relocation reaches to include control streams and beaver ponds that included small and large relict ponds, relocation sites, and long-established sites, we found an increasingly stronger cooling trend as pond sites became more complex, increased in size, and were actively maintained (Figure 3.8). Control streams with no beaver structures exhibited a warming effect of  $\Delta T_{control} = 0.8^{\circ}\text{C}$  (SD =  $1.5^{\circ}\text{C}$ ) between downstream and upstream temperature probes. Vacant relict ponds had a greater warming effect than control streams ( $\Delta T_{relict} = 2.2^{\circ}\text{C}$ , SD =  $2.4^{\circ}\text{C}$ ) and also had fewer overall cooling days. In contrast, vacant relict complexes, established relocation reaches, and well-established beaver pond complexes all exhibited cooling effects of  $\Delta T_{relict-complex} = -1.2^{\circ}\text{C}$  (SD =  $1.3^{\circ}\text{C}$ ),  $\Delta T_{relocation} = -2.0^{\circ}\text{C}$  (SD =  $1.8^{\circ}\text{C}$ ), and  $\Delta T_{complex} = -1.9^{\circ}\text{C}$  (SD =  $2.5^{\circ}\text{C}$ ,  $n = 2$  sites), respectively.

### **3.5. Discussion**

This study demonstrates that the creation of beaver wetland complexes influences water storage and stream temperature, suggesting a positive contributor to climate change resilience. Beavers can rapidly construct dams following relocation that create ponds sufficient to store large amounts of surface water and increase groundwater elevations near beaver ponds. Stream temperatures downstream of dams were substantially cooler than temperatures above dams, especially during summer low-flow conditions. In ponds created from both newly relocated beaver colonies and well-established wetland complexes, site complexity had a strong effect on stream temperature.

#### **3.5.1. *Water storage***

Dams constructed by relocated colonies were initially small in the first few years of our study compared to dam structures in well-established colonies, yet their associated ponds were still able to impound substantial amounts of surface water. Relatively new dams (i.e., constructed within the first year of site colonization) had the potential to impound greater volumes than previously reported. Numerous studies have quantified pond storage and found ponds ranging from very small to over 10,000 m<sup>3</sup>, with a mean pond size near 1000 m<sup>3</sup> (Karran et al. 2016). The relatively small dams created in our study within the first year following relocation lead to the impoundment of 983 m<sup>3</sup> per pond on average, which suggests that beaver relocation as a restoration measure has the potential to increase water storage relatively quickly.

The impoundments at our sites led to an increase in groundwater elevation and overall groundwater storage equivalent to approximately 2.4 times that of the surface water storage at each site. Although, to our knowledge, there have been no previous studies that have reported the

effects of beavers on groundwater storage at relocation sites, some have quantified the effects of beaver damming on groundwater at established beaver sites and found an increase in the water table following beaver damming (Lowry et al. 1994, Westbrook et al. 2006, Hill and Duval 2009). Our findings of groundwater increases of between 0.18 to 0.33 m are similar to studies at naturally-colonized beaver dam sites with documented increases of 0.25 m (Bouwes et al. 2016) to 0.34 m (Majerova et al. 2015). Although all of our successful relocation sites were located within mountainous areas with moderately sized valley cross-sections, we observed a positive relationship between valley width and groundwater storage. Thus, we expect beaver impoundments within areas with wider floodplains to store substantially more groundwater, but this warrants further research.

### **3.5.2. *Stream temperature***

Beaver complexes in headwater streams of the Skykomish River basin have an overall cooling effect on streams. Previous studies report a range of effects from overall warming to cooling of streams below beaver dams. The nature and magnitude of temperature effects tend to vary with environmental factors and dam size and age, but this relationship has only been more recently investigated. For example, early studies (Rasmussen 1941, Patterson 1951, Reid 1952) and recent research (Majerova et al. 2015) have found a warming trend downstream of dams. Other studies that have considered geomorphology have found dams to produce both warming and cooling depending on stream complexity and dam height (Fuller and Peckarsky 2011a). Furthermore, some studies have found a cooling effect and often a dampening of diel variability as beavers occupied a stream reach (Pollock et al. 2007, Błędzki et al. 2011, Bouwes et al. 2016).

In the Pacific Northwest, periodic heavy precipitation events occurred throughout the summers of 2014-2016, supplementing streamflow periodically and decreasing ambient

temperature. Although no relationship was observed between dam height and temperature at relocation sites, it is likely that late-season precipitation events and snowmelt drive cooling in beaver ponds in our study region; these events keep ponds filled and allow for groundwater recharge throughout the summer. It is possible that variation in temperature response depends on whether dams are creating a sufficiently strong hydraulic gradient to drive groundwater upwelling downstream of dams. Regions with periodic precipitation events that continue to supplement ponds and stabilize groundwater tables may have cooler downstream temperature more frequently. Contrary to beaver ponds in more arid areas, which may have less supplementation of flow during low-flow periods (e.g., Majerova et al. 2015), we observed no summer warming trend at pre- or post-relocation sites. This finding further supports our assertion that beaver-influenced systems in our study area maintain sufficient flow and hydraulic gradient to drive downstream cooling throughout low-flow periods.

When we expanded our temperature analysis to include control sites and the beaver site categories of relict ponds, relict complexes, established relocations, and well-established sites, we identified an unanticipated pattern. Although active beaver sites (i.e., established relocation and well-established sites) and relict complexes had a greater cooling effect than control streams, relict ponds were substantially warmer. The differing temperature effect between small relict ponds and large relict complexes – warming versus cooling – supports the findings of Fuller and Peckarsky (2011) that ponds with low dam height to pond area ratio produce more frequent downstream warming. This pattern has a number of management implications for beaver-based restoration strategies. Relocation practitioners often prioritize large, abandoned beaver complexes over small relict ponds in order to create ponds with large surface water and groundwater storage. Our findings suggest that focusing on these areas may enhance storage but

will not necessarily address temperature goals, particularly for streams that face heightened concerns with elevated temperatures. Focusing relocation efforts on beaver ponds that are small, shallow, and abandoned may be more effective in some instances, because restoration in these areas will encourage increases in dam heights, which will drive greater hydraulic gradients and have greater impact on reducing downstream temperature.

### ***3.5.3. Beaver relocation for watershed restoration and climate adaptation***

The role of beavers in stream restoration and climate adaptation has received increased attention in recent years (Pollock et al. 2018). If beaver relocation is to be an effective restoration and climate-change adaptation strategy, however, it is critical to consider whether long-term site fidelity of beaver colonies is a prerequisite to achieving stream temperature and storage restoration goals. Our relocation success rate was consistent with past relocation programs conducted in the American West (Pollock et al. 2018). Despite relocating active, dam-building beavers to sites with high habitat quality potential and food availability, it was often necessary to introduce multiple colonies to a site before permanent colonization could be achieved. In some cases, colonies that abandoned the site may have colonized nearby reaches. Emigration from relocation reaches to nearby areas has been observed in other relocation programs (McKinstry and Anderson 2002, Babik and Meyer 2015). However, depending upon the goals of the relocation program, this may still be considered a success. In other cases, colonies that initially emigrated from a site eventually returned in following seasons. Some initially successful colonization efforts eventually succumbed to high predation rates or dam blow-outs during heavy precipitation events. In these cases, successful colonization and long-term site fidelity were contingent on dam structures with large, stable ponds that reduced predation risk and withstood high winter streamflow. The potential for dam blow-outs may be exacerbated by climate change,

as winter flows increase in intensity in the Pacific Northwest (Das et al. 2011); this emerging concern should be evaluated when prioritizing reaches for relocation.

Habitat quality and water quantity were important factors affecting relocation success and long-term site fidelity. We observed substantial variability in streamflow among sites, with some sites experiencing extreme winter flow events and others nearly drying out during base flow. Major sources of site variation included lithology and substratum type (e.g., colluvial material), soil composition, landscape position (e.g., high, low elevation), hydrogeomorphic variation (e.g., slope, BFW, valley width), and vegetation composition and structure. These factors affect beaver colonization preference, dam and pond size, and the resulting magnitude of hydrologic and temperature change between sites.

Despite repeated relocation at individual sites, permanent colonization and dam-building was only achieved at one-third (5 of 15) attempted relocation sites. To the best of our knowledge, no previous studies exist that document the hydrologic or temperature effects of targeted beaver relocation. Of those that have monitored the initial environmental effects at naturally-colonized sites, sample size is generally low, most often consisting of a single site (Pilliod et al. 2018). Thus, although the sample size of 5 sites, including 19 dams and ponds among sites is still relatively small, it represents an increase in replication from previous studies. Nonetheless, greater replication may have offered additional insight into which site-specific environmental and physical factors are most important in affecting stream temperature. Limited sample size also constrained our ability to evaluate the relatively high temperature variability among sites. Despite these limitations, the randomized selection of our 15 candidate relocation sites from reaches identified by the BIP model (see Chapter 2) as having high potential suitability suggest that they are representative of similar headwater and low-order streams suitable for relocation

within the region. This study focused on beaver relocation within free-flowing streams and did not include relocation within wetland or side-channel habitats. The hydrology and morphology of free-flowing versus wetland and side-channel habitats have different responses to dam-building by beavers. Our study sites were set in a mountainous area, often with localized patches of high-quality potential habitat. This environmental setting differs from lowland areas that have larger, contiguous habitat and potentially dissimilar site characteristics (e.g., lower gradient, broader floodplains, and potentially higher dam and colony density). There may be differences in the hydrologic and temperature effects observed between beaver ponds in upland versus lowland sites, as well as among sites with other sources of variation (e.g., ecoregion, climate regime, lithography and geomorphology).

Despite greater understanding of beaver influences on stream hydrology (Rosell et al. 2005), there remains considerable uncertainty about how regional factors affect water storage and stream temperature. Given the highly variable findings about beaver effects on stream temperature, additional research is needed to further elucidate the underlying mechanisms that drive temperature in beaver-influenced systems and better understand why such variability exists among regions and in different ecological and hydrologic contexts. Furthermore, experimental studies are needed to quantify how thermal heterogeneity is affected within and among beaver pond complexes over time. Sites with older dams often have more pronounced effects on hydrology than newer dams (Meentemeyer and Butler 1999), suggesting that field observations from newly constructed dams may yield a relatively weak signal in some instances. Long-term studies are needed to identify how river systems change over time in response to the dynamics of beaver colonization and movement.

In this study, we examined how beavers may offset some climate-related impacts on water storage and stream temperature, but beavers themselves may be affected directly and indirectly by climate change. For example, reduced summer precipitation in the Pacific Northwest has the potential to cause perennial streams to become intermittent (Reidy Liermann et al. 2011, Van Vliet et al. 2013). In these cases, beavers will likely abandon intermittent reaches and move downstream to find more suitable habitat. Conversely, climate projections predict higher magnitude winter storm events, increased peak stream flows, erosion, and sediment mobilization (CIG 2009). Beaver dams have an increased potential for failure during these events. Similarly, rates of aggradation are also likely to increase, potentially accelerating beaver pond to meadow succession. In some cases, this may promote recovery of riparian ecosystems, but it is unknown how these impacts will affect beaver population and colony dynamics.

Beaver reintroduction provides opportunities for ecosystem restoration and climate adaptation. The creation of wetlands by beaver colonies increases hydrologic stability, thermal variability, geomorphic complexity, species and habitat diversity, and resilience. Active beaver ponds constructed by both long-established and newly relocated colonies caused stream cooling and increased surface and groundwater storage during summer low-flow conditions. These findings in free-flowing streams differ from some other beaver pond-related temperature studies and further research into the regional drivers of stream temperature is needed. When identifying potential reaches for relocation, however, consideration should be given to not only existing habitat and hydrologic conditions, but also those anticipated in the future. Given the reported variability in environmental and hydrologic response to beaver damming, changing climatic conditions will likely further contribute to increased regional variability at beaver sites. Within

watersheds with similar conditions to those in our study area, beaver relocation may be an effective climate adaptation tool to address elevated temperature and reduced watershed storage concerns.

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Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

### 3.7. References

- Avery, E. L. 1983. Bibliography of beaver, trout, wildlife, and forest relationships. Wisconsin Department of Natural Resources. Madison, WI, USA.
- Avery, E. L. 2002. Fish community and habitat responses in a northern Wisconsin brook trout stream 18 years after beaver dam removal. Wisconsin Department of Natural Resources, Madison, WI, USA.
- Babik, M., and W. Meyer. 2015. Yakima basin beaver reintroduction project: 2011- 2015 progress report. Washington Department of Fish and Wildlife, Olympia, WA, USA.
- Bartz, K. K., M. J. Ford, T. J. Beechie, K. L. Fresh, G. R. Pess, R. E. Kennedy, M. L. Rowse, and M. Sheer. 2015. Trends in developed land cover adjacent to habitat for threatened salmon in Puget Sound, Washington, U.S.A. PLoS ONE 10:1–22.
- Baxter, C., F. R. Hauer, and W. W. Woessner. 2003. Measuring groundwater–stream water exchange: new techniques for installing minipiezometers and estimating hydraulic conductivity. Transactions of the American Fisheries Society 132:493–502.
- Beechie, T., H. Imaki, J. Greene, A. Wade, H. Wu, G. Pess, P. Roni, J. Kimball, J. Stanford, P. Kiffney, and N. Mantua. 2012. Restoring salmon habitat for a changing climate. River Research and Applications 7:189.
- Błędzki, L. A., J. L. Bubier, L. A. Moulton, and T. D. Kyker-Snowman. 2011. Downstream effects of beaver ponds on the water quality of New England first- and second-order streams. Ecohydrology 4:698–707.
- Bouwes, N., N. Weber, C. E. Jordan, M. M. Pollock, W. Carl, I. A. Tattam, C. Volk, and J. M. Wheaton. 2016. Ecosystem experiment reveals impacts of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). Nature Publishing Group 7:1–12.
- Burchsted, D., M. Daniels, R. Thorson, and J. Vokoun. 2010. The river discontinuum: applying beaver modifications to baseline conditions for restoration of forested headwaters. Bioscience 60:908–922.
- CIG. 2009. The Washington climate change impacts assessment. (M. McGuire Elsner, J. Littell, and L. Whitely Binder, Eds.). Center for Science in the Earth System, Joint Institute for the Study of the Atmosphere and Oceans, Seattle, WA, USA.
- Consolati-Machen, F. 2016. The role of a beaver in shaping stream channel complexity and

- thermal heterogeneity in a central Oregon stream. Thesis. Utah State University, Logan, UT, USA.
- D'Angelo, P. 2014. Hugin v.2014.0.0. Bielefeld, Germany.
- Das, T., D. W. Pierce, D. R. Cayan, J. A. Vano, and D. P. Lettenmaier. 2011. The importance of warm season warming to western U.S. streamflow changes. *Geophysical Research Letters* 38:1–5.
- Dittbrenner, B. J., M. M. Pollock, J. W. Schilling, J. D. Olden, J. J. Lawler, and C. E. Torgersen. 2018. Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation. *PLoS ONE* 13:e0192538.
- Downes, B., L. Barmuta, P. Fairweather, and D. Faith. 2002. *Monitoring ecological impacts: concepts and practice in flowing waters*. Cambridge University Press, New York, NY.
- Duncan, S. L. 1984. Ecology: Leaving it to Beaver. *Environment: science and policy for sustainable development* 26:41–45.
- Dunham, J., G. Chandler, B. Rieman, and D. Martin. 2005. Measuring stream temperature with digital data loggers: A user's guide. USFS Technical Report:1–18.
- ESRI. 2014. Environmental Systems Research Institute, ArcGIS v. 10.3. Redlands, CA, USA.
- Fuller, M. R., and B. L. Peckarsky. 2011. Does the morphology of beaver ponds alter downstream ecosystems? *Hydrobiologia* 668:35–48.
- Hill, A. R., and T. P. Duval. 2009. Beaver dams along an agricultural stream in southern Ontario, Canada: their impact on riparian zone hydrology and nitrogen chemistry. *Hydrological Processes* 23:1324–1336.
- Huss, M., B. Bookhagen, C. Huggel, D. Jacobsen, R. S. Bradley, J. J. Clague, and M. Vuille. 2017. Toward mountains without permanent snow and ice. *Earth's Future* 5:418–435.
- Johnston, C. A., and R. J. Naiman. 1986. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology 57:47–57.
- Karran, D. J., C. J. Westbrook, J. M. Wheaton, C. A. Johnston, and A. Bedard-Haughn. 2016. Rapid surface water volume estimations in beaver ponds. *Hydrology and Earth System Sciences* 21:1–26.
- Lawler, J. J. 2009. Climate change adaptation strategies for resource management and conservation planning. *Annals of the New York Academy of Sciences* 1162:79–98.
- Littell, J. S., G. S. Mauer, E. P. Salathé, A. F. Hamlet, S. Y. Lee, M. R. Stumbaugh, M. Elsner,

- R. Norheim, E. R. Lutz, and J. Nathan. 2013. Uncertainty and extreme events in future climate and hydrologic projections for the Pacific Northwest: providing a basis for vulnerability and core/corridor assessments. Climate Impacts Group, Seattle, WA, USA.
- Lowry, M. M. 1993. Groundwater elevations and temperature adjacent to a beaver pond in central Oregon. Thesis. Oregon State University, Corvallis, OR, USA.
- Lowry, M. M., R. L. Beschta, McNamara, and M. Michael M. Lowry, Robert L. Beschta. 1994. Effect of a beaver pond on groundwater elevation and temperatures in a recovering stream system. American Water Resources Association:503–513.
- 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.
- Margolis, B. E., R. L. Raesly, and D. L. Shumway. 2001. The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. Wetlands 21:554–563.
- McDowall, D., R. McCleary, E. Meidinger, and R. Hay. 1980. Interrupted Time Series Analysis. SAGE Publications., Thousand Oaks, CA, USA.
- McKinstry, M. C., P. Caffrey, and S. H. Anderson. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American Water Resources Association 37:1571–1577.
- McKinstry, M. C. M., and S. H. S. Anderson. 2002. Survival, fates, and success of transplanted beavers, *Castor canadensis*, in Wyoming. Canadian Field-Naturalist 116:60–68.
- McRae, G., and C. J. Edwards. 1994. Thermal characteristics of Wisconsin headwater streams occupied by beaver: implications for brook trout habitat. Transactions of the American Fisheries Society 123:641–656.
- Meentemeyer, R. K., and D. R. Butler. 1999. Hydrogeomorphic effects of beaver dams in glacier national park, Montana. Physical Geography 20:436–446.
- Naiman, R. J., S. R. Elliott, J. M. Helfield, and T. C. O’Keefe. 2000. Biophysical interactions and the structure and dynamics of riverine ecosystems: The importance of biotic feedbacks. Hydrobiologia 410:79–86.
- NOAA. 2014. National Oceanic and Atmospheric Administration, National Weather Service. Retrieved from [www.weather.gov/phi/localclimate](http://www.weather.gov/phi/localclimate).

- Patterson, D. 1951. Beaver-trout relationships. Wisconsin Conservation Department. Madison, WI, USA.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, S. Heisterkamp, and B. Van Willigen. 2018. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137. Retrieved from <https://cran.r-project.org/package=nlme>.
- Pollock, M. M., G. M. Lewallen, K. Woodruff, C. E. Jordan, and J. M. Castro. 2018. The Beaver Restoration Guidebook: working with beaver to restore streams, wetlands, and floodplains. Page United States Fish and Wildlife Service. V-2.01.
- 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* 1185:1174–1185.
- Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1994. Beaver as engineers: Influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 in C. G. Lawton and J. J. H., editors. *Linking species to ecosystems*. Chapman & Hall, New York, NY, USA.
- Polvi, L. E., and E. Wohl. 2013. Biotic rivers of stream planform: implications for understanding the past and restoring the future. *BioScience* 63:439–452.
- PRISM. 2004. PRISM Climate Group, Oregon State University. Retrieved from <http://prism.oregonstate.edu>.
- Rasmussen, D. I. 1941. Beaver trout relationship in the Rocky Mountain region. *Transactions of the Fifth North American Wildlife Conference* 5:256–263.
- Reid, K. A. 1952. Effects of beaver on trout waters. *Maryland Conservationist* 24:21–23.
- Reidy Liermann, C. A., J. D. Olden, T. J. Beechie, M. J. Kennard, P. B. Skidmore, C. P. Konrad, and H. Imaki. 2011. Hydrogeomorphic classification of Washington State rivers to support emerging environmental flow management strategies. *River Research and Applications*. 1358:1340–1358.
- Rosell, F., O. Bozsér, P. Collen, and H. Parker. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* 35:248–276.
- Rosemond, A. D., and C. B. Anderson. 2003. Engineering role models: do non-human species have the answers? *Ecological Engineering* 20:379–387.

- Scheuerell, M. D., R. Hilborn, M. H. Ruckelshaus, K. K. Bartz, K. M. Lagueux, A. D. Haas, and K. Rawson. 2006. The Shiraz model: a tool for incorporating anthropogenic effects and fish-habitat relationships in conservation planning. *Canadian Journal of Fisheries and Aquatic Sciences* 63:1596–1607.
- Seltman, H. J. 2014. Chapter 15 Mixed Models. Pages 357–378 *Experimental Design And Analysis*. Online at: <http://www.stat.cmu.edu/~hseltman/309/Book/Book.pdf>.
- Shaw, E. L. 2009. Lateral exchange of water and nitrogen along a beaver-dammed stream draining a Rocky Mountain valley. Thesis. University of Saskatchewan, Saskatoon, Canada.
- Snodgrass, J. W., and G. K. Meffe. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. *Ecology* 79:928–942.
- Snohomish Basin Salmon Recovery Forum. 2005. Snohomish River basin salmon conservation plan. Snohomish Basin Salmon Recovery Forum, Everett, WA, USA.
- Stack, W. R., and R. L. Beschta. 1989. Factors influencing pool morphology in Oregon coastal streams. *Headwaters Hydrology* 6:401–411.
- Stewart-oaten, A., and J. R. Bence. 2001. Temporal and spatial variation in environmental impact assessment. *Ecological Monographs* 71:305–339.
- Stewart-Oaten, A., J. R. Bence, and C. W. Osenberg. 1992. Assessing effects of unreplicated perturbations: no simple solutions. *Ecology* 73:1396–1404.
- Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: “pseudoreplication” in Time? *Ecology* 67:929–940.
- USDA. 2014a. U.S. Department of Agriculture, National Agriculture Imagery Program (NAIP). Retrieved from: <https://earthexplorer.usgs.gov/>.
- USDA. 2014b. U.S. Department of Agriculture, Soil Services in Washington. Retrieved from <https://www.nrcs.usda.gov/wps/portal/nrcs/main/wa/soils/>.
- USGS. 2014a. U.S. Geologic Survey National Elevation Dataset.
- USGS. 2014b. U.S. Geologic Survey National Hydrography Dataset Plus. Retrieved from: <https://viewer.nationalmap.gov/basic/>.
- Van Vliet, M. T. H., W. H. P. Franssen, J. R. Yearsley, F. Ludwig, I. Haddeland, D. P. Lettenmaier, and P. Kabat. 2013. Global river discharge and water temperature under climate change. *Global Environmental Change* 23:450–464.
- 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.
- Westbrook, C. J., D. J. Cooper, and B. W. Baker. 2006. Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. *Water Resources Research* 42:1–12.
- White, D. S. 1990. Biological relationships to convective flow patterns within stream beds. *Hydrobiologia* 196:149–158.
- White, S. M., and F. J. Rahel. 2008. Complementation of habitats for Bonneville cutthroat trout in watersheds influenced by beavers, livestock, and drought. *Transactions of the American Fisheries Society* 137:881–894.
- Woo, M.-K., and J. M. Waddington. 1990. Effects of beaver dams on subarctic wetland hydrology. *Arctic* 43:223–230.
- Wright, J., C. Jones, and A. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101.
- WU. 2016. Weather Underground. Retrieved from [www.wunderground.com](http://www.wunderground.com).

### 3.8. Tables

Table 3.1 Beaver relocations within the Skykomish watershed, WA, summarizing the number of colonies and individual beavers introduced, attempted and successful relocations, and number of dams constructed.

Reintroduction	Description	Number
Attempted	- Introduction sites beavers relocated to	13
	- Colonies introduced	22
	- Beavers introduced	69
Successful	- Introduction sites where beavers constructed dams and modified stream hydrology	5
	- Dams built by introduced beavers leading to pond/wetland formation	14

Table 3.2 Study sites grouped by beaver occupancy, condition of complex, and morphology.

Site category	Site type	Number of sites	Description
Control	Control	8	No pre-existing colony, introduction, or subsequent natural colonization
Pre-existing historical dams, but vacant	Relict	6	Site vacant, but historical, unmaintained dams and often shallow ponds present
	Relict complex	4	Similar to relict sites, but evidence of large historical complex
Active site, established dams and ponds	Established relocation	5*	Relocation sites with established colonies and sufficient damming to form pond/wetlands
	Well-established complex	2	Beaver-maintained dams and ponds already present upon initial inspection for many years and through duration of study.

\*Beavers constructed dams at one additional reintroduction site, but this site became inaccessible in 2015 after the access road washed out. See Table S 3.2 for additional details.

Table 3.3 Physical and hydrologic characteristics for 25 sampling reaches in the Skykomish watershed. A full list of environmental data for each site are in Table S 3.1 Physical and hydrologic characteristics at sites.

Variable	Mean	Range	Std. deviation
Elevation (m)	436	225 – 888	200
Stream slope (%)	1.41	0.09 – 3.33	1.12
Drainage area (km <sup>2</sup> )	1.11	0.10 – 3.41	0.77
Bankfull width (m)	2.70	1.20 – 4.38	0.82
Annual precipitation (mm)	2673	2140 – 4000	488
Site length (m)	234	29 - 961	202

Table 3.4 Candidate linear mixed effects models predicting the influence of beaver pond formation and other covariates on stream temperature in the Skykomish watershed, WA, 2014 – 2016. Parsimonious models and the null model are included.

	Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
1.	R + AirT + Precip3	670	0.00	0.47
2.	R + Slope + Precip3	671	0.90	0.30
3.	R + Slope + Vol/m	673	2.69	0.12
4.	R + Slope + AirT	675	4.64	0.05
5.	R + Slope	675	5.04	0.04
6.	R + Slope + DA	676	5.95	0.02
7.	R + Precip3	682	12.29	0.00
8.	R + Precip3 + DA	683	12.71	0.00
9.	R + Precip3 + Vol/m	683	13.03	0.00
10.	R + Vol/m	686	15.70	0.00
11.	R + AirT	686	16.06	0.00
12.	R (null model)	686	16.51	0.00
13.	R + DA	687	16.85	0.00

*Notes:* AIC<sub>c</sub>, Akaike’s Information Criterion for small samples was used to correct for small sample bias, ΔAIC<sub>c</sub> reports the difference between a given model and the highest ranked model, and w<sub>i</sub>, Akaike weights, indicates the most probable model. R: pre- and post-relocation, AirT: air temperature, Precip3: 3-day average precipitation, Slope: log of site elevation change/site length, Vol/m: surface water volume in ponds and streams per meter, DA: drainage area contributing to site from lowest extent of stream reach.

### 3.9. Figures

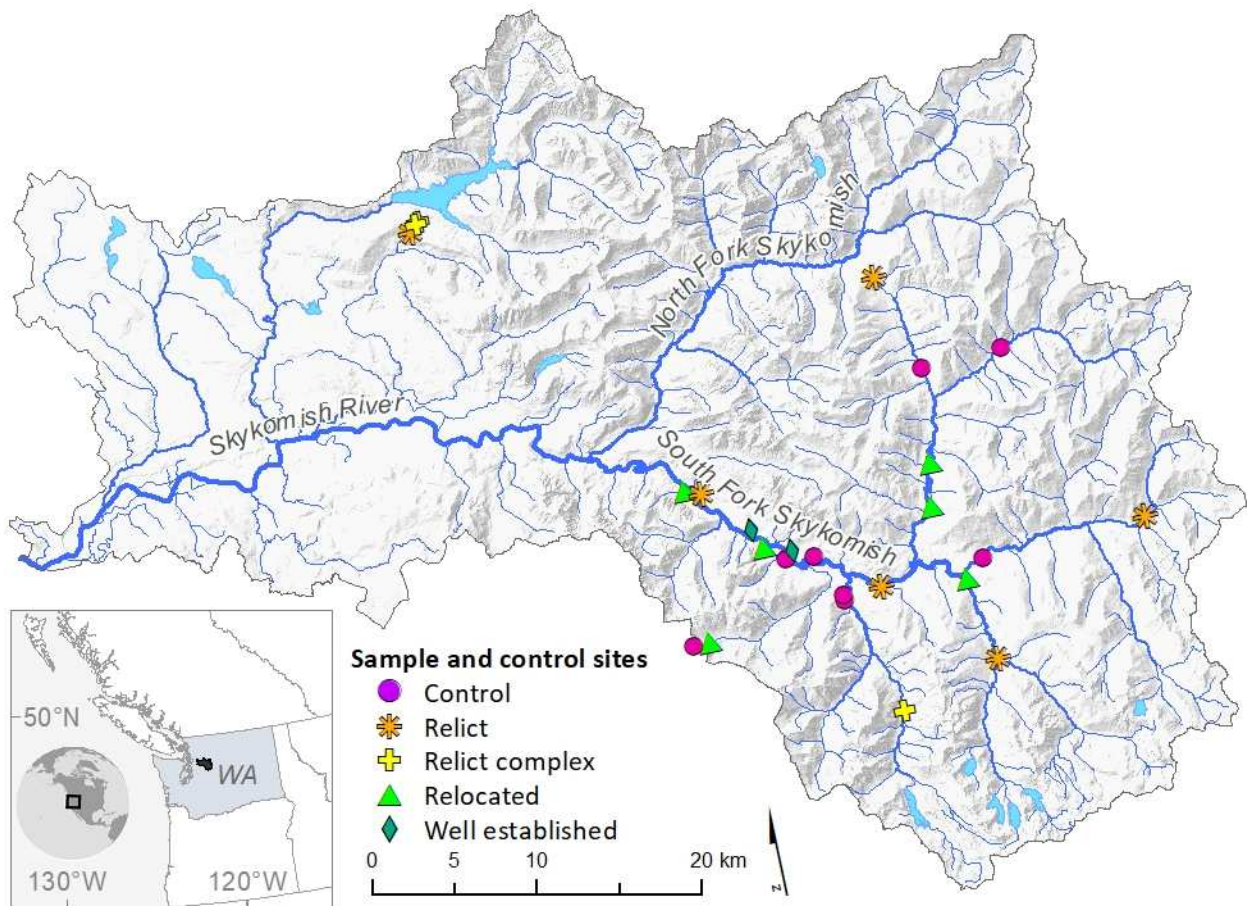


Figure 3.1 Sampling locations within the Skykomish River watershed, Washington State, USA. Of the 25 sites sampled in 2014 through 2016, 8 were free-flowing control reaches with no evidence of beaver modification, 6 were relict reaches consisting of a single small pond with an unmaintained dam, 4 were relict complexes consisting of a series of unmaintained dams and ponds, 2 were naturally colonized and well established beaver complexes, and 5 were relocation sites at which beavers successfully built dams that formed wetland or pond complexes.

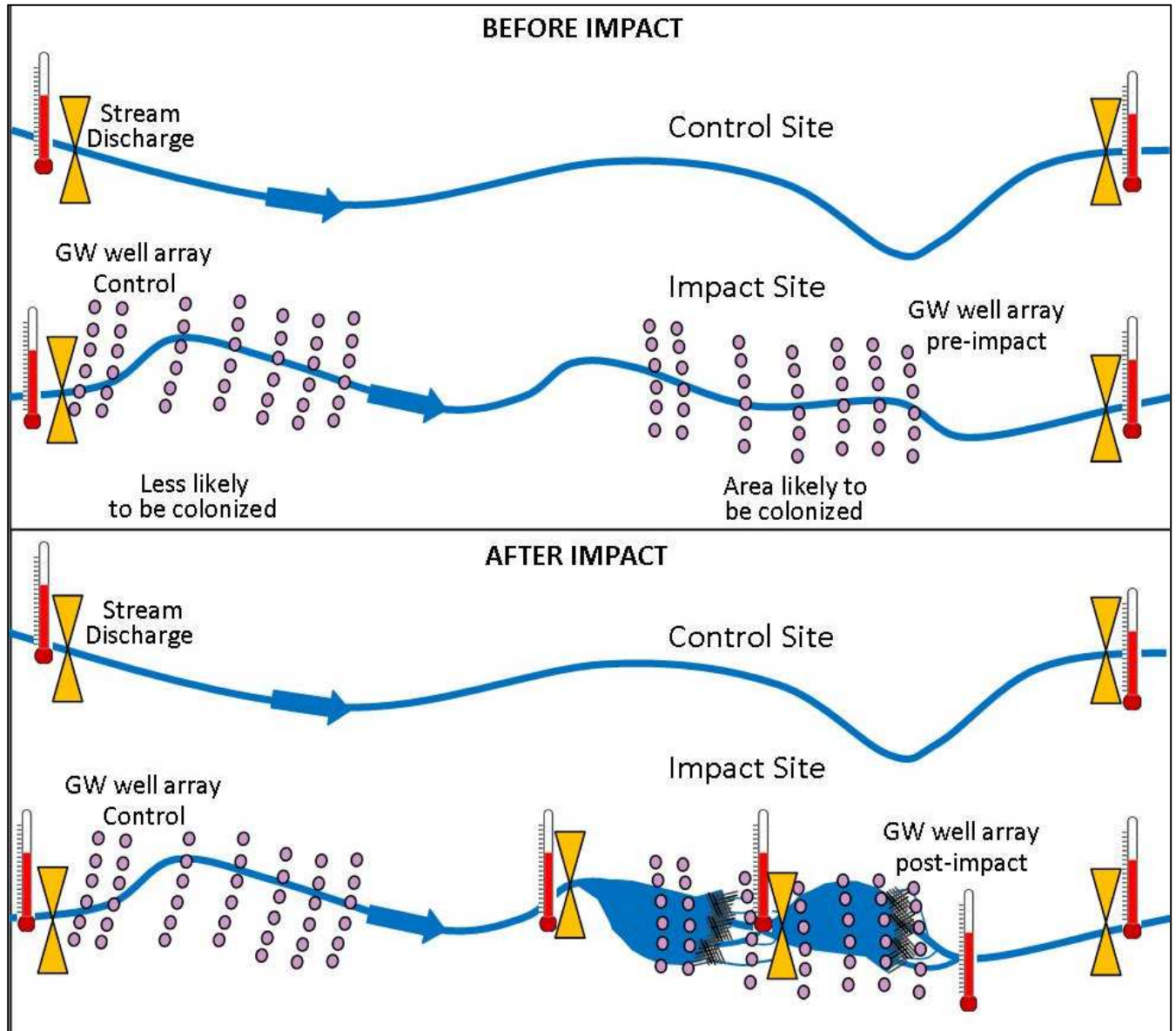


Figure 3.2 Before, after, control, impact (BACI) design for monitoring the effect of beaver relocation on hydrology and stream temperature. Red symbols represent in-stream continuous temperature probes and orange triangles represent flow discharge measurement locations. Arrays of groundwater (GW) wells were installed at anticipated dam sites and in the area upstream of the anticipated impacts site. Additional temperature probes and discharge collection points were installed once a colony was successfully relocated.

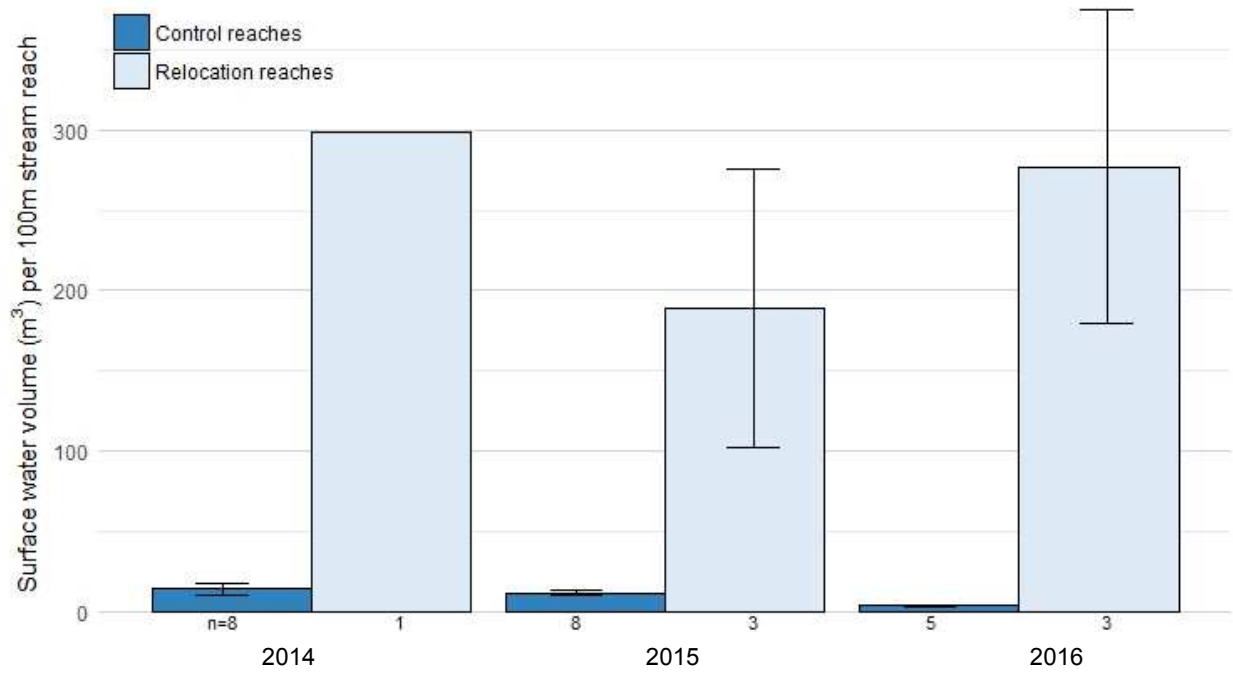


Figure 3.3 Mean surface water storage at control and established relocation reaches during August of 2014-2016.

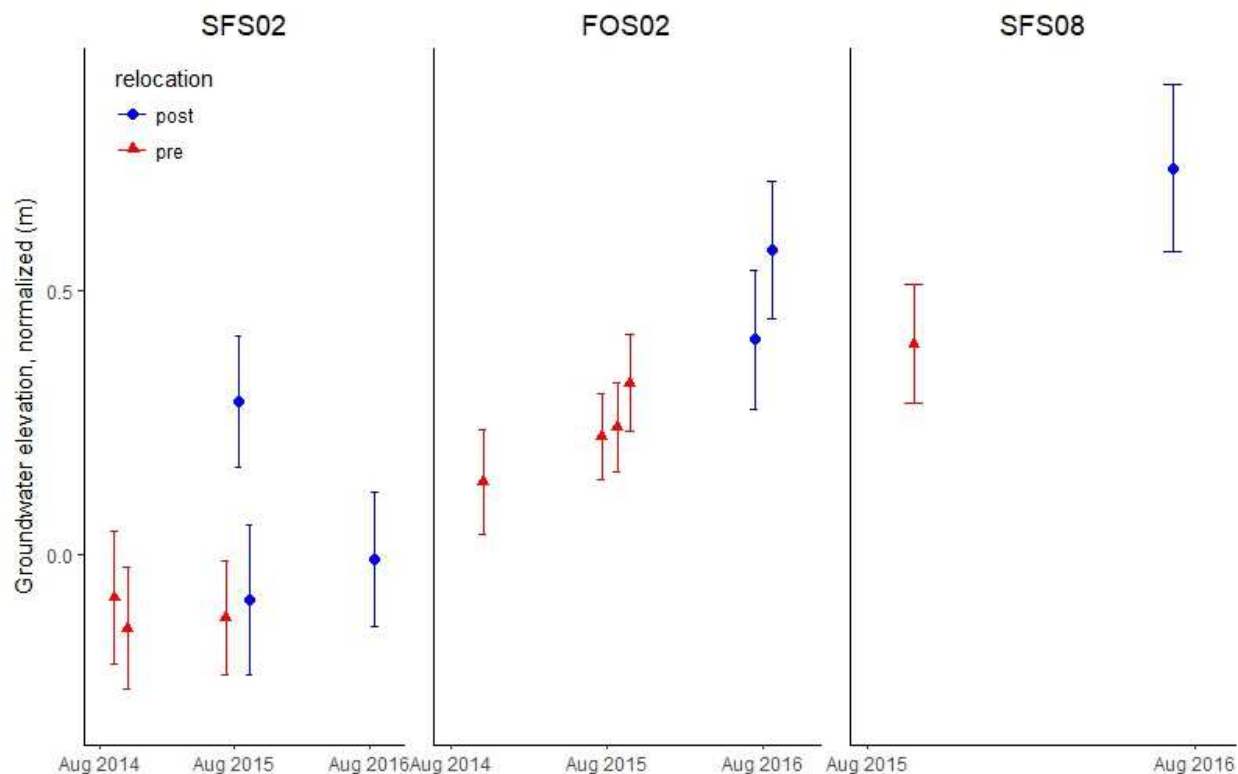


Figure 3.4 Normalized groundwater elevation at beaver relocation sites before and after beaver relocation. Each point represents the site mean of all groundwater wells on the sampling date collected during low-flow conditions. Normalized groundwater elevation at each treatment site was calculated by subtracting the mean groundwater elevation from the upstream mean groundwater elevation (i.e., control) at that site. Elevations are relative to each other within sites only.

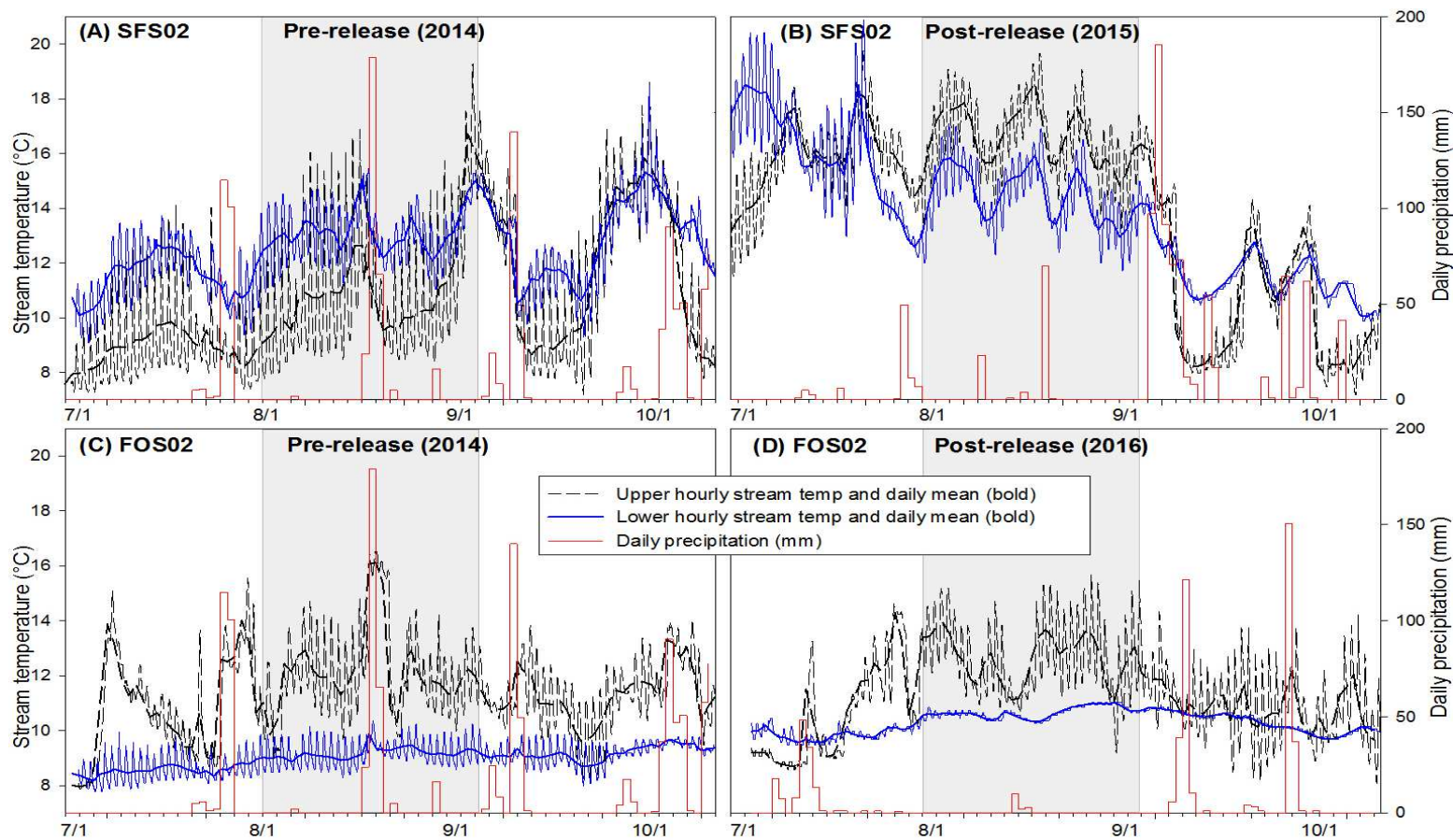


Figure 3.5 Examples of before and after-relocation stream temperature and precipitation time series during low-flow conditions (i.e. July 1 – October 1). Upstream temperature is dashed black, downstream is solid blue, precipitation is red, and the grey box is the period of focus for this study. Prior to relocation, downstream temperature was greater than upstream at the majority of relocation sites (panel A). After relocation, stream temperature was cooler downstream of impoundments in 4 of 5 sites (panel B). In one case (panel C), stream temperature was cooler downstream than upstream prior to relocation. Following relocation (panel D), this site had a diminished cooling effect.

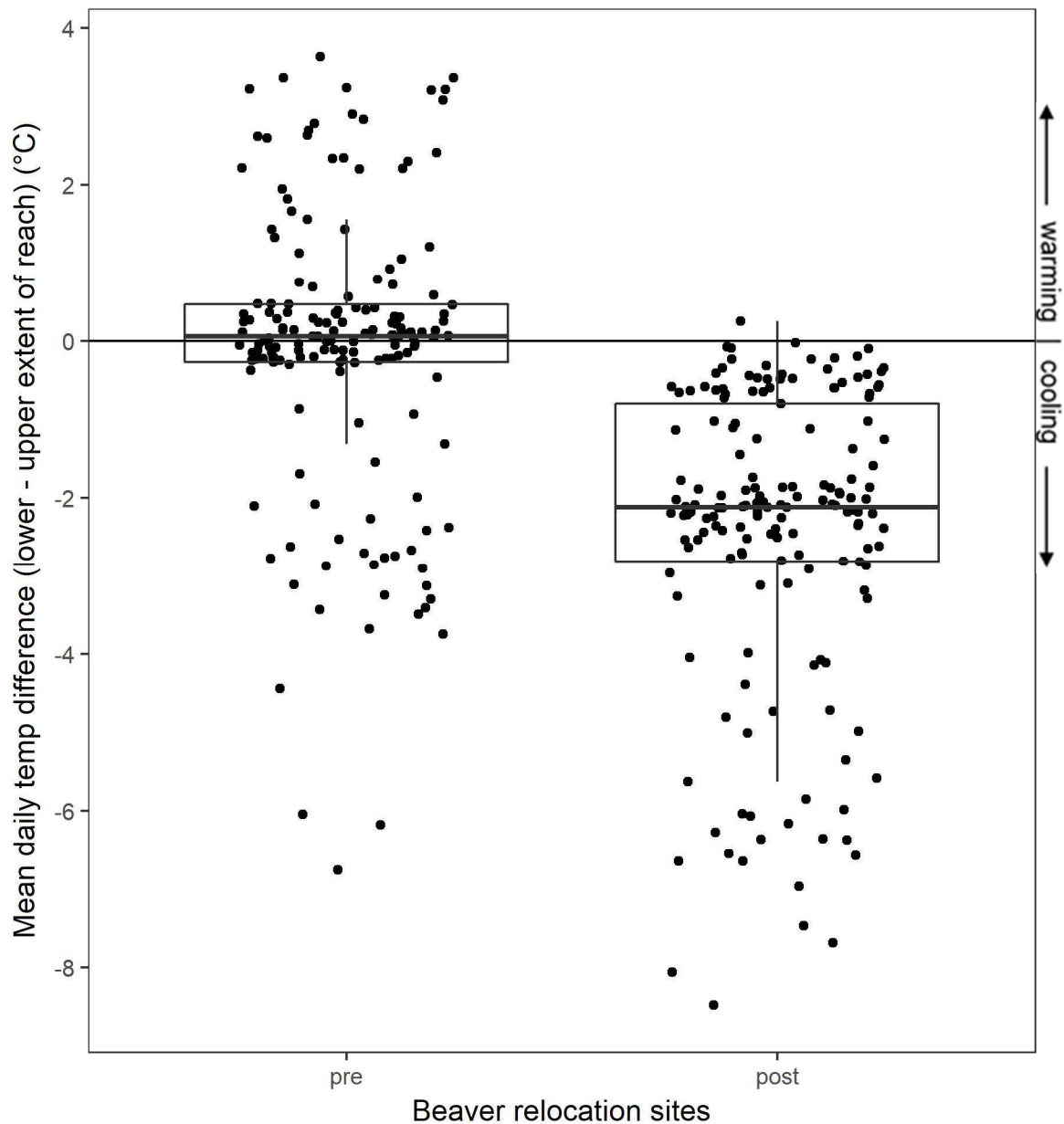


Figure 3.6 Before and after-relocation temperature effect. Each point represents the daily mean of all synoptic differences between stream temperature at the upper and lower extent of each site, collected every 30 minutes. Positive values represent an increase in stream temperature from the site's upper to lower logger, while negative values represent a decrease. Mean pre-relocation stream temperature was  $\Delta T_{\text{before}} = -0.10^{\circ}\text{C}$  (SD =  $1.85^{\circ}\text{C}$ , n = 5) and mean post-relocation stream temperature was  $\Delta T_{\text{after}} = -2.44^{\circ}\text{C}$  (SD =  $1.93^{\circ}\text{C}$ , n = 5).

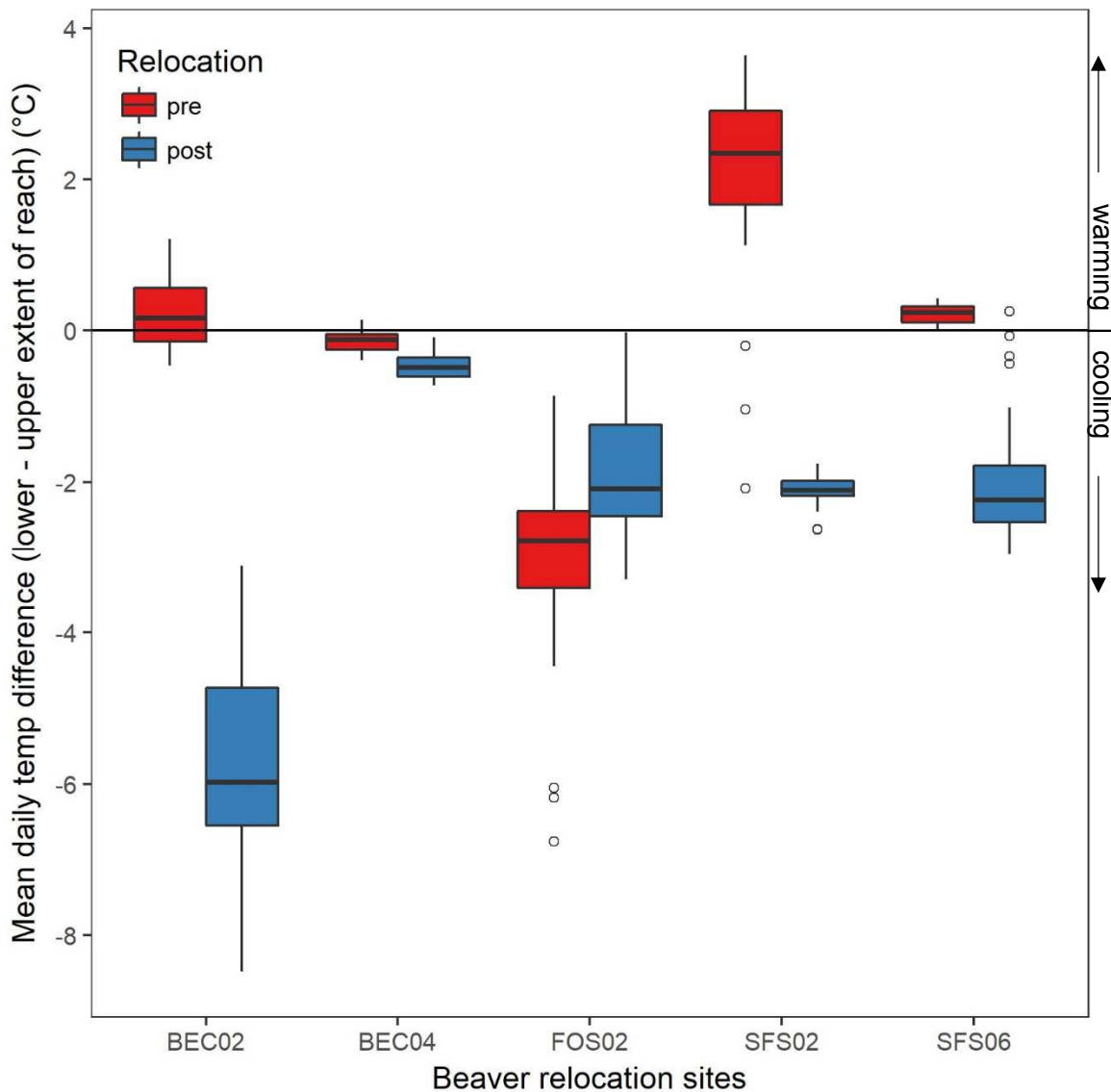


Figure 3.7 Before and after-relocation temperature effect at five sites. Each point represents the mean daily difference between upper and lower temperature probes at each site. Positive values represent an increase in stream temperature from the upper to lower site logger, while negative values represent a decrease.

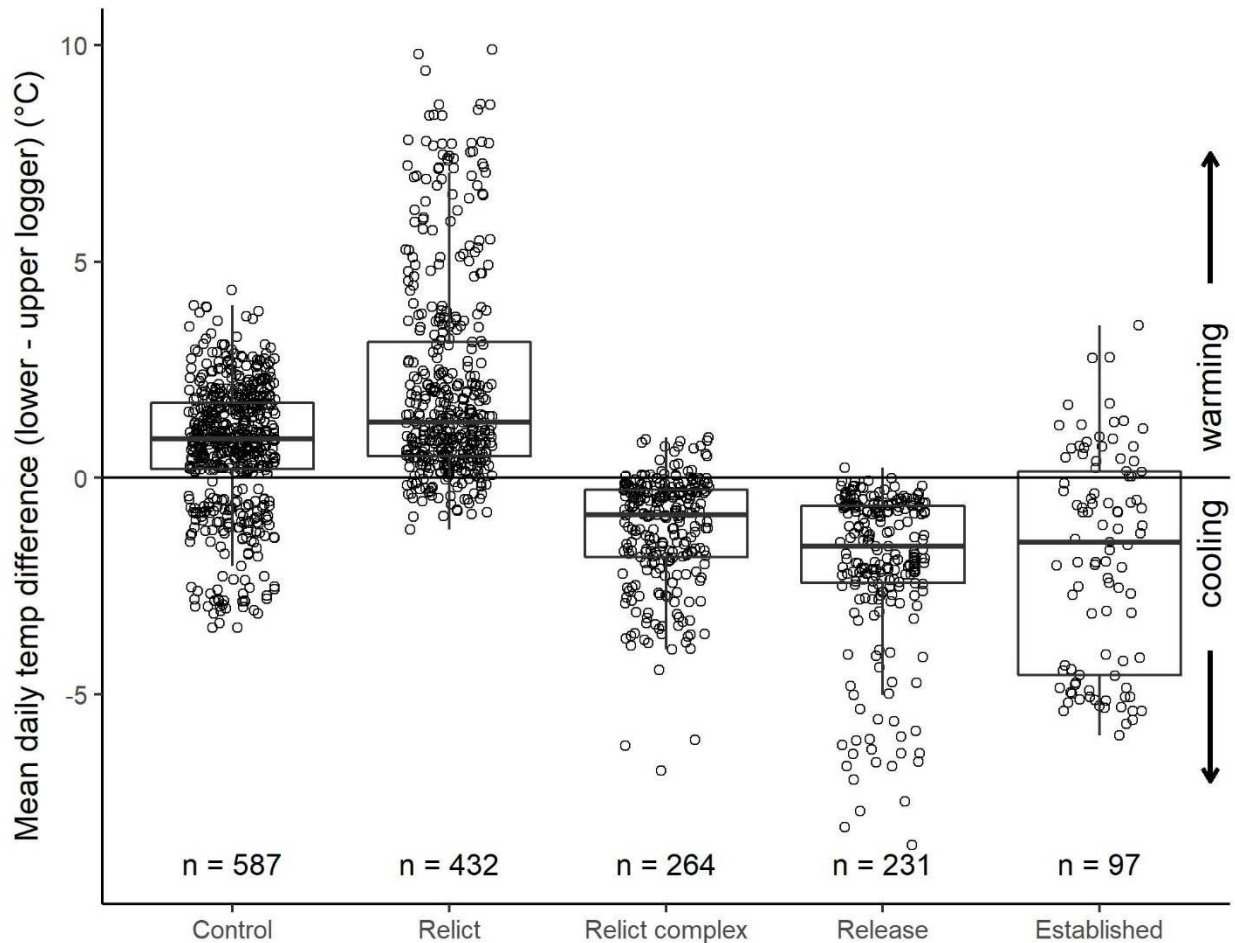


Figure 3.8 Daily mean stream temperature differences between upstream and downstream temperature probes at control reaches and in four categories of beaver complexes. Control sites are free-flowing streams. Relict sites were vacant of beaver and contained small ponds with historical, unmaintained dams. Relict complexes were also vacant but contained multiple or large ponds behind historical, unmaintained dams. Relocation sites had newly constructed dams and ponds, and established sites possessed well-maintained and long-established dams and ponds. Ponds at established sites tended to be much larger than those at relocation sites.

### 3.10. Supplementary Information

Table S 3.1 Physical and hydrologic characteristics at sites.

Site ID	Elevation (m)	Stream slope (%)	Bankfull width (m)	Drainage area (km <sup>2</sup> )	Mean annual precipitation (mm)	Length (m)
SFS01	260	1.84	4.38	2.57	2573	961
OLN01	575	1.78	2.58	0.53	3131	29
OLN02	616	0.10	2.11	0.67	3124	176
OLN03	614	0.14	2.56	0.99	3124	130
FOS01	467	0.40	2.35	0.80	2157	41
BEC01	457	0.37	1.75	0.42	2190	48
BEC02	334	0.45	2.78	1.35	2414	180
BEC04	358	0.59	1.20	0.10	2456	178
SFS02	255	0.50	3.07	1.52	2668	670
TYE01	684	3.16	1.50	0.40	2183	142
BEC03	701	3.33	2.97	1.34	2587	149
SFS03	267	3.01	4.15	2.29	2536	136
MON02	860	2.73	3.08	1.24	3975	234
FOS02	328	0.24	3.10	1.02	2169	302
SFS04	262	2.13	1.79	0.49	2568	244
SFS06	225	1.17	3.15	1.61	2592	146
MON03	497	2.17	3.02	1.19	2740	214
RAP02	542	3.06	4.31	3.41	2301	121
SFS08	244	0.66	3.41	1.78	2820	405
SFS09	282	0.09	2.15	0.53	2590	292
MIL01	296	0.57	2.31	0.61	2577	93
MIL01	294	1.19	2.54	0.78	2577	160
TYE01	371	1.33	2.35	0.62	2140	116
MON01	888	2.92	1.87	0.44	4000	408
SFS10	231	1.29	2.90	1.14	2622	249

Table S 3.2 Study's 25 sample sites, reported by beaver presence, influence, mode of site colonization, and relocation outcome.

Site ID	Control	Historical dams present		Naturally colonized		Treatment		
		Relict site	Relict complex	Pre-existing colony, dams	Colonized after study initiation	Relocation	Dam not built	Dam built
HUC12 + site number	No pre-existing colony, introduction, or subsequent natural colonization	Site initially vacant, but historical un-maintained dams present	Similar to Relict site, but evidence of large historical complex	Beavers & dams already present upon initial inspection	No beavers introduced, but site was colonized naturally & dams built	Colony(s) actually introduced	No dams were built by introduced beavers	Dams built by introduced beavers
BEC01	x							
SFS03	x							
SFS04	x					2	2	
RAP02	x							
MIL01	x							
MIL01	x							
TYE01	x							
MON01	x							
OLN01		x				1	1	
FOS01		x				1	1	
TYE01		x				1	1	
BEC03		x						
SFS09		x				1	1	
SFS10		x			x			
OLN02			x			3	3	
OLN03			x			1	1	
MON03			x			1	1	
SFS01				x				
SFS08				x				
BEC04					x			
BEC02			x			2		3
FOS02			x			3		5
SFS02						4		3
MON02						1		2
SFS06						1		1
25	8	6	5	2	2	22	11	14

Table S 3.3 Groundwater well levels at control, pre- and post-relocation, and long-term established beaver sites.

Site	Site status	Sample date	Number of wells		GW depth, site mean (m)		Standard deviation of GW depth		Standardized GW depth at treatment site (t - c) (m)	Mean summer low-flow depth (m)	Post-relocation GW change (m)
							t	c			
							t	c			
SFS02	Pre	9/8/14	40	18	-0.781	-0.681	0.410	0.372	-0.099		
		7/8/15	40	18	-1.003	-0.825	0.309	0.359	-0.178	-0.277	
SFS02	Post	8/12/15	23	18	-0.710	-1.000	0.503	0.287	0.291		
		9/11/15	23	18	-0.685	-0.599	0.516	0.394	-0.086		
		8/17/16	23	18	-0.733	-0.725	0.470	0.341	-0.009	0.065	0.343
FOS02	Pre	10/16/14	19	17	-0.685	-0.823	0.318	0.270	0.138		
		7/21/15	19	17	-0.715	-0.939	0.307	0.172	0.224		
		8/26/15	19	17	-0.734	-0.975	0.332	0.152	0.242		
		9/25/15	19	17	-0.599	-0.925	0.353	0.174	0.325	0.232	
FOS02	Post	7/12/16	19	17	-0.379	-0.785	0.485	0.287	0.407		
		8/23/16	19	17	-0.267	-0.843	0.513	0.232	0.577	0.492	0.260
SFS08	Inactive	9/22/15	14	23	-0.091	-0.490	0.286	0.397	0.399	0.399	
		7/7/16	14	23	0.138	-0.593	0.483	0.434	0.731	0.516	0.116

t: treatment, c: control sites

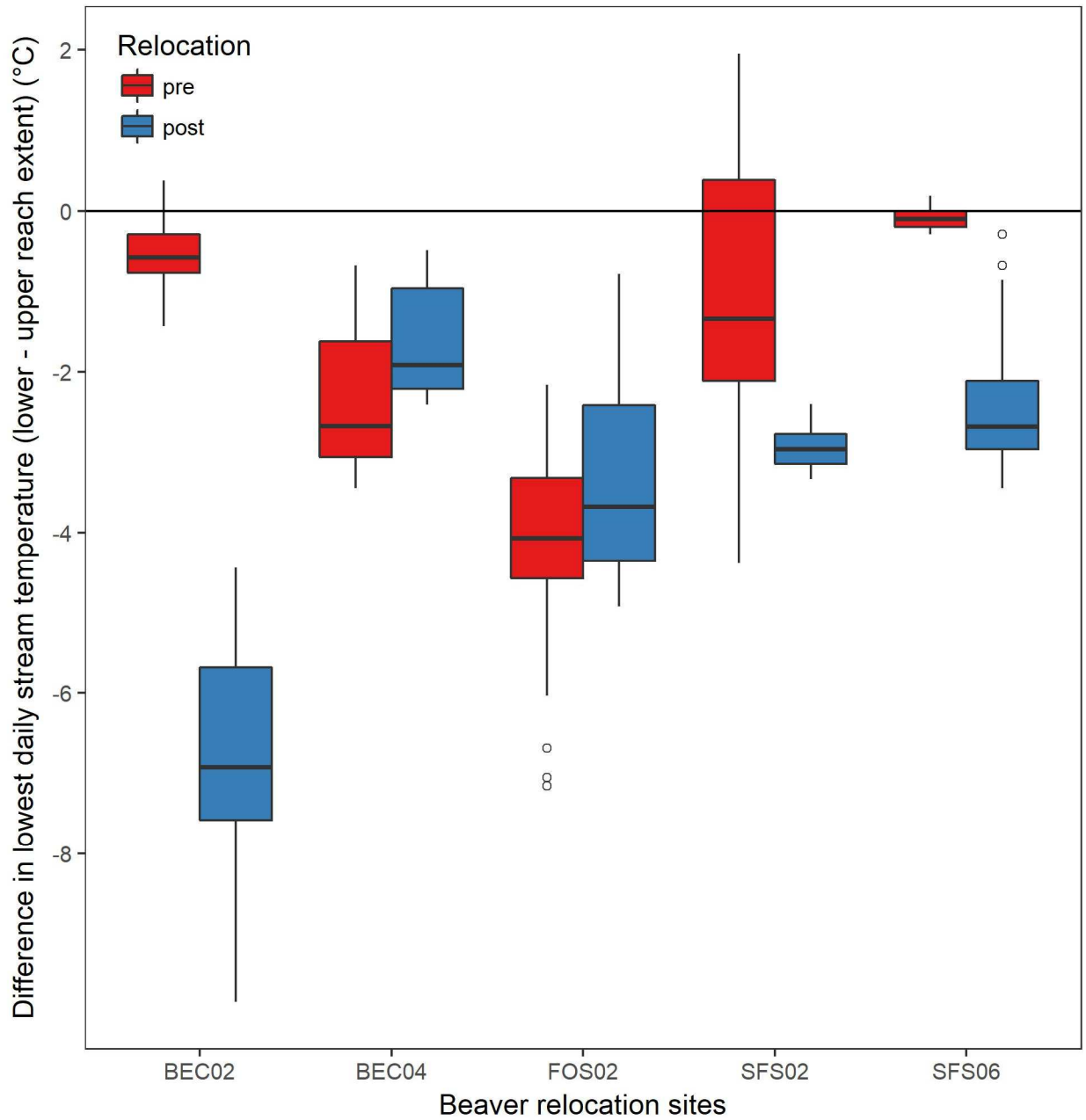


Figure S 3.1 Maximum stream cooling effect at pre and post-relocation sites. Maximum cooling effect reports the greatest daily cooling effect of all synoptic temperature differences between the lower and upper end of each reach.

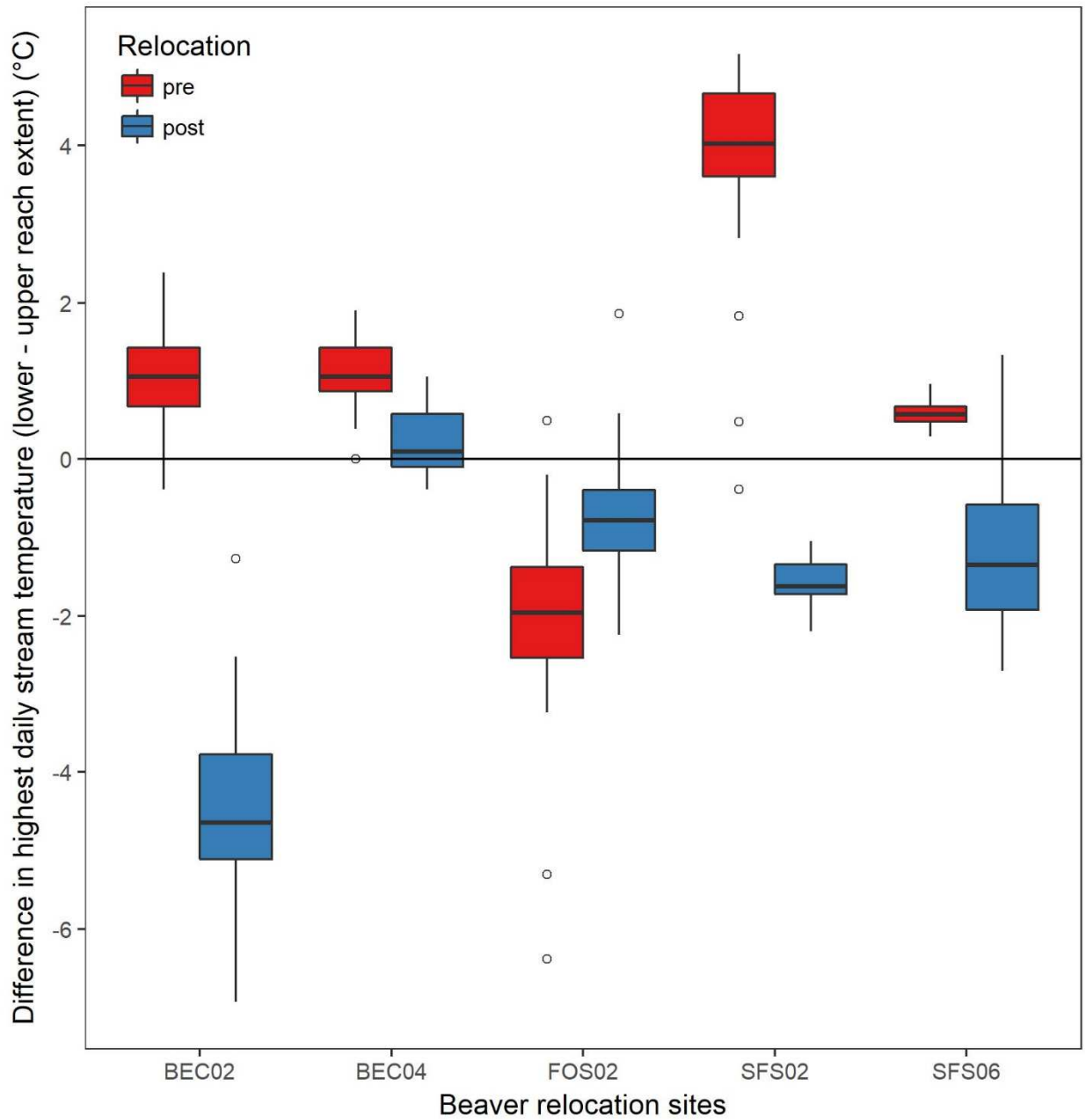


Figure S 3.2 Maximum stream warming effect at pre and post-relocation sites. Maximum warming effect reports the greatest daily warming effect of all synoptic temperature differences between the lower and upper end of each reach.

## Chapter 4. **Modeling regional-scale hydrologic effects of beaver impoundments: Can beaver mitigate the effects of climate change?**

### **4.1. Abstract**

Warming in the Pacific Northwest has resulted in reduced summer rain and winter snowpack. This trend is predicted to continue. The decrease in spring snowmelt and summer water availability will likely result in warmer stream temperatures and decreased perennial flow in headwater streams, causing stress to aquatic and riparian species. Beaver (*Castor canadensis*) have the potential to reduce this stress by increasing ecological resilience to disturbance through the creation of pond complexes. Thus, reintroducing beaver has been cited as an important climate change adaptation strategy. It is not clear, however, the degree to which beaver could offset climate-induced reductions in precipitation or snowpack. Here, we created a regional model for western Washington and Oregon, USA, to assess the degree to which beaver ponds and groundwater storage can offset snowpack loss and supplement summer water availability under a number of future climate scenarios. We first constructed a beaver intrinsic potential habitat model and used it to predict where colonies and dams might exist if populations were near carrying capacity. We delineated ponds behind these dams and identified surface and groundwater storage based on terrain and location. Water storage was compared to predicted losses in snowpack and summer precipitation in 2050 and 2080 for climate projections based on RCP 4.5 and 8.5. Although beaver could store substantial amounts of surface and groundwater, this could only offset small amounts of the relatively large projected snowpack loss in the region. Beaver were able to supplement summer water availability, however, and have the potential to increase summer availability by up to 20% in some basins. We conclude that at high densities

likely nearing carrying capacity, beaver have the potential to increase hydrologic resilience in many stream reaches and some basins. We identify where beaver relocation and policies that encourage expansion can be directed to have the greatest impact.

#### **4.2. Introduction**

Climate change is altering hydrologic regimes in the American West, and climate models predict that these changes will continue and intensify over the next century (Dalton et al. 2013, Mote and Salathé 2010, IPCC 2013). Annual temperatures are projected to increase by 1.1°C to 4.7° C by 2080 (Dalton et al. 2013). In the Pacific Northwest, the greatest changes are expected to occur at higher elevations of the Cascade Mountains on west and southwest facing slopes (Littell et al. 2009). The timing of annual precipitation is expected to continue to shift, with a greater percentage of precipitation falling during the winter, and summer precipitation decreasing by up to 34% of historical levels by 2080 (Mauger et al. 2015). Elevated winter temperatures will cause a greater percentage of precipitation to fall as rain instead of snow and will lead to earlier snowmelt at higher elevations (Reidy Liermann et al. 2011). In these places, snowpack may decline by as much as 100% of historical levels by 2080 (Mauger et al. 2015) with some basins transitioning from being snow dominated to being rain dominated in the western Cascades (Elsner et al. 2010).

The predicted changes in precipitation timing, intensity, and phase (i.e., snow or rain), will likely have substantial impacts on stream hydrology. Winter storm events are likely to be stronger, producing more erosive flows (Mauger et al. 2015). Many streams in the American West rely on spring snowmelt to supplement summer stream flows (Stewart et al. 2004). As warming temperatures continue to decrease annual snowpack, the duration of summer low flow

will expand. These trends have already been observed in many places (Stewart et al. 2005, Luce and Holden 2009) and will continue to worsen in many areas (Mauger et al. 2015). Reduced summer low flows are likely to result in warmer stream temperature (Margolis et al. 2001a), and some perennial reaches that have historically relied on summer supplementation from snowpack may transition to seasonal streams (Stewart et al. 2004, 2005).

The alteration of hydrologic regimes in streams will likely have some adverse impacts on riparian habitats and species. For example, increased bed and bank erosion resulting from increased winter storm intensity has the potential to cause scouring and sedimentation of salmonid redds and loss of large woody debris and complex geomorphology, such as braided streambeds. Floodplain disconnection resulting from channel down-cutting may promote drying of riparian vegetation and increased fire susceptibility (Pollock et al. 2014). Decreased summer water quantities and warmer temperatures will likely promote lower dissolved oxygen levels, and reduced habitat availability (Mantua et al. 2010). These changes will increase stress to aquatic organisms and will also affect their movement, distribution, and phenology. Riparian vegetation and species will be similarly affected by decreased soil moisture. Both hydrologic stability and ecosystem resilience will be substantially reduced by these changes

Beaver (*Castor canadensis*) populations in North America have witnessed a dramatic decline and resurgence over the previous four centuries. Prior to the onset of industrial-scale trapping efforts, North American beaver (*Castor canadensis*) populations were estimated to number up to 400 million individuals (Seton 1929, Naiman et al. 1986). Following local extirpation in many areas of eastern North America, the demand for fur drove westward expansion in search for new populations (Mackie 1997). Beaver were trapped intensively throughout most of their former range until about 1900 when populations, reaching only a small

fraction of historical levels, were sufficiently depressed to make trapping unprofitable. Despite the decline of the fur trade, beavers continued to be systematically removed from many areas as beaver complexes were drained and converted to agriculture. Beaver complexes and surrounding areas have often been attractive for human development because they frequently occur in relatively flat areas, with productive soils, and a perennial water source. In more recent years, these areas have often been converted to development and other human-dominated land uses.

Beaver populations have begun to rebound in many areas, due in part to changes in how beaver are managed. The decline in recreational trapping, increased use of nonlethal management strategies, and adoption of regulations (e.g., Revised Code of Washington 2001) that decrease trapping efficiency have together reduced the total number of beaver being killed annually. Additionally, a changing public perception and greater understanding of the beaver's ability to provide ecosystem benefits has prompted many jurisdictions to adopt a policy of tolerance (Bailey et al. 2018). Worldwide, rapidly increasing beaver populations have grown to an estimated  $3.0 \times 10^7$  (Whitfield et al. 2015). Although they are unlikely to reclaim areas of their historical range that have been converted to human land uses (Dittbrenner et al. 2018), rebounding populations in North America are currently estimated at 15 to 50 million (Naiman et al. 1986, Whitfield et al. 2015). Despite this resurgence, populations remain below carrying capacity in many remaining areas. For example, beaver are currently vacant from as much as 70% of available stream habitat in some basins of the Pacific Northwest (Dittbrenner et al. 2018).

Beaver have long been recognized for their ability to increase the ecological function of riparian and aquatic ecosystems (Rosell et al. 2005). Through their dam-building, they create pond complexes that influence geomorphology, hydrology, and water quality. Beaver ponds reduce stream velocity, allowing for increased sediment aggradation and channel complexity

(Pollock et al. 2014). In streams that have experienced downcutting, this can result in floodplain reconnection. Beaver have been found to increase the riparian width of streams from 10.5 m to 33.9 m (McKinstry et al. 2001) as well as the number and size of pools in reaches downstream of dams (Stack and Beschta 1989). Beaver pond complexes can store substantial amounts of surface and groundwater (Johnston and Naiman 1987) with up to 30% of some stream's summer water was stored in beaver ponds (Duncan 1984). Beaver ponds can also result in lost storage due to evaporative or transpiration losses, however, and some have found that a 1.25 ha beaver pond reduced annual discharge by 8% (Correll et al. 2000). Dammed stream reaches have been shown to extend the lateral extent of the hyporheic zone by up to 7.5 m beyond control reaches (Shaw 2009) and by over 50 m when adjacent to larger ponds (Lowry 1993).

Beaver complexes influence flow timing and stabilize stream discharge by slowing stream velocity during high flow events, impounding high flows, and releasing that water during low flows. Ponds have the potential to increase stream flow downstream of dams during summer low flow periods Parker (1986), and some (Yeager and Hill 1954, Rutherford 1955, Frickel 1972) have suggested and observed that beaver complexes may convert intermittent flows into perennial streams. These effects may be related to dam age, with older dams having a greater influence on hydrology (Meentemeyer and Butler 1999). Beaver complexes have also been found to affect stream temperature, but these effects often vary by geomorphic setting and regime. Some have found that beaver complexes lead to downstream warming (Patterson 1951, Avery 1992), warming and cooling depending upon season (Avery 1983), or no relationship between dam presence and temperature (McRae and Edwards 1994). Other studies have evaluated stream temperatures at larger scales and found that beaver ponds increase thermal

heterogeneity, but have a net cooling effect, largely from groundwater recharge and upwelling (White 1990, Weber et al. 2017)(Chapter 2).

Combined increases in morphological complexity, surface and groundwater storage, and thermal heterogeneity created by beaver pond complexes can result in increased habitat and biological diversity, and ecosystem resilience. Pond complexes create a variety of pond depths, flow velocities, and thermal regimes. Beaver's ongoing herbivory promotes an increase in the diversity of vegetation species and communities, and successional states, creating specialized habitat (Naiman et al. 2000). When these changes occur in low-order and headwater stream reaches, lower productivity reaches are often altered by introducing high productivity pond habitats (Anderson and Rosemond 2007, Fuller and Peckarsky 2011b). These changes have been shown to promote and improve nutrient cycling and water quality (Smith et al. 1991). The increased provisioning and variability in pond and community types often leads to an increase in species and community diversity (Pollock et al. 1995, Gibson and Olden 2014). As ecosystem engineers, beaver have the capacity to not only increase existing ecological function but also buffer against future changes and habitat alterations (Naiman et al. 2000). For example, during summer months when stream temperature is elevated, deep ponds and downstream cooling may offer areas of thermal refugia (Steel et al. 2017). During winter storm events, ponds can reduce potentially erosive stream velocity and spread flows into the floodplain to be dispersed (Pollock et al. 2014).

Some studies have suggested that, as populations expand, the ability of beaver to increase hydrologic stability, total riparian habitat area (Naiman et al. 2000), community (Pollock et al. 1995) and patch diversity (Wright et al. 2002, 2012), and ecosystem resistance and resilience (Naiman et al. 1986) could reduce some of the impacts associated with climate change. Whereas

the majority of research into the effects of beaver on hydrology and ecosystems has come from direct observation at the reach level, less is known about how groups of beaver colonies at sufficient numbers may collectively affect riparian areas and whole stream basins. The ecological implications of observed and predicted changes to stream hydrology and water availability have placed an increased emphasis on identifying approaches that reduce impacts to ecological communities, life history patterns of species, and the processes that maintain them. Given these needs, further analysis of the role of beaver as an ecosystem engineer and as a mechanism to retain ecological resilience in aquatic systems at the larger landscape scale is warranted.

In this study, we evaluate the effect of beaver populations at or near carrying capacity on watershed and region-scale measures of surface and groundwater storage. Our objectives were to (1) construct a spatially explicit hydrologic model to quantify the watershed-scale effect of beaver at carrying capacity on water surface and groundwater storage, (2) compare the potential hydrologic effects of beaver to anticipated impacts of climate change on snowpack to determine whether beaver can offset some loss of late-season water storage, and (3) assess to what degree beaver-created storage can increase summer water availability, particularly in rain-dominated basins. We assess whether beaver conservation and reintroduction can be used to reduce some climate change impacts and increase hydrologic stability and riparian resilience to reduce anticipated disturbances. We close by exploring how beaver modify ecological processes at scales not traditionally evaluated, and how they may be best utilized by restoration practitioners and planners for prioritizing management and long-term conservation decisions.

### **4.3. Methods**

#### ***4.3.1. Study area***

Our study area encompassed Washington and Oregon, USA, west of the Cascade Mountain crest, comprising an area of approximately 140,000 km<sup>2</sup> (Figure 4.1). The region is topographically and climatically diverse, transitioning from lowlands adjacent to the Pacific Ocean on the west to the Cascade crest on the east. Elevation varies from 0 m to 4,392 m above sea level. Mean annual precipitation ranges from 670 millimeters in the San Juan Islands basin (Hydrologic Unit Code (HUC) 17110003) of Washington state to 3,364 mm in the Queets-Quinault basin (HUC 17100102) on the Olympic Peninsula of Washington. Coastal areas and lowland regions are predominantly rain dominated (i.e. 70% of study region), whereas more mountainous basins towards the upper reaches of the Cascades and Olympic mountains are mixed rain-snow (25%) or snow dominated (5%) (Elsner et al. 2010).

The variability of topography and climate includes six distinct level III ecoregions within the study area (Wiken et al. 2011). Upland areas are dominated by conifer forests, whereas lowland areas are dominated by mixed-deciduous vegetation communities. The study area consists of 64 hydrologic unit code (HUC) 8-digit basins, each with at least one large river system present. The proximity to Pacific Ocean and Puget Sound coastal lowlands, in part, results in a high density of wetlands and estuaries throughout the study area.

Land use varies throughout the region, ranging from densely human-dominated landscapes to large tracts of relatively natural lands. Lowland areas predominantly consist of intensive land uses such as developed areas and agriculture. Mid-upland areas consist of a matrix of rural residential, private timberlands, and forested natural areas. More mountainous areas are most frequently owned by the US federal government and have designated uses of national forests, and national park and wilderness areas.

Beaver were historically prevalent throughout the region and could be found in most perennial streams, lakes, and estuaries (Mackie 1997). Following European colonization, beaver were intensively harvested and approached local extirpation by the early 1900s. Many lowland areas were converted to human land uses such as development or agriculture after removal of beaver. Much of these areas remain in use and represent lost habitat potential for recovering beaver populations. Beaver have returned to parts of their historical range but remain below carrying capacity in many areas (Dittbrenner et al. 2018)(Chapter 2).

#### **4.3.2. *Model overview***

The creation of the beaver watershed storage model and subsequent analyses can be divided into four overarching categories (Figure 4.2). First, we created a beaver intrinsic potential (BIP) habitat model to identify and rank potential beaver habitat. Next, we identified stream reaches that could support colonies and we placed dams within these reaches. We then delineated beaver ponds at each dam based on the surrounding topography. We estimated the extent of groundwater inundation as a result of damming from topography and existing groundwater literature. We then applied a mask to exclude areas of human-dominated land uses to account for that fact that these areas are unlikely to support widespread beaver colonization. Finally, to assess the potential for beaver to offset the impacts of climate change on water availability, we compared measures of beaver-created surface and groundwater storage with estimates of snowpack and precipitation under various future climate scenarios. We used ArcGIS 10.5 (ESRI 2014), and the Python and R programming languages for model creation and analyses.

### 4.3.3. *Beaver intrinsic potential model to identify potential habitat*

We created a BIP model to identify stream segments that were potentially suitable for beaver colonization. The model consists of three input parameters: stream gradient, bankfull width (BFW), and valley width as described in Dittbrenner et al. (2018). At each stream segment, the three parameters were given a score based on site condition that were then summed to produce a raw BIP score (see Table S 4.1). The model output consisted of a ranking of intrinsic habitat potential, 0 – 3 (corresponding to no BIP, low, moderate, and high BIP).

We used the National Hydrography Dataset NHDPlusHR (NHD) flowline layer (USGS 2019) as a base layer for all spatial stream data and the Watershed Boundary Dataset (WBD) (USGS 2019) for HUC 4 and HUC 8 boundaries. Human-created conveyances (e.g., irrigation canals) were excluded from the preliminary NHD stream layer (preserving NHD FTypes 460 and 558). We used stream gradient data contained in the NHD data table NHDFlowlineVAA. In cases where data were missing or erroneous, we calculated stream gradients from 10 m NED DEMs (USGS 2014a).

We extrapolated bankfull width for each stream segment using an empirical equation adapted from Barnard et al. (2013) for small streams in western Washington:

$$BFW = 0.29 \times 0.39DA^{0.45} \times 0.39 P^{0.61}, \quad \text{Equation 1}$$

where  $BFW$  is in meters,  $DA$  is the upstream drainage area ( $\text{km}^2$ ) measured from the lower extent of the stream segment, and  $P$  is mean annual precipitation (cm/year). We obtained the calculated drainage area for each segment from the NHDFlowlineVAA table, and precipitation from 800-m resolution PRISM data (PRISM 2004).

We estimated valley width using the Valley Confinement Algorithm tool developed by Nagel et al. (2014). This tool creates a GIS polygon data layer depicting the shape and extent of unconfined valley bottoms or the lateral extent of the valley floor. As inputs for the Valley Confinement Algorithm tool, we used NHD flowlines, 10-m DEMs, and mean annual precipitation from PRISM data averaged across each HUC 8 basin. To find the valley width for each stream segment, we calculated the average width of stream cross sections, spaced every 10 m along segments, intersecting the extent of the Valley Confinement Algorithm polygon.

#### ***4.3.4. Colony and dam placement***

We identified stream reaches that were suitable for colonization using beaver intrinsic potential habitat scores and assigned points representing beaver colonies to a geographic information system (GIS) based on known colony densities. Prior to designating colony points, we excluded stream segments that intersected features that were unlikely to be suitable for dam-building colonies using the NHD waterbody data layer. These features included large waterbodies such as lakes and ponds greater than 0.05 km<sup>2</sup>, reservoirs, and estuaries (NHD Waterbody FTtypes 390, 436, 493, respectively). We based our estimates of colony density on existing literature documenting colony distribution within stream systems in areas where populations have approached carrying capacity or demonstrated equilibrium (see Table S 4.2, Table S 4.6). This corresponded to densities of 1.5 colonies per stream km in BIP-3 streams, 1.0 colony per km in BIP-2 streams, 0.5 colonies per km in BIP-1 streams, and no colonies in BIP-0 streams. Colony points were assigned to streams by generating random points within stream segments of each BIP class using the specified colony density.

We placed beaver dam points within stream reaches containing colonies using a dam density estimate from the literature (see Table S 4.3, Table S 4.6). We assumed the colony home

range, or area in which dam building is likely to take place for each colony, to be one-half of the colony density (e.g., 0.5 km for colonies in BIP 2 streams), and a dam spacing of no less than 100 m between dams. We randomly generated dam points using these criteria within each colony's home range. As such, the number of dams per colony was dependent on the suitable stream length of each colony.

In some cases, the NHD flow path layer is an approximation of the actual stream location and may not lie within the lowest point of the valley. In these circumstances, the mismatch between stream location and topography would likely adversely affect the modeling of pond size and area by under-estimating the dam's contributing area. To account for this issue, we created a synthetic stream analog at each stream segment based on a flow accumulation modeling approach and compared the location of the NHD streamline with a topography-based stream line. In cases where there was a substantial difference between the NHD stream line and this synthetic stream, we snapped the previously generated dams to the modeled stream layer.

#### ***4.3.5. Beaver pond and groundwater storage***

We generated a pond at each dam point. At each dam, we found the contributing area, or drainage area, using a flow-accumulation approach. We used an estimated dam height of 0.91 m based on existing literature documenting dam characteristics within well-established colonies (see Table S 4.4, Table S 4.6). To delineate each pond, we identified the elevation of the dam crest above the valley floor to define a horizontal plane. All cells within each dam's contributing area that intersected this plane were considered to be part of the pond. This method allows for the estimation of both pond area and depth. Our model produced ponds that intersected other ponds when dams were in close proximity, as commonly occurs in actual beaver ponds. In cases where

two pond raster cells overlapped, we counted the larger of the two, simulating complexes with multiple ponds.

We estimated ground water storage within the area surrounding each pond using data from existing literature and empirical results from our previous work on beaver-driven groundwater storage (Chapter 2). We estimated that the lateral extent of increase in the water table resulting from beaver damming was determined by the floodplain width and as a function of pond size. Lateral extent was calculated as the lesser of valley width, calculated during BIP development (see section 4.3.3) or a width of approximately 2.4 times that of the radius of the associated beaver pond, or:

$$GW_{extent} = 2.4 \times \sqrt{\frac{A_{pond}}{\pi}}, \quad \text{Equation 2}$$

where  $GW_{extent}$  is lateral extent (m) of groundwater effected by beaver and  $A_{pond}$  is pond area ( $m^2$ ). In ponds located outside floodplains, lateral extent was based on a 25 m buffer around the pond, consistent with empirical data (see Table S 4.4, Table S 4.6). We estimated groundwater storage by multiplying the lateral extent by the change in water table height and soil porosity. We assumed an increase of 0.42 m in the height of the water table based on estimates from the literature (see Table S 4.5, Table S 4.6). Spatially explicit soil porosity was obtained from the USDA Natural Resource Conservation Service State Soil Geographic Database (STATSGO) (Miller and White 2002) using porosity measures at a depth of L6 (40-60 cm depth).

#### **4.3.6. Landscape and human land-use analysis**

We combined surface and groundwater storage and summarized total beaver complex storage at the HUC 4 and HUC 8 levels. We evaluated estimates of regional storage potential using the full

model, and with a mask that omitted a number of human-dominated land-use types. The mask omitted pond complexes within lands dominated by agriculture using the 2011 National Land Cover Database (NLCD) (Homer et al. 2015), defined as Pasture/Hay and Cultivated Crops (NLCD categories 81 and 82, respectively) and developed land uses, including the NLCD categories Developed Open Space, Developed Low Intensity, Developed Medium Intensity, and Developed High Intensity. We applied this mask when performing all subsequent analyses.

#### ***4.3.7. Calculating the potential for beaver to offset climate impacts on water availability***

We compared beaver complex storage to April 1 snowpack volume in snow-dominated basins under a number of future climate scenarios to identify whether increases in storage by beaver could offset some losses from declining snowpack. In all climate-related analyses, we used beaver storage estimates with an agricultural and development land use mask applied. We compared this storage to projected loss of April 1 snow water equivalent (SWE) in historical (1950-2005), 2050 (2040-2069), and 2080 (2070-2099) time periods under representative concentration pathways (RCP) 4.5 and 8.5. Snow volume was calculated using data from the Climate Scenarios Project (Mote et al. 2014), which used the Variable Infiltration Capacity Macroscale Hydrologic model (VIC) (Liang et al. 2004, Hamman et al. 2018) and Unified Land Model (Livneh et al. 2011) to calculate April 1 SWE on a 1/16<sup>th</sup> degree grid throughout the study area. The model used an ensemble of 10 Coupled Model Inter-Comparison Project 5 (CMIP5) global climate models (GCM) (see Table S 4.7) that were downscaled with Multivariate Adaptive Constructed Analogues (MACAv2) (Abatzoglou and Brown 2012). We aggregated April 1 snow volume by HUC 8 basins by multiplying the sum of April 1 SWE among all grid cells within each basin by cell size. Beaver-related storage contribution was calculated by

dividing total beaver complex storage by total snow volume per HUC 8 basin for each time period and emission scenario.

We also compared beaver complex storage to summer precipitation in rain-dominated basins in the same time periods and RCPs used in the snowpack analysis. Accumulated future summer precipitation (i.e. June, July, August) was calculated using data from the Climate Scenarios Project (Mote et al. 2014) using an ensemble of 20 CMIP5 GCMs (see Table S 4.7) downscaled with MACAv2 – gridMET (Abatzoglou 2013) on a 1/24<sup>th</sup> degree grid throughout the study area. Total summer precipitation volume was aggregated by HUC 8 basins. Beaver-related storage contribution was calculated by dividing total beaver complex storage by total summer precipitation volume per HUC 8 basin for each time period and climate scenario.

#### **4.4. Results**

##### ***4.4.1. Beaver intrinsic potential habitat***

Across the entire study area, approximately 17% or 52,925 km of streams were suitable for beaver (Table 4.1). Upon evaluation of BIP scores in streams throughout the study area, however, the distribution of potentially habitable streams was highly regionally variable. Although the Oregon Coast region has the greatest number of stream segments, its predominantly rough terrain and relatively low stream density results in the highest proportion of unsuitable streams of all HUC-4 basins in the study area (Table 4.1). Conversely, while the Puget Sound region had the least dense stream network and smallest total stream length of the HUC 4 basins in the study, the prevalence of lowlands resulted in both the highest proportion and greatest total length of suitable stream habitat for beaver (Table 4.1). At the HUC 8 level, the percent of streams suitable for colonization (i.e., BIP 1-3) varied from 2% in the Chetco basin to

70% in the Strait of Georgia (see Table S 4.8). In general, basins towards the Pacific Coast region and those clustered around the Puget Sound had the highest proportion of suitable streams, while basins along the Cascade Mountains had lower levels of suitability.

#### ***4.4.2. Colony and dam placement***

We estimated that the number of colonies the study area could support, regardless of currently existing land uses, was approximately 56,000. At the HUC 4 level, colony estimates ranged from 5,685 colonies in the Columbia basin to 14,213 colonies in the Puget Sound basin. This corresponds to a mean colony density within the study area of 1.1 colonies per stream km in suitable streams or 0.40 colonies per km<sup>2</sup>.

The study area was capable of supporting approximately 381,000 beaver dams, or 1.2 dams per stream kilometer, or 2.7 dams per km<sup>2</sup>. At the HUC-4 basin level, the number of dams per basin ranged from 37,875 in the Lower Columbia to 95,814 in the Puget Sound basin. Basins with low densities of suitable streams frequently also had shorter stretches of suitable habitat, limiting the number of dams in those areas substantially. Conversely, areas with large numbers of dams frequently had a higher density of suitable streams and also longer suitable stream reaches.

#### ***4.4.3. Beaver pond and groundwater storage***

We estimated that the study area is capable of supporting approximately 219,000 beaver complexes—excluding areas dominated by human land uses (Table 4.2). Beaver ponds in those complexes impounded a total of  $353 \times 10^6 \text{ m}^3$  or 1,347 m<sup>3</sup> per beaver dam. The increase in water table from damming in the area surrounding ponds created an increase in total groundwater storage of approximately  $467 \times 10^6 \text{ m}^3$  or 1,782 m<sup>3</sup> of groundwater per dam. The total combined surface and groundwater storage was  $819 \times 10^6 \text{ m}^3$  or 3,127 m<sup>3</sup> per pond. The contribution of

groundwater and surface water storage to total complex storage varied depending on local morphology as shown in Figure 4.3, which provides a conceptual example of our model.

When we applied the land-use mask to evaluate beaver presence and storage potential under this scenario, the exclusion of complexes in both agricultural and developed lands from the full model decreased storage volume by 44% or  $645 \times 10^6 \text{ m}^3$  (Table 4.2). The majority of these lands were found in low-lying areas, where beaver complexes tended to have the greatest storage potential.

When summarizing beaver complex storage by HUC 8 basins, total basin-level storage ranged from  $0.5 \times 10^6 \text{ m}^3$  in the Chetco basin (Oregon Coast subregion) to  $54.2 \times 10^6 \text{ m}^3$  in the upper Chehalis basin (Washington Coast subregion) (Figure 4.4). When these data were normalized by area per basin, the Chetco basin remained the least dense ( $309 \text{ m}^3/\text{km}^2$ ) and the Grays Harbor basin had the greatest potential total storage at  $25,835 \text{ m}^3/\text{km}^2$  (Figure 4.4). There appears to be a general trend in the distribution and total volume of pond storage with higher levels of storage towards the coast where topography is gentler and floodplains are wider. This is also pronounced within the Puget Sound basin, which has a disproportionately high amount of coastal areas from the Pacific Ocean on the west and the Puget Sound, which intersect the majority of the HUC 8 basins within that sub-region.

#### ***4.4.4. Climate change analysis***

Of the 64 HUC-8 basins in the study area, the majority of basins, 47 (73%), were rain-dominated as defined by Elsner et al. (2010), 14 basins (22%) were mixed rain-snow, and 3 basins (5%) were snow-dominated. When we evaluated the potential storage by dominant precipitation type, rain-dominated basins had 86% of total beaver-created storage ( $702 \times 10^6 \text{ m}^3$ ), mixed basins had 13% of total storage ( $105 \times 10^6 \text{ m}^3$ ), and snow-dominated basins had 1% of total storage ( $12 \times$

$10^6 \text{ m}^3$ ) (Figure 4.5). Furthermore, when we normalized storage by area for each dominant precipitation type, beaver complexes in rain-dominated basins stored approximately 4 times as much water as snow-dominated basins ( $7,209 \text{ m}^3/\text{km}^2$  vs.  $1,770 \text{ m}^3/\text{km}^2$ ), and mixed rain-snow dominated basins stored approximately 2 times as much water as snow-dominated basins ( $2,974 \text{ m}^3/\text{km}^2$ ) (Figure 4.5). Storage volume per pond in rain and snow-dominated basins were similar ( $3,222$  vs  $3,273 \text{ m}^3/\text{complex}$ ), while ponds in mixed-basins had about 20% less ( $2,554 \text{ m}^3/\text{complex}$ ).

We evaluated the potential for beaver ponds to replace storage in snow-dominated basins for RCP 4.5 and RCP 8.5 in 2050 and 2080. Although beaver complexes could store substantial quantities in mixed and snow-dominated basins, the severity of snowpack loss under all future climate scenarios resulted in beaver ponds being able to make up for a small amount of lost snow water volume. Beaver made up for a maximum of approximately 4% of total loss, and their contribution was negligible in many basins (Figure 4.6).

We evaluated the potential for beaver ponds to supplement summer hydrology as a percentage of total summer precipitation. We included both rain-dominated basins and those currently designated as mixed and snow-dominant because climate models suggest that all basins within the study area will transition to rain-dominated by 2080 in the RCP 8.5 emission scenario (Littell et al. 2013). Climate projections indicated that by 2080 the study area will experience an 18% decrease in mean summer precipitation based on the RCP 8.5 scenario. Beaver complex storage had the potential to supplement summer precipitation to provide approximately 5% additional storage on average. This contribution was highly variable between HUC 8 basins, however, and ranged from negligible amounts ( $\sim 1\%$ ) up to a 20% increase in some basins (Figure 4.7).

When we evaluated this effect by dominant precipitation type (i.e., rain, mixed, and snow-dominated basins), changes in summer precipitation were more pronounced in rain-dominated basins with a decrease of  $10.1 \times 10^6 \text{ m}^3/\text{km}^2$  compared to  $8.0 \times 10^6 \text{ m}^3/\text{km}^2$  in mixed basins and  $6.4 \times 10^6 \text{ m}^3/\text{km}^2$  in snow-dominated basins. Beaver complexes have the potential to supplement summer precipitation in these areas by 7.3%, 2.4% and 1.1%, respectively.

#### **4.5. Discussion**

As interest in ecosystem service provisioning by natural systems grows, beaver-created ponds and wetlands continue to be a central focus. The role of beaver in generating ecosystem services at reach scales has been well documented, but there has been less attention on provisioning at larger scales. Spatial models predict how beaver populations and beaver-created water storage vary across the landscape. Here, we modeled the magnitude of ecosystem service provisioning by beaver populations near carrying capacity, and we investigated how they influence hydrology and water availability in the Pacific Northwest. This approach allows for an analysis of beaver's potential to influence natural systems currently and to offset the effects of climate change on hydrology under various climate scenarios and time frames. The spatially-explicit nature of the model allows for basin-specific management recommendations and restoration prioritization.

##### **4.5.1. *Beaver populations***

We estimated that the study area is capable of accommodating up to 56,000 beaver colonies outside of areas dominated by human land use (i.e., 0.40 colonies per  $\text{km}^2$ ). This estimate is consistent with the available literature and is most likely lower than expected densities. For example, Whitfield et al. (2015) predicted a density of 0.6 colonies per  $\text{km}^2$  across areas of North America with favorable habitat, but this was largely based on data from studies of recovering

beaver populations. Few studies have documented populations with densities at or near carrying capacity. Typically, density estimates range from 0.76 colonies per km<sup>2</sup> (Voigt et al. 1976) to 3.0 colonies per km<sup>2</sup> (Novak 1999). There has not been a comprehensive survey of beaver populations in the Pacific Northwest. We suggest that addressing this a critical knowledge gap would identify growth rates and spatial variability within populations, allow for the prediction of potential infrastructure conflicts as populations continue to expand, and assist in more informed and targeted beaver-based restoration efforts.

We estimated that a modeled population of 56,000 beaver colonies would create approximately 381,000 dams or 7.2 dams per stream km of suitable stream. Studies that have characterized stable populations have found dam densities ranging from 2.5 dams per km (Naiman et al. 1988) to 41.6 dams per km (Warren 1926) with an average of 15.2 dams per km (see Table S 4.3 literature review). Our model methodology had the potential to over- or underestimate the number of colonies and dams on the landscape. We did not consider off-channel beaver habitat, nor was the model capable of anticipating how prolonged beaver damming might alter geomorphology (e.g., aggradation leading to channel widening and migration) and, in turn, influence future beaver habitat. Our method of randomized assignment of colonies and dams to stream segments potentially erred in assigning colonies to some areas that were highly suitable and would attract beaver. Conversely, it may have placed colonies and dams in areas with only a small amount of suitable habitat making their colonization unlikely. These errors are minimized, however, because the ponds that were delineated in these areas were most likely very small due to the topography.

#### 4.5.2. *Water*

Beaver were capable of storing substantial quantities of surface and groundwater, despite having habitat limited to only about 17% of all streams. We estimated that the combined volume of beaver-created surface and groundwater storage in our study area was  $819 \times 10^6 \text{ m}^3$ . For reference, this volume is approximately 1.5 times that impounded in Lake Washington by the Hiram M. Chittenden Dam (DOE 2019) in Seattle WA. The majority of storage was located in low-lying areas with wide floodplains, resulting in a large range in storage among basins. Basins surrounding the Puget Sound, for example, stored much more water than some basins in southern Oregon, which had fewer floodplains and low-gradient streams.

The mean modeled pond surface area within our study region was  $2,429 \text{ m}^2$ , and the modeled average surface water volume was  $1,346 \text{ m}^3$  per pond. Karran et al. (2016) evaluated 40 beaver ponds throughout various physiographic settings and regions and found mean pond area and volumes of  $2,321 \text{ m}^2$  and  $943 \text{ m}^3$ , respectively, suggesting that our modeled pond size and area align well with others. We used a dam height of 0.91 m for all dams, thereby limiting the depth of ponds to that measure as well. Although this represents an average pond depth that agrees well with the literature (Fuller and Peckarsky 2011b), it is likely another area of underestimation. In most ponds, beaver excavate mud for dam construction from the pond bottom, progressively increasing pond depth and storage potential over time.

The modeled groundwater surrounding pond complexes stored  $1,346 \text{ m}^3$  on average, comprising about 60 percent of the total site storage (i.e., surface water and groundwater). Literature evaluating the effects of beaver dams on groundwater storage is highly variable; there is little replication, and the results are often conflicting (see Table S 4.5), making it difficult to compare with other studies. The extent of groundwater inundation and potential for storage is dependent on a number of site-specific factors (e.g., porosity, soil depth, transmissivity, width of

valley floor, etc.). We used empirical findings from our previous field-based beaver research (Chapter 2), located within the study area, to inform our groundwater analysis. These data, although locally based, do not capture the full extent of conditions throughout the study area and may over- or underestimate potential groundwater storage in some cases.

Beyond the creation of additional water storage, beaver ponds in the study region modify riparian areas in a number of ways. The creation of 381,000 ponds in the study area and up to 11,400 ponds in some basins could increase forage, refugia, and rearing space for salmonids and other fish species. The addition of ponds of various depths and morphologies would add thermal heterogeneity (Means 2018) and downstream cooling (Chapter 2). The creation of 43,930 km of pond fringe habitat, up to 2,600 km in some basins, would promote riparian and wetland vegetation, and expand spawning and rearing habitat for species such as amphibians and birds.

#### ***4.5.3. Climate adaptation***

Some basins could offset up to 4% of April 1 snowpack loss under the most extreme climate scenario that we analyzed (RCP 8.5, 2080). However, beaver-created storage was insufficient to offset levels of climate-change-induced snow pack loss in any of the future climate-change scenarios that we evaluated (i.e., RCP 4.5, RCP 8.5, 2050, 2080). The contribution of beaver to future water storage was small due to (1) the relatively sparse concentration of beaver ponds in snow-dominated basins and (2) the large amount of snowpack loss during any future climate scenario in Pacific Northwest. In all scenarios, it is projected that the study area will experience losses in April 1 snow volume of at least  $14,200 \times 10^6 \text{ m}^3$  and likely up to  $26,375 \times 10^6 \text{ m}^3$  by 2080 (versus total beaver storage of  $819 \times 10^6 \text{ m}^3$ ). Hafen (2017) evaluated whether modeled beaver populations in Utah, USA could offset lost snowpack in future climate scenarios and similarly found that beaver could offset up to about 5% of loss. Like this study, potential errors

in our model were largely due to the reduced pond sizes and proportion of habitable streams found in mountainous regions. The relationship between beaver and snowpack loss in the Pacific Northwest cannot be extrapolated to other areas, however. The predicted loss in Pacific Northwest snow volume is much greater than that projected for other areas in the American West. Other areas, such as eastern Oregon and Washington, for example, will likely lose a substantial amount of April 1 SWE during the same time frame, but the magnitude of that loss is considerably less (Mantua et al. 2010, Das et al. 2011, Luce et al. 2014, Gergel et al. 2017). The storage contribution of beaver in these areas, and especially where topography is not steep, may be substantially greater.

Although the ability of beaver to offset storage from Cascade Mountains snowpack loss was small, beaver have the potential to displace substantial amounts of water in many basins. For example, although the Snoqualmie basin was only able to offset approximately 2% of April 1 snowpack loss in RCP 8.5 2080, this nevertheless represents  $15.7 \times 10^6 \text{ m}^3$  of storage. This volume is equivalent to about 25% of the basin's largest reservoir, the Tolt Reservoir, which is one of two reservoirs that provide drinking water to 1.2 million people in the Seattle metropolitan area.

Beaver have the potential to supplement summer hydrology with up to a 20% increase in storage in some basins. In these cases, unlike offsetting the loss of snowpack, by capturing, storing, and slowly releasing rainfall, beaver can increase total summer water availability over what is currently available and in future scenarios. Although rain-dominated basins within the study area are expected to experience less total hydrologic change than snow-dominated basins, the increase in summer water availability across all basins in the study area has the potential to benefit many aquatic species. At the stream reach level, the increase in summer water availability

and deep pools may provide cool, perennial water to reaches that might otherwise go dry. This is especially true in many basins of the Pacific Northwest where the magnitude of summer precipitation makes any future decreases particularly important. The increase in summer water availability can be leveraged to restore degraded systems and enhance existing high-value habitat. The greatest level of summer storage supplementation was seen in basins around the Puget Sound, which tend to be relatively flat with wide valleys. Targeting relocation and prioritizing management actions that encourage colonization of these areas may allow populations to continue to expand and storage benefits realized.

Over 20% of historically suitable habitat in the region is currently under human-dominated land use. Although only 20% of habitat is displaced, this results in a 56% reduction in total potential beaver-derived water storage because of the relatively high quality of potential beaver habitat occupied by humans. Human settlement in core areas of beaver's historical range reduces the potential storage volume from  $1,464 \times 10^6 \text{ m}^3$  to  $819 \times 10^6 \text{ m}^3$ . Most of the land that is appropriate for colonization by beaver exists on non-federal and non-tribally owned lands. Thus, if beaver are used as a method to increase watershed storage, it will be necessary to provide greater outreach to private landowners explaining the potential benefits of beaver, and to provide management options other than non-lethal removal in areas where there are periodic conflicts with infrastructure or other land uses. Although beaver can enhance systems in many ways, they can also create conflicts when in close proximity to homes and infrastructure. Identifying priority areas for beaver habitat and developing contingencies for inevitable conflicts with humans may facilitate long-term ecosystem enhancements.

Prior to their population decline, beaver were attributed with maintaining 519,000 ha of ponds and wetlands estimated to have been lost or degraded by human land uses in Oregon and

Washington (Dahl 1990, 2011). As beaver populations continue to recover in many areas, they may be able to restore some of these systems and preserve remaining wetlands. In these places, the potential of beaver for affecting basin-scale processes is becoming more evident. The widespread use of beaver as a restoration tool, however, has a number of barriers. Opposition to possible infrastructure conflicts, competing restoration priorities, and in some cases, misinformation all have the potential to delay a more widespread use of beaver. Nonetheless, there are few other restoration options that can address stream degradation and climate-change impacts at such a low cost, across varied political and ownership boundaries, and with minimal long-term maintenance. At sufficient levels, beaver have the potential to maintain current and future ecosystem and hydrologic stability.

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#### 4.7. References

- Abatzoglou, J. T. 2013. Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology* 33:121–131.
- Abatzoglou, J. T., and T. J. Brown. 2012. A comparison of statistical downscaling methods suited for wildfire applications. *International Journal of Climatology* 32:772–780.
- Anderson, C. B., and A. D. Rosemond. 2007. Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia* 154:141–153.
- Avery, E. L. 1983. Bibliography of beaver, trout, wildlife, and forest relationships. Wisconsin Department of Natural Resources:28.
- Avery, E. L. 1992. Effects of removing beaver dams upon a northern Wisconsin brook trout stream. Fish Research Section, Bureau of Research, Wisconsin Department of Natural Resources.
- Bailey, D. R., B. J. Dittbrenner, and K. P. Yocom. 2018. Reintegrating the North American beaver (*Castor canadensis*) in the urban landscape. *WIREs Water*:e1323.
- Barnard, R. J., J. Johnson, P. Brooks, K. M. Bates, B. Heiner, J. P. Klavas, D. C. Ponder, P. D. Smith, and P. D. Powers. 2013. *Water Crossing Design Guidelines*. Washington Department of Fish and Wildlife. Olympia, WA, USA.
- Correll, D. L., T. E. Jordan, and D. E. Weller. 2000. Beaver pond biogeochemical effects in the Maryland Coastal Plain. *Biogeochemistry* 49:217–239.
- Dahl, T. E. 1990. Wetlands losses in the United States, 1780's to 1980's. Report to the Congress. National Wetlands Inventory, St. Petersburg, FL (USA).
- Dahl, T. E. 2011. Status and trends of wetlands in the conterminous United States 2004 to 2009. US Department of the Interior, US Fish and Wildlife Service.
- Dalton, M.M., P.W. Mote, A. K. Snover. 2013. *Climate Change in the Northwest: Implications for Our Landscapes, Waters, and Communities*. Island Press, Washington, DC.
- Das, T., D. W. Pierce, D. R. Cayan, J. A. Vano, and D. P. Lettenmaier. 2011. The importance of warm season warming to western U.S. streamflow changes. *Geophysical Research Letters* 38:1–5.
- Dittbrenner, B. J., M. M. Pollock, J. W. Schilling, J. D. Olden, J. J. Lawler, and C. E. Torgersen. 2018. Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform

- restoration and climate change adaptation. PLoS ONE 13.
- DOE-WA. 2019. Inventory of Dams Report for Select Washington Counties and Selected Dam Hazard Categories. Washington Department of Ecology, Olympia, WA, USA.
- Duncan, S. L. 1984. Ecology: Leaving it to Beaver. *Environment: Science and Policy for Sustainable Development* 26:41–45.
- Elsner, M. M., L. Cuo, N. Voisin, J. S. Deems, A. F. Hamlet, J. A. Vano, K. E. B. Mickelson, S. Y. Lee, and D. P. Lettenmaier. 2010. Implications of 21st century climate change for the hydrology of Washington State. *Climatic Change* 102:225–260.
- ESRI. 2014. Environmental Systems Research Institute, ArcGIS v. 10.3. Redlands, CA, USA.
- Frickel, D. G. 1972. Hydrology and effects of conservation structures, Willow Creek basin, Valley County, Montana 1954-1968. US Geological Survey Water-Supply Paper 1532-G, US Geological Survey. 42.
- Fuller, M. R., and B. L. Peckarsky. 2011. Ecosystem engineering by beavers affects mayfly life histories. *Freshwater Biology* 56:969–979.
- Gergel, D. R., B. Nijssen, J. T. Abatzoglou, D. P. Lettenmaier, and M. R. Stumbaugh. 2017. Effects of climate change on snowpack and fire potential in the western USA. *Climatic Change* 141:287–299.
- 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.
- Hafen, K. 2017. To What Extent Might Beaver Dam Building Buffer Water Storage Losses Associated with a Declining Snowpack? Thesis. Utah State University.
- Hamman, J. J., B. Nijssen, T. J. Bohn, D. R. Gergel, and Y. Mao. 2018. The variable infiltration capacity model version 5 (VIC-5): Infrastructure improvements for new applications and reproducibility. *Geoscientific Model Development* 11:3481–3496.
- Homer, C. G., J. A. Dewitz, S. Yang, L., Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, and 2015 Wickham, J.D., and Megown, K. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing* 81:345–354.
- Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. *Landscape Ecology* 1:47–57.

- Karran, D. J., C. J. Westbrook, J. M. Wheaton, C. A. Johnston, and A. Bedard-Haughn. 2016. Rapid surface water volume estimations in beaver ponds. *Hydrology and Earth System Sciences* 21:1–26.
- Liang, X., D. P. Lettenmaier, E. F. Wood, and S. J. Burges. 2004. A simple hydrologically based model of land surface water and energy fluxes for general circulation models. *Journal of Geophysical Research* 99:14.
- Littell, J. S., M. Elsner, L. C. W. Binder, and A. Snover. 2009. The Washington climate change impacts assessment: evaluating Washington's future in a changing climate. Climate Impacts Group, Seattle, WA, USA.
- Littell, J. S., G. S. Mauger, E. P. Salathé, A. F. Hamlet, S. Y. Lee, M. R. Stumbaugh, M. Elsner, R. Norheim, E. R. Lutz, and J. Nathan. 2013. Uncertainty and extreme events in future climate and hydrologic projections for the Pacific Northwest: providing a basis for vulnerability and core/corridor assessments. Climate Impacts Group, Seattle, WA, USA.
- Livneh, B., P. J. Restrepo, and D. P. Lettenmaier. 2011. Development of a unified land model for prediction of surface hydrology and land–atmosphere interactions. *Journal of Hydrometeorology* 12:1299–1320.
- Lowry, M. M. 1993. Groundwater elevations and temperature adjacent to a beaver pond in central Oregon. Thesis. Oregon State University, Corvallis, OR, USA.
- Luce, C. H., and Z. A. Holden. 2009. Declining annual streamflow distributions in the Pacific Northwest United States, 1948-2006. *Geophysical Research Letters* 36:2–7.
- Luce, C. H., V. Lopez-Burgos, and Z. Holden. 2014. Sensitivity of snowpack storage to precipitation and temperature using spatial and temporal analog models. *Water Resources Research* 50:9447–9462.
- Mackie, R. S. 1997. *Trading Beyond the Mountains: The British Fur Trade on the Pacific, 1793-1843*. UBC Press, Vancouver, BC.
- Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climatic Change* 102:187–223.
- Margolis, B. E., M. S. Castro, and R. L. Raesly. 2001. The impact of beaver impoundments on the water chemistry of two Appalachian streams. *Canadian Journal of Fisheries and Aquatic Science* 58:2271–2283.

- Mauger, G. S., J. H. Casola, H. A. Morgan, R. L. Strauch, B. Jones, B. Curry, T. M. B. Isaksen, L. W. Binder, M. B. Krosby, and A. K. Snover. 2015. State of Knowledge: Climate Change in Puget Sound. Climate Impacts Group, Seattle, WA, USA.
- McKinstry, M. C., P. Caffrey, and S. H. Anderson. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. *Journal of the American Water Resources Association* 37:1571–1577.
- McRae, G., and C. J. Edwards. 1994. Thermal characteristics of Wisconsin headwater streams occupied by beaver: implications for brook trout habitat. *Transactions of the American Fisheries Society* 123:641–656.
- Means, C. D. O. 2018. Stream temperature variability in headwater beaver dam complexes in relation to hydrologic and environmental factors. University of Washington.
- Meentemeyer, R. K., and D. R. Butler. 1999. Hydrogeomorphic effects of beaver dams in glacier national park, Montana. *Physical Geography* 20:436–446.
- Miller, D. A., and R. A. White. 2002. A Conterminous United States Multilayer Soil Characteristics Dataset for Regional Climate and Hydrology Modeling. *Earth Interactions* 2.
- Mote, P., D. Turner, D. P. Lettenmaier, D. Bachelet, and J. Abatzoglou. 2014. Integrated Scenarios of Climate, Hydrology, and Vegetation for the Northwest. Corvallis, OR, USA.
- Mote, P. W., and E. P. Salathé. 2010. Future climate in the Pacific Northwest. *Climatic Change* 102:29–50.
- Nagel, D. E., J. M. Buffington, S. L. Parkes, S. Wenger, J. R. Goode, E. David, M. John, L. Sharon, and R. Jaime. 2014. A Landscape Scale Valley Confinement Algorithm: Delineating Unconfined Valley Bottoms for Geomorphic, Aquatic, and Riparian Applications, Gen. Tech. Rep. RMRS- GTR-321. Fort Collins, CO.
- Naiman, J. R., J. M. Melillo, J. E. Hobbie, R. J. Naiman, J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67:1254–1269.
- Naiman, R. J., S. R. Elliott, J. M. Helfield, and T. C. O’Keefe. 2000. Biophysical interactions and the structure and dynamics of riverine ecosystems: The importance of biotic feedbacks. *Hydrobiologia* 410:79–86.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver: The structure and dynamics of streams are changing as beaver recolonize their

- historic habitat. *BioScience* 38:753–762.
- Novak, M. 1999. Beaver. Pages 282–312 in M. E. O. and B. M. M. Novak, J. A. Baker, editor. Wild furbearer management and conservation in North America. Queen's Printer, Ontario, Canada.
- Parker, M. 1986. Beaver, water quality, and riparian systems. Pages 28–30 Wyoming Water 1986 and Streamside Zone Conference. The Center, Casper, Wyoming (USA).
- Patterson, D. 1951. Beaver-trout relationships. Wisconsin Conservation Department. Madison, WI, USA.
- Pollock, M. M., T. J. Beechie, J. M. Wheaton, C. E. Jordan, N. Bouwes, N. Weber, and C. Volk. 2014. Using beaver dams to restore incised stream ecosystems. *BioScience* 64:279–290.
- Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1995. Beaver as engineers: Influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 in C. G. Lawton and J. J. H., editors. *Linking species to ecosystems*. Chapman & Hall, New York, NY, USA.
- PRISM. 2004. PRISM Climate Group, Oregon State University. Retrieved from <http://prism.oregonstate.edu>.
- RCW (Revised Code of Washington). 2001. Unlawful traps § 77.15.192. Olympia, WA.
- Reidy Liermann, C. A., J. D. Olden, T. J. Beechie, M. J. Kennard, P. B. Skidmore, C. P. Konrad, and H. Imaki. 2011. Hydrogeomorphic classification of Washington State rivers to support emerging environmental flow management strategies. *River Research and Applications*. 1358:1340–1358.
- Rosell, F., O. Bozsér, P. Collen, H. Parker, O. Bozser, P. Collen, and H. Parker. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* 35:248–276.
- Rutherford, W. H. 1955. Wildlife and environmental relationships of beavers in Colorado forests. *Journal of Forestry* 53:803–806.
- Seton, J. R. 1929. *Lives of game animals*. Vol. 4, Part 2, Rodents, etc. Page (D. Doubleday, Ed.). Garden City, NY, USA.
- Shaw, E. L. 2009. Lateral exchange of water and nitrogen along a beaver-dammed stream draining a Rocky Mountain valley. Thesis. University of Saskatchewan, Saskatoon, Canada.
- Smith, M. E., C. T. Driscoll, B. J. Wyskowski, C. M. Brooks, and C. C. Cosentini. 1991.

- Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Canadian Journal of Zoology* 69:55–61.
- Stack, W. R., and R. L. Beschta. 1989. Factors influencing pool morphology in Oregon coastal streams. *Headwaters Hydrology* 6:401–411.
- Steel, E. A., T. J. Beechie, C. E. Torgersen, and A. H. Fullerton. 2017. Envisioning, Quantifying, and Managing Thermal Regimes on River Networks. *BioScience* 67:506–522.
- Stewart, I., D. Cayan, and M. Dettinger. 2004. Changes in snowmelt runoff timing in western North America under a business as usual climate change scenario. *Climatic Change* 1:8–9.
- Stewart, I. T., D. R. Cayan, and M. D. Dettinger. 2005. Changes toward earlier streamflow timing across western. *North American Journal of Climatology*. 18:10.
- USGS. 2014. U.S. Geologic Survey National Elevation Dataset.
- USGS. 2019. U.S. Geologic Survey National Hydrography Dataset High Resolution. Retrieved from:  
<https://viewer.nationalmap.gov/basic/?basemap=b1&category=nhd&title=NHD%20View>.
- Voigt, D. R., G. B. Kolenosky, and D. H. Pimlott. 1976. Changes in summer foods of wolves in central Ontario. *Journal of Wildlife Management* 40:663–668.
- Warren, E. R. 1926. A study of the beaver in the Yancy Region of Yellowstone National Park. *Roosevelt Wildlife Annals* 1:5–191.
- 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.
- White, D. S. 1990. Biological relationships to convective flow patterns within stream beds. *Hydrobiologia* 196:149–158.
- Whitfield, C. J., H. M. Baulch, K. P. Chun, and C. J. Westbrook. 2015. Beaver-mediated methane emission: The effects of population growth in Eurasia and the Americas. *AMBIO* 44:7–15.
- Wiken, E., F. Jiménez-Nava, and G. Griffith. 2011. North American Terrestrial Ecoregions—Level III.
- Yeager, L. E., and R. R. Hill. 1954. Beaver management problems in western public lands. Pages 462–479 *Transactions of the North American Wildlife and Natural Resources Conference*.

#### 4.8. Tables

Table 4.1 Beaver intrinsic potential (BIP) habitat in study area streams by hydrologic unit code 4 (HUC) subregion.

HUC 4 subregion	HUC4	Stream segments (no.)	Total stream length (km)	Length per BIP class (%)				
				No BIP <sup>†</sup>	Low	Mod.	High	Total BIP <sup>††</sup>
Lower Columbia	1708	140,858	41,472	87	4	7	3	13
Oregon Coast	1710	455,168	119,308	90	3	5	2	10
Puget Sound	1711	97,727	31,745	59	8	19	14	41
Washington Coast	1710	173,505	41,493	76	5	13	6	24
Willamette River	1709	205,064	66,244	81	4	9	7	19
Subregion total		1,089,998	307,310	83	4	9	5	17

Notes: Oregon and Washington coast HUCs share the same HUC 4 ID, but were separated for this study due to differences in topography and climate. Headwater stream segments with a drainage area of less than 0.05 km<sup>2</sup> or percent slope greater than 50% were excluded from this summary table.

<sup>†</sup> No BIP indicates that the stream reach is unlikely to support beaver.

<sup>††</sup> Total BIP is the sum of Low, Moderate, and High BIP percentages, representing all possible beaver habitat.

Table 4.2 Beaver complex storage potential in western Washington and Oregon by land use and ownership.

	Pond complexes (no.)	Pond area (x10 <sup>6</sup> m <sup>2</sup> )	Pond volume (x10 <sup>6</sup> m <sup>3</sup> )	Groundwater volume (x10 <sup>6</sup> m <sup>3</sup> )	Total storage (x10 <sup>6</sup> m <sup>3</sup> )	Storage per complex (m <sup>3</sup> )
All study area	277,549	1,216	631	833	1,464	3,841
Excluding agricultural lands	249,780	918	421	555	977	3,227
Excluding all human-dominated lands	219,111	636	353	467	819	3,127
Public & tribal lands without human uses	61,202	173	96	127	224	3,081

Table 4.3 Beaver-created surface and groundwater storage, and potential to offset April 1 snow water equivalent (SWE) snowpack loss in 2050 and 2080 under CMIP5 RCP 8.5 climate projections in mixed and snow-dominated basins.

Scenario	Beaver storage (10 <sup>6</sup> m <sup>3</sup> )	April 1 SWE (10 <sup>6</sup> m <sup>3</sup> )	April 1 SWE change (10 <sup>6</sup> m <sup>3</sup> )	Beaver storage contribution to SWE loss (%)
Historical	44.2	18,576	na	na
RCP 4.5, 2050	44.2	9,420	-9,156	0.48
2080	44.2	6,226	-12,350	0.36
RCP 8.5, 2050	44.2	7,067	-11,509	0.38
2080	44.2	244	-18,332	0.24

Table 4.4 Beaver-created storage potential to summer precipitation during historical conditions (1970-2005) and in 2080 CMIP5 RCP 8.5 climate projection in all basins in the study area. Summer precipitation includes total accumulation in June, July, and August.

Scenario	Beaver storage (x10 <sup>6</sup> m <sup>3</sup> )	Summer precipitation (x10 <sup>6</sup> m <sup>3</sup> )	Increase from beaver storage (%)	Range in increase in HUC- 8 basins (%)
Historical	819.4	18,471	4.4	0.2–15.6
RCP 8.5, 2080	819.4	15,134	5.4	0.3–19.3

#### 4.9. Figures

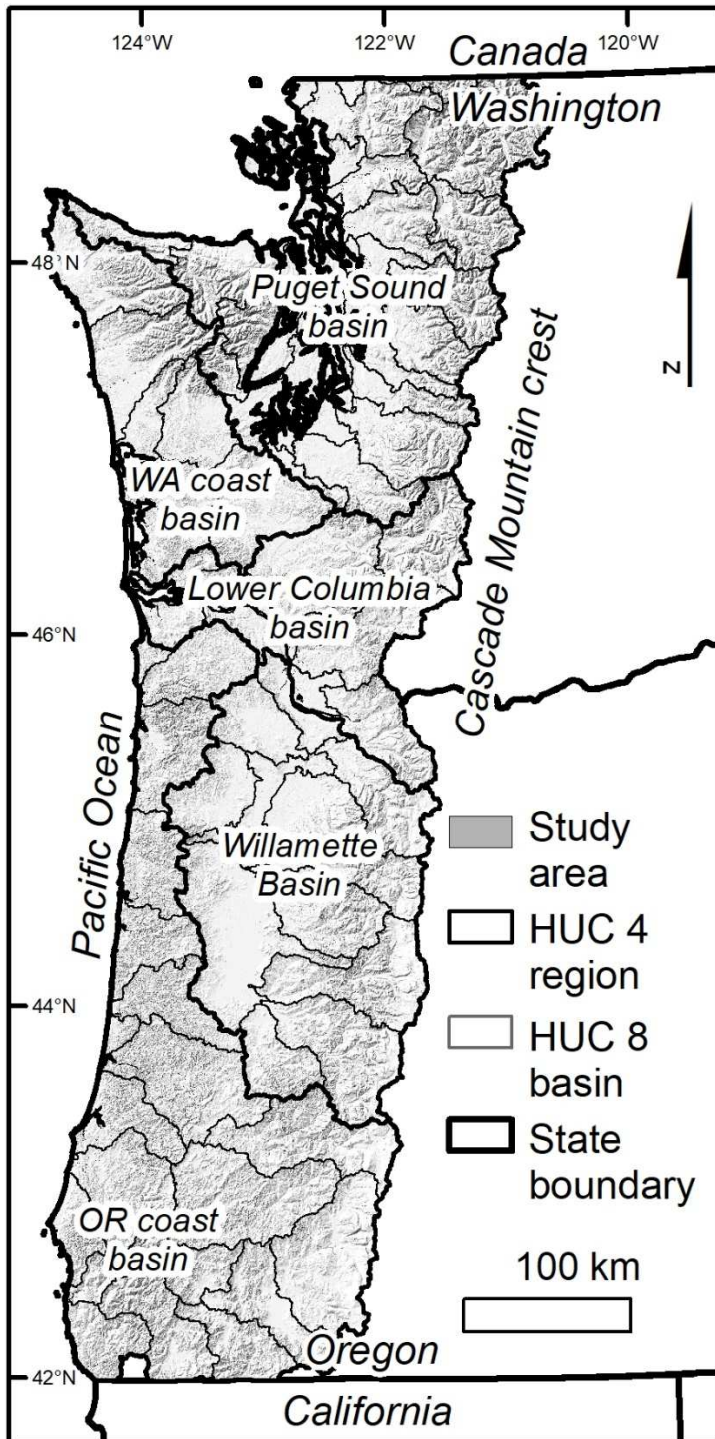


Figure 4.1 Study region including all watersheds west of the Washington and Oregon Cascade Mountain crest. We evaluated beaver storage potential at the hydrologic unit code (HUC) 4 and HUC 8 level.

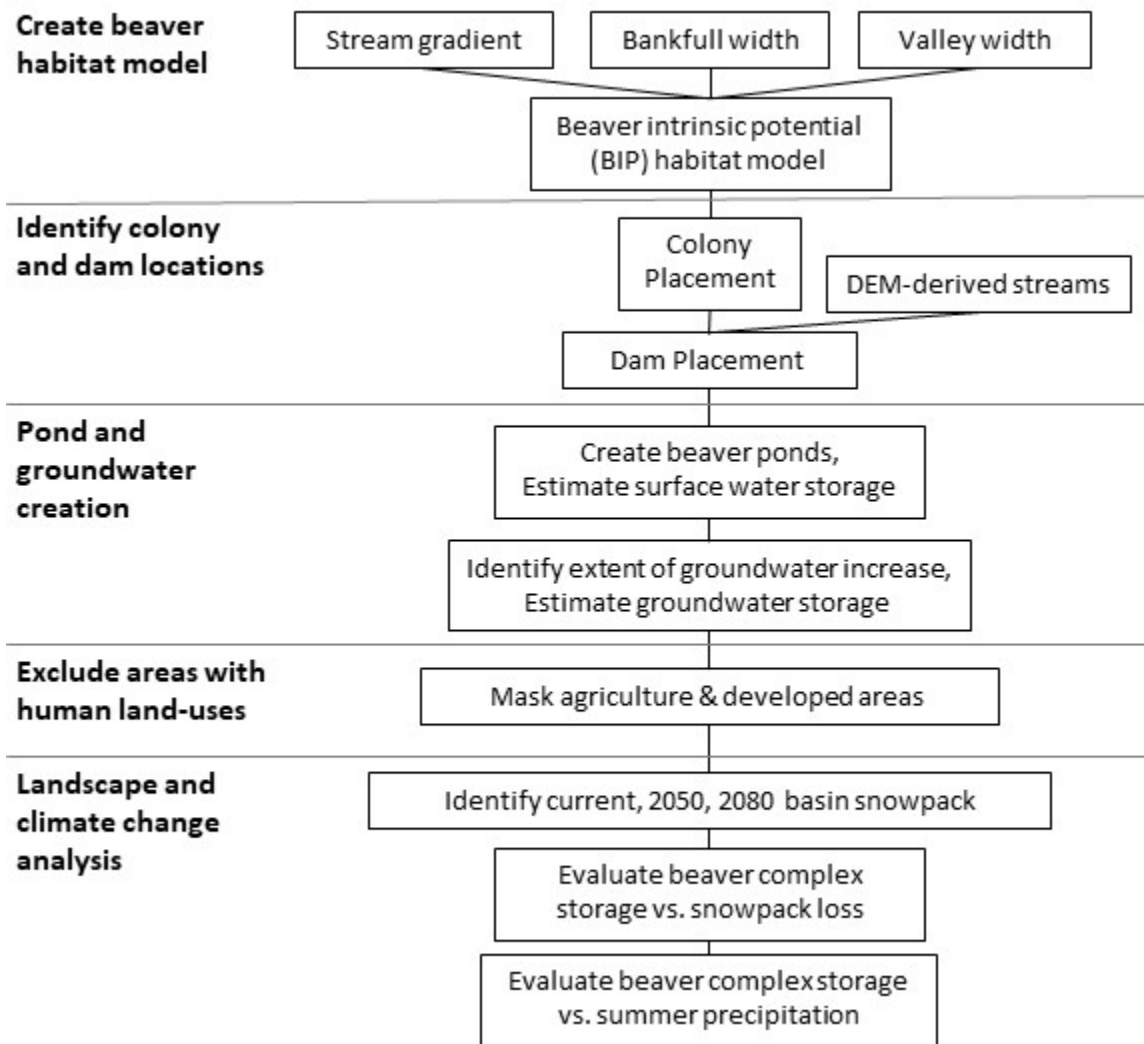


Figure 4.2 Flowchart showing steps in model predicting inputs and outputs.

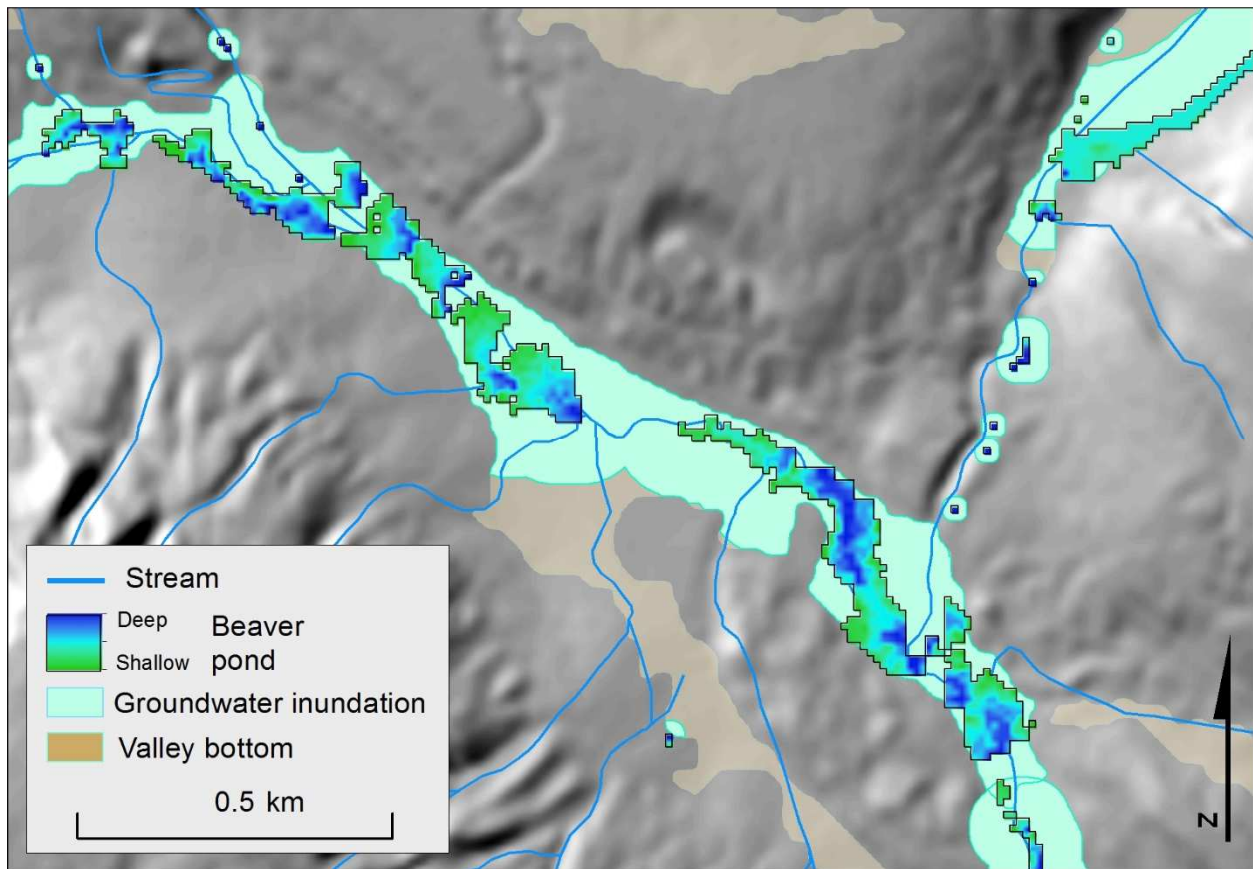


Figure 4.3 Example of beaver-created pond complexes and extent of groundwater inundation in a reach of Roesiger Creek in the Skykomish River watershed. Groundwater extent was constrained by valley bottoms within unconfined stream segments. Ponds and groundwater extent were generally small within confined segments.

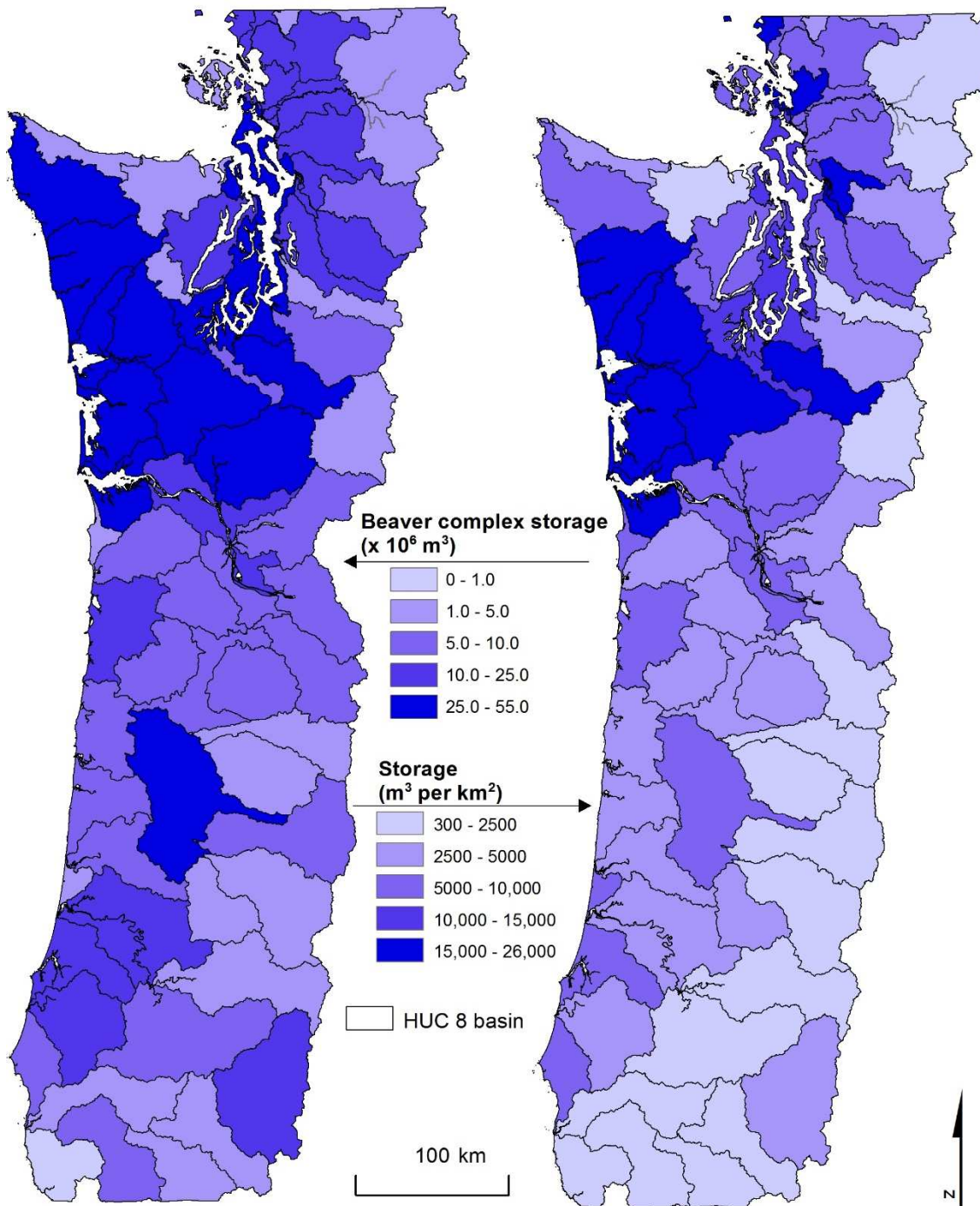


Figure 4.4 Total beaver-derived water storage per HUC 8 (hydrologic unit code) basin (left) and storage per km<sup>2</sup> (right), excluding pond complexes on lands with agricultural or human-dominated land uses.

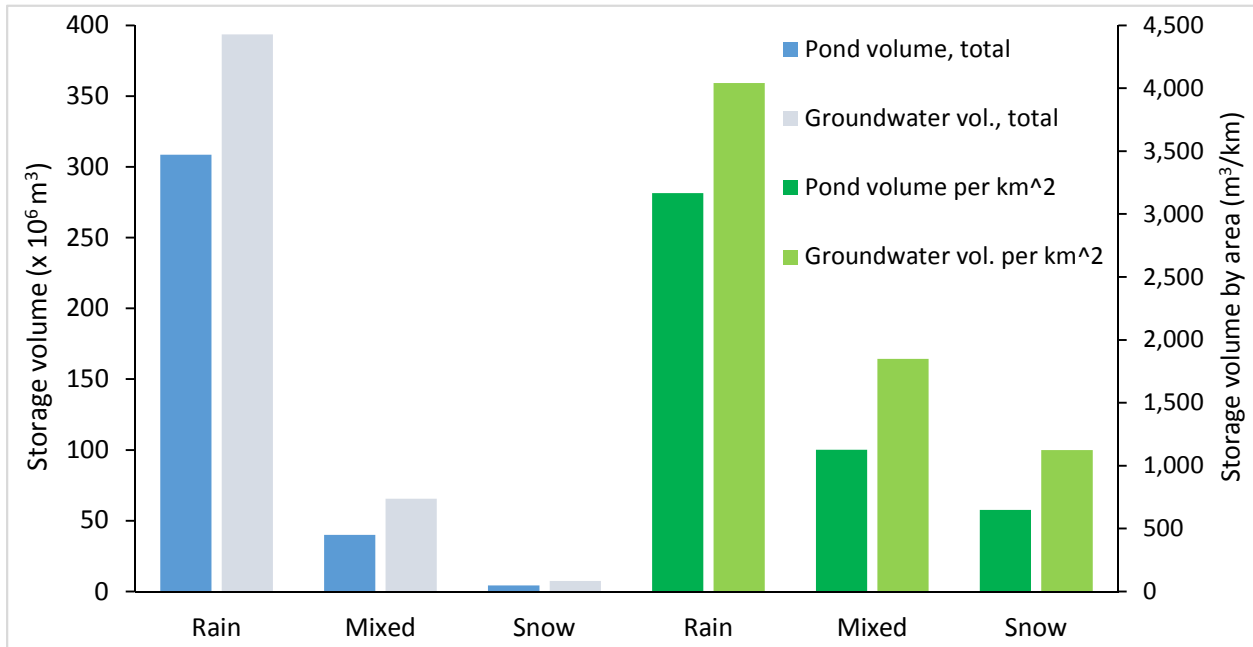


Figure 4.5 Total beaver-generated surface and groundwater storage within rain, mixed, and snow-dominated basins within the study region. The majority of the study region (70%) consists of rain-dominated subbasins.

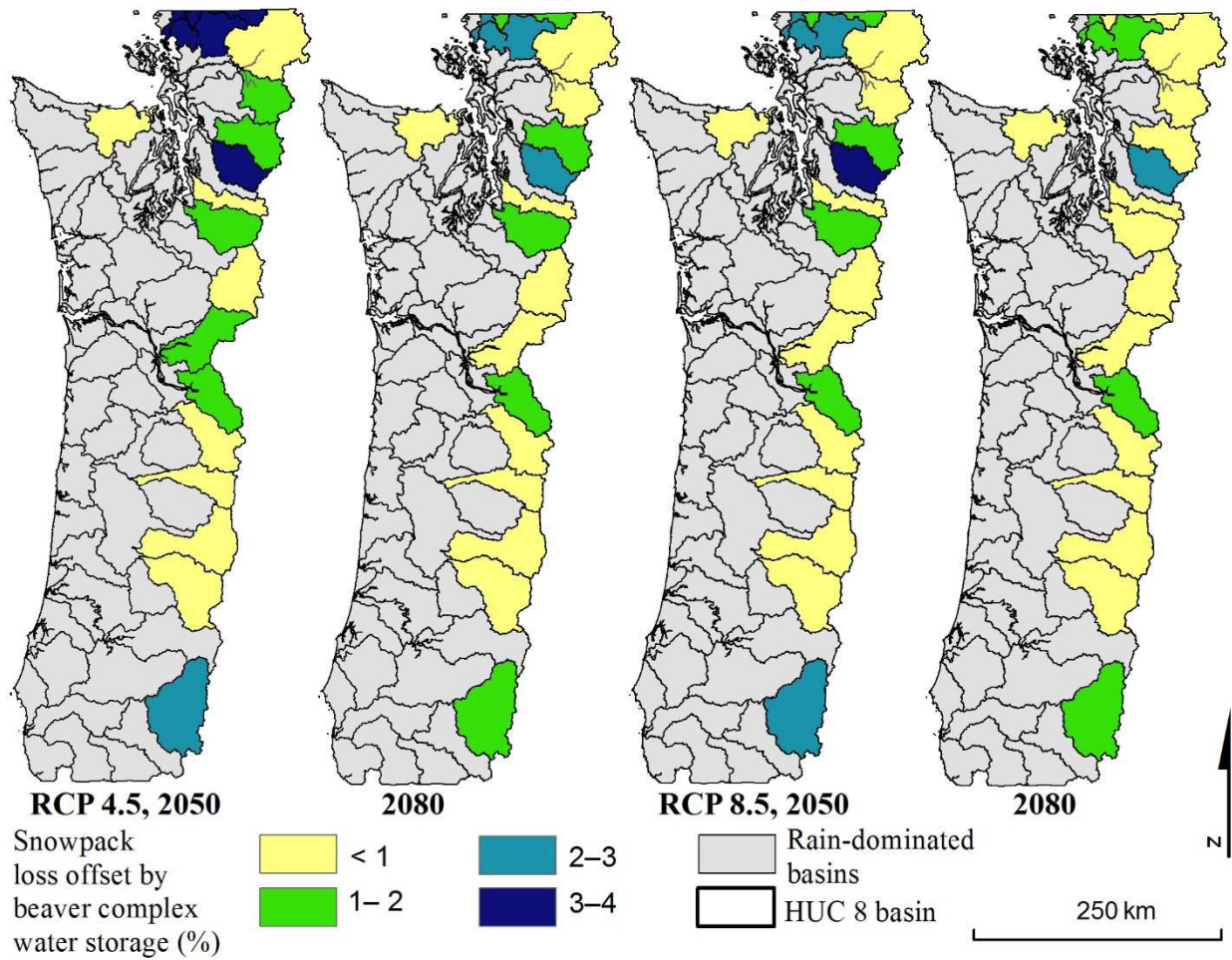


Figure 4.6 Snowpack loss offset by modeled beaver-created surface and groundwater storage. Offset is expressed as a percentage of April 1 snow water equivalent (SWE) under two future climate scenarios – representative concentration pathway (RCP) 4.5 and RCP 8.5 – in 2050 and 2080.

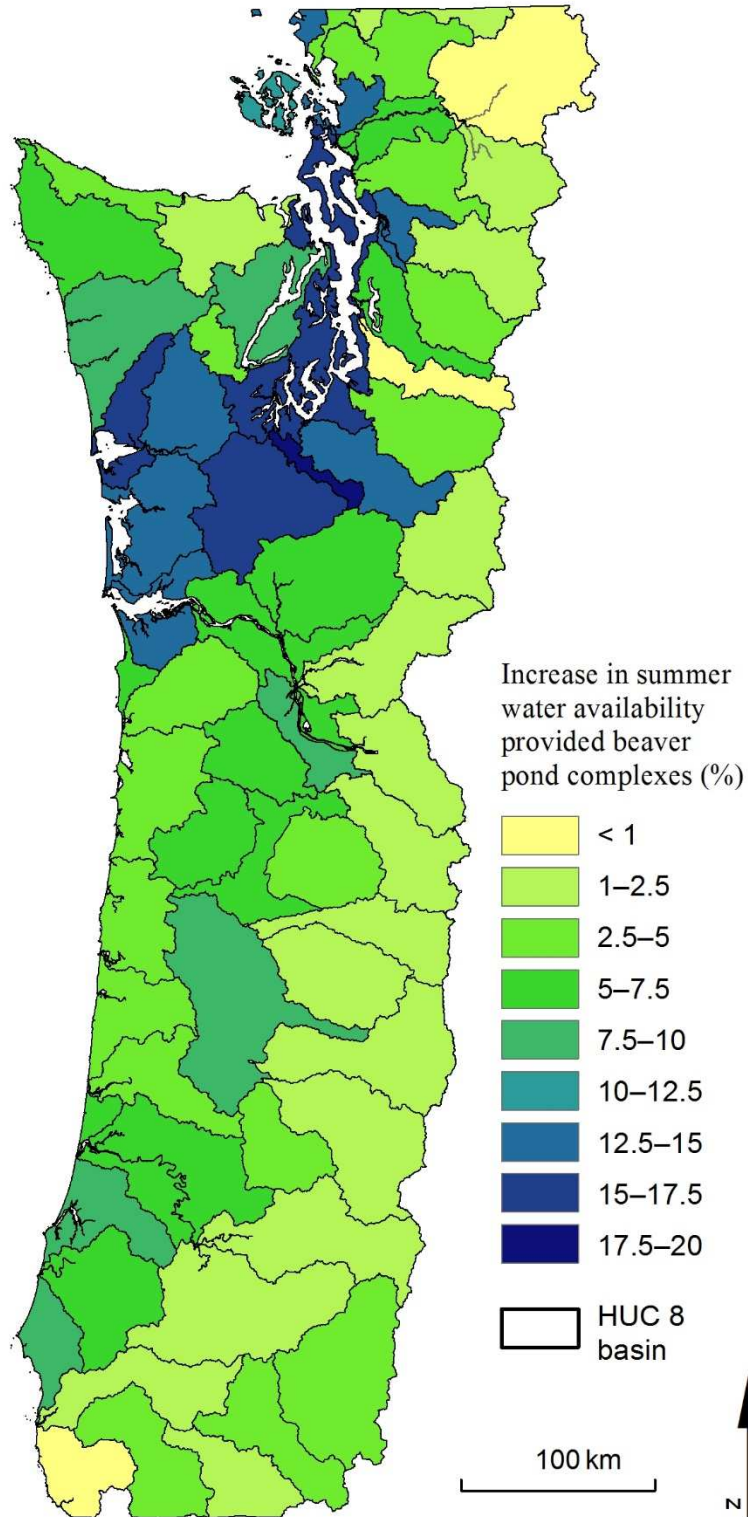


Figure 4.7 Increase in summer water availability supplemented by storage in beaver pond complexes in 2080, RCP 8.5. Summer water storage is expressed as a percentage of mean summer precipitation (i.e., June, July, August).

#### 4.10. Supplementary information

Table S 4.1 Beaver intrinsic potential habitat scoring criteria and methodology.

Stream slope		Stream bankfull width (m)		Valley width (m)		Cumulative score	Adjusted score	BIP category
< 1 %	4	<7	4	> 30	4	12	3	High
< 2 %	3	<10	3	< 30	2	10,11	2	Med
< 4 %	2	<13	2	< 20	0	9	1	Low
< 6 %	1	<17	1			<9	0	No BIP
< 10 %	0.5	>=17	0					
> 10%	0							

Table S 4.2 Colony densities identified in beaver (*Castor canadensis*) population studies throughout North America.

Study	Col/km range	State, province, or ecoregion
Beier and Barrett 1987	0.74	California
Beier and Barrett 1987	0.38	northwestern forested mountains
Boyce 1981	0.63	Alaska
Broschart et al. 1989	1.82 - 2.23	Minnesota
Collins 1976	0.9	Wyoming
Cox and Nelson 2009	0.4	Illinois
Dennington and Johnson 1974	0.35	taiga
Fleming 1977	0.76	eastern temperate forests
Hill 1976	1.9	Alabama
Howard and Larson 1985	0.83	Massachusetts
Leidholt-Bruner et al. 1992	0.38	marine west coast forests
McComb et al. 1990	0.05	great plains
Müller-Schwarz and Sun 2003	0.4 - 1.09	taiga
Mumma et al. 2018	0.44 - 0.88	BC, CA
Naiman et al. 1986	0.83 - 3.53	northern forests
Nelson and Nielsen 2010	0.4	Illinois (Central)
Nordstrom 1972	1.25	New Brunswick
Nordstrom 1972	1.25	northern forests
Novakowski 1965	0.44	great plains
Ribic et al. 2017	0.226	Wisconsin
Ritter et al. 2012	0.49 - 1.14	Montana (Beaverhead)
Ritter 2018	0.25 - 0.42	Montana (Gallatin)
Robel et al. 1993	0.39	Kansas
Ruedemann and Schoonmaker 1938	1.66	northwestern forested mountains
Scrafford et al. 2018	1.33	Montana
Sough & Sadlier 1977	1.53 - 2.59	BC, CA
Sough & Sadlier 1977	2.59	BC, CA
Woo and Waddington 1990	4.77	Hudson plain

Table S 4.3 Dam density estimates from studies evaluating areas in which beaver populations have either stabilized or reached carrying capacity. Adapted from Pollock et al. (2003).

Source	Dams/km	Location	Comments
Leidholt-bruner et al. 1992	1.1	Oregon	Recovering, but healthy
Naiman et al. 1986	10.6	Quebec	Pristine
Naiman et al. 1988b	2.5	Minnesota	Protected population
Scheffer 1938	7.5	Washington	Relocated population
Scheffer 1938	35.4	Washington	Relocated population
Skinner et al. 1984	9.6	Wyoming	Remote
Smith 1950	12.0	Colorado	Remote
Smith 1950	19.1	Colorado	Includes inactive dams
Warren 1926	41.6	Colorado	Pristine
Woo and Waddington 1990	14.3	Quebec	Remote, pristine
Average	15.4		

Table S 4.4 Heights of well-established beaver dams in lowland reaches or areas with wide valleys.

Author	Year	Location	Dam count	Dam height (m)		Terrain
				Mean	Range	
Dittbrenner et al.	2019	WA, USA	11	0.92	0.38 - 2.13	Wide valleys
Karran et al.	2016	AB, CAN	10	1.56	0.85 - 2.00	Wide valleys
Karran et al.	2016	MN, USA	6	0.86	0.40 - 1.10	Lowlands
Westbrook et al.	2006	CO, USA	2	1.25	0.8 - 1.7	Wide valleys
Meentenmeyer and Butler	1999	MT, USA	5	1.14	0.59 - 1.37	Wide valleys
Beedle	1991	AK, USA	44	0.70	0.5 - 1.5	Lowlands
Bryant	1983	AK, USA	7	1.00	0.8 - 2.2	Lowlands
Beard	1953	MI, USA	1	0.90	0.90	Lowlands
Scheffer	1938	WA, USA	23	0.94	0.3 - 1.5	Wide valleys
			109	0.91*		

\*A weighted mean was used to calculate the mean dam height of all studies.

Table S 4.5 Studies documenting the effect of beaver dams on groundwater elevation, storage, and lateral extent.

Study	location	GW elevation change (m)	GW storage (m <sup>3</sup> /pond)	Lateral extent of effect (m)	sample size
Bouwes et al. 2016	OR, USA	0.25	-	-	8 BDAs, 1 control reach
Chapter 3	WA, USA	0.26	655	31	5 reaches, 19 ponds, 5 control reaches
Hafen 2017	UT, USA	-	163	-	3 reaches
Hill and Duval 2009	ON, Canada	1.00	-	20	1 reach
Lowry et al. 1994	OR, USA	0.18	446	50	1 pond
Majerova et al. 2015	UT, USA	0.34	-	-	10 ponds in 1 reach
Shaw 2009	AB, Canada	-	-	7.5	2 reaches with ponds, 1 control reach
Westbrook et al. 2006	CO, USA	0.6	-	80 - 600	1 reach with ponds
Woo and Waddington 1990	ON, Canada	0.29	-	-	1 wetland complex with ponds
Summary		0.42	421	7.5 - 600	

Table S 4.6 Model parameter summary used to established data for parameterization of the regional beaver model.

Model parameter	No. of studies or surveys evaluated	Ref. table	Data mean	Data range	Bootstrapped 95% confidence intervals	Data or processing method used for parameterization
Colony density (col./km)	37	S 4.2	1.1	0.4 - 4.77	(0.80, 1.52)	1.5 for BIP-3, 1.0 for BIP-2, 0.5 for BIP-1, 0 for BIP-0
Dam density (dam/km)	10	S 4.3	15.4	1.1 - 41.6	(8.92, 26.23)	Randomized placement within colony home range*, constrained by a maximum dam capacity of (length of BIP > 0 streams in home range (km) / 0.15) and minimum dam spacing of >= 90 m. Modeled dam density was 7.2
Dam height (m)	109	S 4.4	0.91	0.3 - 2.2	(0.90, 1.22)	0.91
Lateral extent of groundwater storage (m)	4	S 4.5	27	7.5 - 50	(15.3, 37.6)	Outside floodplain: 25 m extent. Within floodplains: lesser of 2.4 x radius of beaver pond or floodplain extent. Modeled GW extent in floodplain was 13.6 m
Groundwater table (m)	7	S 4.5	0.42	0.25 - 1.00	(0.27, 0.73)	0.42 increase within affected area surrounding pond

\*home range is defined here as the area where the majority of the colony's dam-building occurs and is modeled as a (0.5 x colony density) radius buffer around each colony center point.

Table S 4.7 Global climate models (GSM) that contributed to phase 5 of the Coupled Models Inter-comparison Project (CMIP5) were used to model spatially-explicit future precipitation and April 1 snow water equivalent (SWE).

GCM	GCM origin	Used in analysis of:	
		Precipitation	April 1 SWE
bcc-csm1-1	China	y	
bcc-csm1-1-m	China	y	y
BNU-ESM	China	y	
CanESM2	Canada	y	y
CCSM4	USA	y	y
CNRM-CM5	France	y	y
CSIRO-Mk3-6-0	Australia	y	y
GFDL-ESM2G	USA	y	
GFDL-ESM2M	USA	y	
HadGEM2-CC365	United Kingdom	y	y
HadGEM2-ES365	United Kingdom	y	y
inmcm4	Russia	y	
IPSL-CM5A-LR	France	y	
IPSL-CM5A-MR	France	y	y
IPSL-CM5B-LR	France	y	
MIROC5	Japan	y	y
MIROC-ESM	Japan	y	
MIROC-ESM-CHEM	Japan	y	
MRI-CGCM3	Japan	y	
NorESM1-M	Norway	y	y

Table S 4.8 BIP habitat rankings and stream summary by HUC 8 basins.

Sub-region & Huc 8 basin	HUC-8 ID	Stream segments	Total stream length (km)	BIP 0, no BIP	BIP 1, low BIP	BIP 2, mod BIP	BIP 3, high BIP	BIP 1-3, suitable
<b>Lower Columbia</b>								
Lewis	17080002	21,403	7,238	90%	4%	5%	1%	10%
Lwr. Columbia	17080006	20,212	4,337	82%	4%	7%	6%	18%
Clatskanie	17080003	24,530	6,890	82%	5%	10%	4%	18%
Lwr. Columbia-Sandy	17080001	17,272	5,190	90%	3%	5%	2%	10%
Lwr. Cowlitz	17080005	40,339	11,739	85%	4%	8%	4%	15%
Upper Cowlitz	17080004	17,102	6,077	94%	2%	3%	1%	6%
Basin summary		<b>140,858</b>	<b>41,472</b>	<b>87%</b>	<b>4%</b>	<b>7%</b>	<b>3%</b>	<b>13%</b>
<b>Oregon Coast</b>								
Alsea	17100205	23,112	5,655	94%	2%	3%	1%	6%
Applegate	17100309	17,439	5,292	93%	3%	4%	1%	7%
Chetco	17100312	11,020	3,613	98%	1%	1%	0%	2%
Coos	17100304	21,417	5,034	90%	2%	5%	3%	10%
Coquille	17100305	34,380	8,012	91%	2%	5%	2%	9%
Illinois	17100311	14,988	5,199	91%	2%	6%	2%	9%
Lwr. Rogue	17100310	21,687	6,387	94%	2%	4%	0%	6%
Middle Rogue	17100308	27,805	7,269	85%	3%	8%	3%	15%
Necanicum	17100201	2,662	859	87%	3%	7%	3%	13%
Nehalem	17100202	17,536	4,577	85%	5%	8%	2%	15%
North Umpqua	17100301	21,740	7,469	92%	3%	4%	1%	8%
Siletz-Yaquina	17100204	26,686	6,307	91%	2%	5%	2%	9%
Siltcoos	17100207	5,268	758	87%	3%	6%	4%	13%
Siuslaw	17100206	28,790	6,292	92%	2%	4%	2%	8%
Sixes	17100306	13,275	3,493	90%	2%	5%	3%	10%
South Umpqua	17100302	52,207	13,703	92%	2%	5%	1%	8%
Umpqua	17100303	50,231	11,694	89%	2%	6%	2%	11%
Upper Rogue	17100307	27,037	9,574	85%	6%	8%	2%	15%
Wilson-Trusk-Nestuccu	17100203	37,888	8,122	92%	2%	4%	2%	8%
Basin summary		<b>455,168</b>	<b>119,308</b>	<b>90%</b>	<b>3%</b>	<b>5%</b>	<b>2%</b>	<b>10%</b>

*Continued on following page*

Table S 4.8 continued

Sub-region & Huc 8 basin	HUC-8 ID	Stream segments (no.)	Total stream length (km)	BIP 0, no BIP	BIP 1, low BIP	BIP 2, mod BIP	BIP 3, high BIP	BIP 1-3, suitable
<b>Puget Sound</b>								
Crescent-Hoko	17110021	4,672	1,352	75%	7%	14%	3%	25%
Deschutes	17110016	2,111	545	60%	7%	15%	18%	40%
Dungeness-Elwha	17110020	3,972	1,721	71%	9%	14%	6%	29%
Duwamish	17110013	3,471	1,130	58%	8%	16%	19%	42%
Hood Canal	17110018	5,727	2,162	63%	9%	20%	8%	37%
Lake Washington	17110012	3,915	1,595	43%	10%	31%	16%	57%
Lwr. Skagit	17110007	3,247	1,224	58%	6%	18%	18%	42%
Nisqually	17110015	7,392	2,295	52%	7%	20%	22%	48%
Nooksack	17110004	6,253	1,925	60%	6%	16%	19%	40%
Puget Sound	17110019	8,314	3,837	34%	13%	37%	17%	66%
Puyallup	17110014	9,044	2,436	71%	8%	15%	7%	29%
San Juan Islands	17110003	1,118	315	33%	6%	12%	49%	67%
Sauk	17110006	5,636	1,132	81%	5%	8%	6%	19%
Skokomish	17110017	1,642	507	77%	6%	8%	8%	23%
Skykomish	17110009	7,091	1,744	71%	8%	14%	7%	29%
Snohomish	17110011	2,353	1,014	37%	7%	31%	25%	63%
Snoqualmie	17110010	6,594	1,900	59%	10%	18%	13%	41%
Stillaguamish	17110008	6,504	2,161	66%	8%	16%	10%	34%
Strait of Georgia	17110002	1,638	744	30%	7%	29%	33%	70%
Sumas River	17110001	1,053	377	51%	8%	17%	24%	49%
Upper Skagit	17110005	5,980	1,630	85%	4%	6%	5%	15%
<b>Basin summary</b>		<b>97,727</b>	<b>31,745</b>	<b>59%</b>	<b>8%</b>	<b>19%</b>	<b>14%</b>	<b>41%</b>
<b>Washington coast</b>								
Grays Harbor	17100105	14,537	3,556	66%	7%	17%	10%	34%
Hoh-Quillayute	17100101	26,679	7,447	79%	5%	12%	3%	21%
Lwr. Chehalis	17100104	20,745	5,518	69%	7%	15%	9%	31%
Queets-Quinault	17100102	19,383	6,260	72%	6%	16%	6%	28%
Upper Chehalis	17100103	44,303	10,501	77%	5%	11%	7%	23%
Willapa Bay	17100106	47,858	8,211	81%	5%	9%	5%	19%
<b>Basin summary</b>		<b>173,505</b>	<b>41,493</b>	<b>76%</b>	<b>5%</b>	<b>13%</b>	<b>6%</b>	<b>24%</b>
<b>Willamette River</b>								
Clackamas	17090011	16,577	5,042	88%	4%	6%	1%	12%
Coast Fork Willamette	17090002	13,490	4,322	90%	3%	6%	2%	10%
Lwr. Willamette	17090012	6,279	1,784	74%	6%	13%	8%	26%
Mckenzie	17090004	23,329	8,262	94%	3%	3%	1%	6%
Middle Fork Willamette	17090001	21,072	7,719	95%	2%	2%	1%	5%
Middle Willamette	17090007	5,348	2,409	47%	8%	26%	19%	53%
Molalla-Pudding	17090009	16,997	4,992	70%	6%	15%	10%	30%
North Santiam	17090005	19,351	5,897	90%	2%	4%	3%	10%
South Santiam	17090006	30,432	7,992	89%	2%	6%	3%	11%
Tualatin	17090010	16,869	4,457	71%	4%	13%	12%	29%
Upper Willamette	17090003	18,603	8,467	58%	6%	16%	20%	42%
Yamhill	17090008	16,717	4,901	74%	6%	14%	6%	26%
<b>Basin summary</b>		<b>205,064</b>	<b>66,244</b>	<b>81%</b>	<b>4%</b>	<b>9%</b>	<b>7%</b>	<b>19%</b>
<b>Region total</b>	<b>1,089,998</b>	<b>1,089,998</b>	<b>307,310</b>	<b>4%</b>	<b>9%</b>	<b>5%</b>	<b>5%</b>	<b>17%</b>

#### 4.11. Supplementary information references

- Beard, E. B. 1953. The importance of beaver in waterfowl management at the Seney National Wildlife Refuge. *Journal of Wildlife Management* 17:398–436.
- Beedle, D. 1992. Physical Dimensions and Hydrologic Effects of Beaver Ponds on Kuiu Island. Thesis. Oregon State University. OR, USA
- Beier, P., and R. H. Barrett. 1987. Beaver habitat use and impact in Truckee River Basin, California. *Journal of Wildlife Management*:794–799.
- Bouwes, N., N. Weber, C. E. Jordan, M. M. Pollock, W. Carl, I. A. Tattam, C. Volk, and J. M. Wheaton. 2016. Ecosystem experiment reveals impacts of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). *Nature Publishing Group* 7:1–12.
- Boyce, M. S. 1981. Habitat ecology of an unexploited population of beavers in interior Alaska. Pages 155–186 *Worldwide Furbearer Conf. Proc.*
- Broschart, M. R., C. A. Johnston, and R. J. Naiman. 1985. Predicting beaver colony density in boreal landscapes. *The Journal of Wildlife Management* 4:929–934.
- Bryant, M. D. 1984. The role of beaver dams as coho salmon habitat in southeast Alaska streams. Pages 183–192 *Proceedings of the Olympic Wild Fish Conference. Fisheries Technology Programme. Peninsula College, Port Angeles, Washington.*
- Collins, T. C. 1976. Population characteristics and habitat relationships of beavers, *Castor canadensis*, in northwest Wyoming. University of Wyoming, Laramie, USA.
- Cox, D. R., and T. A. Nelson. 2009. Beaver Habitat Models for Use in Illinois Streams. *Transactions of the Illinois State Academy of Science* 102:55–64.
- Dennington, M., and B. Johnson. 1974. Studies of beaver habitat in the Mackenzie Valley and northern Yukon. Information Canada, 1974 [c1975].
- Dittbrenner, B. J., M. M. Pollock, J. W. Schilling, J. D. Olden, J. J. Lawler, and C. E. Torgersen. 2018. Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation. *PLOS ONE* 13:e0192538.
- Fleming, M. W. 1977. Induced sterility of the adult male beaver (*Castor canadensis*) and colony fecundity. Thesis. University of Massachusetts. MA, USA
- Hafen, K. 2017. To what extent might beaver dam building buffer water storage losses associated with a declining snowpack? Thesis. Utah State University. UT, USA

- Hill, A. R., and T. P. Duval. 2009. Beaver dams along an agricultural stream in southern Ontario, Canada: their impact on riparian zone hydrology and nitrogen chemistry. *Hydrological Processes* 23:1324–1336.
- Hill, E. P. 1976. Control methods for nuisance beaver in the southeastern United States. *Proceedings of the 7th Vertebrate Pest Conference*:25.
- Howard, R. J., and J. S. Larson. 1985. A Stream Habitat Classification System for Beaver. *The Journal of Wildlife Management* 49:19–25.
- Karran, D. J., C. J. Westbrook, J. M. Wheaton, C. A. Johnston, and A. Bedard-Haughn. 2016. Rapid surface water volume estimations in beaver ponds. *Hydrology and Earth System Sciences* 21:1–26.
- Leidholt-bruner, K., D. E. Hibbs, and W. C. McComb. 1992. Beaver dam locations and their effects on distribution and abundance of Coho salmon fry in two coastal Oregon streams. *Northwest Science* 66:218–223.
- Lowry, M. M., R. L. Beschta, McNamara, and M. Michael M. Lowry, Robert L. Beschta. 1994. Effect of a beaver pond on groundwater elevation and temperatures in a recovering stream system. *American Water Resources Association*:503–513.
- 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.
- McComb, W. C., J. R. Sedell, and T. D. Buchholz. 1990. Dam-site selection by beavers in an eastern Oregon basin. *The Great Basin Naturalist* 50:273–281.
- Meentemeyer, R. K., and D. R. Butler. 1999. Hydrogeomorphic effects of beaver dams in glacier national park, Montana. *Physical Geography* 20:436–446.
- Müller-Schwarze, D., and L. Sun. 2003. *The beaver: Natural history of a wetlands engineer*. Cornell University Press.
- Mumma, M. A., M. P. Gillingham, C. J. Johnson, and K. L. Parker. 2018. Where beavers (*Castor canadensis*) build: testing the influence of habitat quality, predation risk, and anthropogenic disturbance on colony occurrence. *Canadian Journal of Zoology* 904:cjz-2017-0327.
- Naiman, J. R., J. M. Melillo, J. E. Hobbie, R. J. Naiman, J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67:1254–1269.

- Naiman, R., C. Johnston, and J. Kelley. 1988. Alteration of North American streams by beaver. *BioScience* 38:753–762.
- Nelson, T. A., and C. K. Nielsen. 2010. Population ecology of beavers in Illinois. Carbondale, IL, USA.
- Nordstrom, W. R. 1972. Comparison of trapped and untrapped beaver populations in New Brunswick. Thesis (M. Sc.)--University of New Brunswick.
- Novakowski, N. S. 1965. Population dynamics of a beaver population in northern latitudes. University of Saskatchewan.
- Pollock, M. M. M. M., M. Heim, and D. Werner. 2003. Hydrologic and Geomorphic Effects of Beaver Dams and Their Influence on Fishes. *American Fisheries Society Symposium* 37:20.
- Reudemann, R., and W. J. Schoonmaker. 1938. Beaver dams as geologic agents. *Science* 88:524–525.
- Ribic, C. A., D. M. Donner, A. J. Beck, D. J. Rugg, S. Reinecke, and D. Eklund. 2017. Beaver colony density trends on the Chequamegon-Nicolet National Forest, 1987 -2013. *PLoS ONE* 12:1–15.
- Ritter, T. D. 2018. Ecosystem pioneers: beaver dispersal and settlement site selection in the context of habitat restoration. Thesis. Montana State University. MT, USA
- Robel, R. J., L. B. Fox, and K. E. Kemp. 1993. Relationship between habitat suitability index values and ground counts of beaver colonies in Kansas. *Wildlife Society Bulletin* 21:415–421.
- Scheffer, P. M. 1938. The beaver as an upstream engineer. *Soil Conservation* 3:178–181.
- Scrafford, M. A., D. B. Tyers, D. T. Patten, and B. F. Sowell. 2018. Beaver habitat selection for 24 years since reintroduction north of Yellowstone National Park. *Rangeland Ecology and Management* 71:266–273.
- Shaw, E. L. 2009. Lateral exchange of water and nitrogen along a beaver-dammed stream draining a Rocky Mountain valley. Thesis. University of Saskatchewan, Saskatoon, Canada.
- Skinner, Q. D., J. E. Speck, M. Smith, and J. C. Adams. 1984. Stream water quality as influenced by beaver within grazing systems in Wyoming. *Journal of Range Management* 37:142–146.
- Slough, B. G., and F. S. Sadleir. 1977. A land capability classification system for beaver (*Castor canadensis Kuhl*). *Canadian Journal of Zoology* 55:1324–1335.
- Smith, A. E. 1950. Effects of water runoff and gradient on beaver in mountain streams.

University of Michigan, Ann Arbor.

Warren, E. R. 1926. A study of the beaver in the Yancy Region of Yellowstone National Park.

Roosevelt Wildlife Annals 1:5–191.

Westbrook, C. J., D. J. Cooper, and B. W. Baker. 2006. Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. *Water Resources Research* 42:1–12.

Woo, M.-K., and J. M. Waddington. 1990. Effects of beaver dams on subarctic wetland hydrology. *Arctic* 43:223–230.

## Chapter 5. **Synthesis and future directions**

Humans and beaver have been intertwined for well beyond recorded history. The fossil record indicates that early beaver were likely cutting wood to build dams as early as 25 million years ago (Rybczynski 2007, 2008). Early Mesolithic and Neolithic Europeans are believed to have settled in beaver-influenced areas for the hunting and fishing resources that they provided (Liarsou 2013). Beaver are featured prominently in the mythology of many Native American tribes, reflecting the value that they associated with them. In one Blackfoot origin myth, the earth was saved by a beaver who sacrificed himself during a great flood (Backhouse 2019). The beaver swam to the depths of the flood waters to bring up a piece of earth, which would restore the land. The water was too deep and he drowned in the attempt, but his lifeless body floated to the surface with a clump of mud clutched in one paw. The earth was renewed and the beaver was given his life back for his sacrifice. In the 17th century, the Catholic church ruled that beaver were classified as fish and therefore acceptable for the Québécois of Canada to eat on Fridays during lent when consumption of meat is forbidden. The decimation of North American beaver populations on the east coast prompted exploration of the American West for more fur. The trappers that explored these areas mapped the west, established trade routes, and allowed for westward expansion (Mackie 1997). Just as humans have relied on beaver throughout history, they are likely to continue to depend on the ecosystem services, biodiversity, and resilience that beaver provide well into the future.

Beaver's ability to alter aquatic ecosystems, often in dramatic ways, has long garnered attention. Despite over a century of scientific investigation into their natural history and the ecological and hydrologic implications of their actions, disagreement and unanswered questions remain surrounding their role in these systems. Specifically, as beaver populations have

remained suppressed in many areas, findings on how they influence water storage and stream temperature are often variable and contradictory. Likewise, the effects that beaver populations have at larger scales have been difficult to test. As new environmental challenges emerge, beaver's role in aquatic systems may need to be re-examined for fresh perspectives.

In this dissertation, my objective was to increase our understanding of how beaver modify the environment and to explore the potential implications of these modifications in a changing climate. Despite these efforts, it is clear that the ways in which beaver influence aquatic systems are largely dependent upon geographic context, climate, topography, surrounding land use, successional states, and the probability of stochastic events. In this concluding chapter, I highlight the key points of preceding chapters and discuss the implications of these findings. I also identify unanswered questions that have arisen from this research and propose new directions that warrant further attention to advance the science and management of beaver in a changing world.

## **5.1. Major findings**

### ***5.1.1. Evaluation of beaver habitat and populations***

- Habitat models that use an intrinsic potential approach are an effective tool for identifying possible beaver habitat.
- Stream-based beaver habitat models cannot identify all types of beaver habitat.
- There are unknown factors influencing and potentially limiting beaver dispersal and occupation of suitable habitat.

Beaver habitat models facilitate the evaluation of habitat distribution, basin population capacity, and prioritization of relocation and beaver-assisted restoration. Several different types of beaver

habitat models exist. Intrinsic potential models are able to identify habitable stream reaches regardless of the current state of existing environmental factors, such as condition of the vegetation community. This modeling approach is particularly useful for species such as beaver because they modify the landscape to directly alter extrinsic factors. It has the advantage over more traditional habitat suitability models in that it allows for the forecasting of restoration and colonization potential, regardless of existing conditions.

Beaver's ability to alter the landscape allows them to establish colonies in a variety of hydrogeomorphological settings beyond stream systems, however, and existing models are currently unable to predict occupation across this entire range (e.g., streams, side channels, wetlands). Because many of these areas are created by beaver, it may be difficult to predict where beaver might occur in off-channel habitats. As higher resolution data (e.g., lidar topography) become increasingly available, identifying these areas may be more realistic. Until these model types become more widely applicable, existing models are likely to underestimate habitat potential, in some cases, substantially.

Within the Skykomish River basin, where I tested the BIP model, I found population density and site vacancy to be highly variable. In some instances, existing colonies were found near high quality, vacant habitat. It is unknown why dispersing members from established beaver colonies are not colonizing nearby vacant habitat. This lack of occupation appears to be consistent in other basins of the Pacific Northwest as well. Based on my experience translocating colonies to sites selected using the BIP model, it appears that intrinsic potential models are well-suited for identifying potential habitat, but a secondary fine filter should also be used to evaluate whether planned relocation sites require modification, such as the placement of beaver dam analogues (BDAs) to create pools.

### ***5.1.2. Beaver relocation and its effect on reach-scale hydrology and water quality***

- Newly relocated beaver may produce cooling downstream of ponds.
- Beaver relocation efficiency and natural colonization rates may be increased by site modification.
- Post-relocation dam building may not occur immediately.

I observed that dams built by recently relocated beaver were associated with cooler temperatures downstream. These systems also raised groundwater tables adjacent to ponds after dam establishment. Although other studies have found that the ecological functions associated with beaver dams increase over time, my findings suggest that hydrologic and water quality benefits may be realized immediately after dam construction. There may be trade-offs, however, in targeting potential relocation sites for restoration of hydrology and water quality. For example, in systems with small, abandoned ponds, which often contribute to substantial warming, beaver colonization may lower stream temperature but may not lead to appreciable amounts of additional water storage. Conversely, in abandoned complexes new beaver establishment may lead to a large increase in storage, but they may not necessarily contribute to additional cooling. Prioritizing stream reaches for beaver-based restoration will require the articulation of desired outcomes and potentially also a decision-making framework to achieve restoration goals.

Over the course of the study, I trapped approximately 100 beaver and relocated them to vacant stream reaches. Approximately 50% of relocated beaver remained on-site for at least a year and constructed dams. In addition to the relocation techniques discussed in Chapter 3, I believe that the initial presence of deep pools is a primary contributor to increased site fidelity. These pools provide cover from predation and may assist beaver in identifying where to initiate dam construction. The creation of pools using human-initiated techniques such as BDAs at sites

that have been modeled as high quality may substantially increase relocation success rates. In some cases, beaver colonies that I relocated to presumably high-quality sites emigrated from the site soon after release. In subsequent years, I found that some of these beaver returned to the site, but did not initially build dams. At one site, a colony began dam-building three years after relocation. This suggests that the current method of measuring relocation success – by whether dams are constructed that season – may underestimate rates of long-term site fidelity. It also fails to capture any potential secondary benefits, such as dispersal and colonization of new sites by young from productive colonies.

### ***5.1.3. Synergistic effects of beaver populations***

- Beaver dams can potentially store large quantities of water at the basin scale.
- Beaver activities may not offset snowpack losses in areas where future climate change alters precipitation regimes.
- Beaver dams may increase summer water availability.

Results from my model suggest that beaver may store substantial quantities of surface and groundwater. Storage is largely dependent on the density of suitable stream habitat and topography. In basins with large floodplains and low gradient streams, beaver may be able to impound a volume of water equivalent to a human-built reservoir. Most of the historically snow-dominated basins of the western Cascade Mountains are projected to transition to rain-dominated basins. Beaver-created storage will be unable to offset these losses due to the large volumes of snow that they receive. In other snow-dominated basins with greater amounts of potential beaver habitat and less predicted snow loss, beaver may be able to offset climate-driven reductions in

snow pack. Beaver may supplement summer water availability in many basins, however, by increasing the storage potential of summer precipitation. This potential can be realized at reach, section, and basin scales as populations expand. Although beaver relocation and natural colonization in basins with high storage potential may increase hydrologic stability, local beaver management policies and perspectives may need to be revised to facilitate re-colonization.

## **5.2. Anticipated research needs and next steps**

### ***5.2.1. Regional beaver population assessment***

Current beaver populations are patchy throughout their historical range. The lack of information on beaver distribution limits our understanding of their population size, how they are dispersed on the landscape, and the degree to which they have occupied available habitat. This information would contribute to a better understanding of population dynamics and allow for more informed restoration prioritization. Previous population assessments have used aerial counts of beaver lodges (Bergerud and Miller 1977, Peterson and Payne 1986, Svendsen 1989). This approach could be automated with remotely sensed imagery to track lodges over time. If successful, it might be possible to conduct monitoring surveys across large areas. Although it might not be feasible to conduct such a survey throughout their entire range, repeated surveys in one or more long-term monitoring regions would provide valuable information on trends.

### ***5.2.2. Evaluating effects of beaver on stream temperature***

A large number of studies exist that have evaluated how beaver affect stream temperature. These findings have shown a warming effect, a cooling effect, mixed effects, or no effect at all. The discrepancy in these findings may stem from disagreement regarding the site-specific underlying mechanisms that drive the observed temperature effect. These factors include the type and size of

dams and beaver impoundments present, geographic context, topography, geomorphic setting, and climactic factors and weather patterns. In Chapter 3, I found that beaver had a cooling effect at relocation reaches. At these sites, summer stream temperature was influenced by ambient air temperatures, storm events, and topography. In abandoned reaches, however, stream temperature was most influenced by pond morphology. Other studies have found, for example, that dam height is the primary driver of stream cooling (Fuller and Peckarsky 2011b), with greater cooling associated with taller dams. Given the variability in these findings, further studies are needed to identify primary drivers of stream temperature and determine how these factors vary by region or topographic setting.

### ***5.2.3. Monitoring well-established beaver populations***

Many studies have documented beaver-related metrics, including interactions, proximity to other colonies, colony mixing among relatives, site modification, such as dam dimensions and densities, counts and measure of pond hydrology, and effects on local morphology, habitat creation for other species, and measures of biodiversity. These data may be useful in the parameterization of models. Most of these data, however, have been collected from populations that are still recovering, so their utility may be limited. For example, they may not adequately document the successional state of the colony or wetland complex from which data were collected.

Beaver pond complexes advance through a general order of succession: as new dams are progressively augmented, they impound more water and sediment, increasing morphological complexity and heterogeneity, until they eventually aggrade sufficient material to transition into a beaver meadow. Site conditions will vary based on the site's position in the successional continuum. For example, dam dimensions may be different when measured shortly after

construction than when measured after multiple generations of beaver construction and maintenance. Failure to consider or document the successional stage of a complex has led to the reporting of highly variable beaver-related metrics. More accurate accounting of context, including site morphology and successional state, would make it possible to use these data more appropriately and would reduce discrepancies between studies.

Furthermore, studies and collection of beaver-related metrics are needed in areas where populations have either stabilized or are nearing carrying capacity. Few studies have documented conditions in areas with well-established colonies. The limited data that exist have been collected primarily from areas where beaver were not intensively trapped in previous centuries, such as the Boundary Waters of northern Minnesota (USA) or northern Canada (see Naiman et al. 1986, Woo and Waddington 1990). These data are frequently cited or used in other studies without providing context on geographic, topographic, or climatic factors. Although the lack of available populations near carrying capacity make it difficult to evaluate conditions in this state, greater efforts are needed to obtain these metrics to predict future conditions in areas where populations are rebounding.

#### ***5.2.4. Tracking restoration success***

Beaver-assisted restoration practices are most frequently implemented through relocation, assisted colonization, or as an unintended consequence of restoring suitable habitat. Guidance on beaver restoration is increasingly available to assist in these efforts. For example, the beaver restoration guidebook (Pollock et al. 2018) provides detailed information on many aspects of beaver-related restoration. Although these guidance documents provide an excellent resource for practitioners, information is also needed from those who have implemented these approaches. This includes documenting the experiences of success and failures, the challenges encountered,

and evolving conditions at these sites. Many local and state jurisdictions have adopted restoration reporting systems that track project status, site conditions, and outcomes. Similar systems could be used to track beaver-based restoration actions. In some cases, these systems can be expanded from what already exists. Tracking, reporting, and disseminating this information is needed to promote education and implementation among practitioners.

### 5.3. Evaluating beaver effects at multiple scales

In the preceding chapters, I have primarily focused on contributing to our understanding of how beaver influence aquatic systems to reduce climate impacts. I have approached this question with the intention of addressing the problem at multiple spatial scales. Through this work, it has become apparent that, although beaver modify ecological processes at a variety of scales, most studies focus on the reach scale (i.e., approximately 100-250 m length). In the following section, I argue that the lack of attention beyond the reach scale is a systematic oversight, and that closing this critical information gap will allow for a greater understanding of beaver ecology and restoration.

Beaver have been of interest to naturalists and the scientific community for centuries. There has been continued focus on beaver natural history and how they influence stream morphology, hydrology, water quality and chemistry, nutrient cycling, and ecology. However, despite the breadth of the body of literature that has evaluated how beaver influence these aspects of aquatic ecosystems, most studies focus on the reach scale. The reach scale typically consists of interactions that occur within the territory of a single beaver colony, i.e., a pond or wetland complex generally consisting of a number of dams and their surrounding foraging area. The reach scale is also sometimes referred to as the *human scale*, since it is the level at which we most easily perceive our environment. For this reason, many observational studies examine phenomena from this frame of reference.

Dam building by beaver is most conspicuous at the reach scale, but hierarchical levels exist within riverscapes from which the influence of beaver can be evaluated. A spatially-nested hierarchical classification of the scales at which riparian ecosystems operate was first proposed by Frissell et al. (1986). In this classification system, watersheds are generally organized in an ordered group, moving from small-scale pool-riffle complexes that are contained within stream

reaches, followed by stream segments, sub-basins, and finally watersheds. This scheme identifies distinct mechanisms operating at each level that control ecosystem processes. Each level provides direct and indirect controls on the level below. The dynamics that maintain riparian ecosystems are complex, and scale-dependent processes operate in both top-down and bottom-up directions.

Beaver pond complexes influence ecosystem-forming processes at multiple scales. Grasse (1951) demonstrated that at the segment scale, multiple colonies and dams could affect discharge patterns and potentially moderate peak flows. Other studies have evaluated nutrient cycling (Correll et al. 2000) and sediment transport and retention (Meentemeyer and Butler 1999) and found that beaver had substantial effects both at the reach scale and broader scales. Investigations into landscape-scale productivity (Correll et al. 2000), community diversity (Pollock et al. 1995, McMaster and McMaster 2000), and succession (Pastor et al. 1984, Johnston and Naiman 1990) have found similar levels of influence.

Beaver also interact with the landscape at temporal scales ranging from hourly, daily, seasonally, yearly, and up to geologic time scales. Petro (2013) tracked beaver in the Alsea watershed in Oregon's Coast Range, which has a flashy seasonal hydrograph. Beaver responded by building summer dams to retain water for protection but ceased building in the fall and allowed high winter flows to completely breach dams, thereby altering the system on a seasonal scale. Beechie et al. (2010) notes that erosion and runoff processes are fairly constant at decadal scales and are dictated by climate patterns. At the century scale, large fires in the Pacific Northwest cause the release of pulses of sediment, nutrients, and debris. Catastrophic beaver dam blowouts mimic this process but on a much shorter time period—over decades as opposed to centuries. Polvi and Wohl (2012) reported that beaver were responsible for building soil and

sediment layers in a watershed in Colorado over a 4,300 year period. These examples illustrate how beaver influence ecosystem processes across spatial and temporal scales. There are many more contexts and environmental settings which require further exploration.

### ***5.3.1. Beaver restoration and the shifting habitat mosaic of riverine landscapes***

Climate change has the potential to alter riverine processes, many of which have already been altered by anthropogenic disturbance. Changes to large-scale processes may have cascading impacts at each subsequent level resulting in ecosystem impairments that may be difficult to address. Faced with greater uncertainty and variability, restoration projects will need to be more robust and consider multiple spatial scales and longer time periods (Welch 2005, Julius et al. 2008). Management actions can be taken to reduce potential impacts to riparian systems and the processes that regulate them. Given the types of impacts and scales across which they are occurring, there are a number of challenges for the restoration of riparian ecosystems. Future conditions are unlikely to look like the past. Competitive relationships among plants are likely to change with changing CO<sub>2</sub> concentrations (Schlesinger and Clark 2001). As plant associations change, it may be difficult to identify reference states from which to gauge restoration success. It may not be possible to restore riparian systems to pre-disturbance conditions (Lawler 2009). A shift in focus from a species-based restoration approach to a process-based restoration approach can allow for greater surety of achieving restoration goals (Beechie et al. 2010). Process-based restoration identifies what types of disturbances are altering overarching ecosystem processes, and then seeks to remove that disturbance and restore the process.

Traditional stream restoration is most often performed at the reach scale (Roni et al. 2008). This is because most stream assessments are designed to evaluate stream reaches and restoration project costs make reach scales most feasible. Additionally, a reach is much more

likely to fall within the property boundaries of a single landowner or jurisdiction, making planning and implementation easier (Hannah et al. 2002). Restoration projects do occur at larger scales, but the logistics and cost of these projects increase exponentially, making them more rare. The concept of process-based restoration has gained traction and is recognized as the preferred method for framing restoration prioritization and project planning (Beechie and Bolton 1999, Beechie et al. 2010). However, many smaller entities lack the funding and other resources to address degraded larger-scale processes. Whereas it is better to perform a number of small-scale restoration projects than none at all, it is essential to address disrupted large-scale river processes. Because these overarching processes control smaller-scale function, it is improbable that riverscapes can be restored and preserved using reach-scale restoration alone.

Beaver dam-building activities occur at the reach scale, but the cumulative effect of multiple beaver throughout a watershed has been shown to enhance ecosystem processes at multiple scales and increase the resilience of these systems (Rosell et al. 2005). Beaver have the potential to act as a novel restoration and preservation tool because they influence and support many of these overarching ecosystem processes. This may be particularly relevant to ameliorate anticipated climate-change impacts, which influence large-scale processes. Human-based riparian restoration may be effective at the reach-scale but may be less effective at addressing higher scale processes. In these cases, beaver may be an effective restoration tool (DeVries et al. 2012). For example, both human- and beaver-based projects increase biodiversity within the restoration area (Jones et al. 1997). However, beaver also increase biodiversity at the landscape scale (Wright et al. 2002) by increasing the number of non-wetland patch types. Beaver impoundments also offer specialized habitat types, which increase resilience to disturbance (Naiman et al. 1988). Beaver readily inhabit human dominated landscapes and create vegetated

riparian corridors in these areas. These corridors have the potential to allow other species to migrate more easily. Although human-based restoration also has the potential to restore riparian corridors, humans are far more constrained by ownership boundaries. Additionally, in areas in which beaver have become established, colonizing individuals will identify new marginal habitat and convert it to productive wetlands and pond complexes. In this way, beaver-based restoration can produce compounding results. Traditional restoration cannot restore the same area without large resource expenditures. Beaver are highly adapted to disturbance because they are generalists and can tolerate a range of conditions, from extreme northern latitudes to deserts. Their tolerance to changing conditions and disturbances suggests that they will be able to adapt to unknown future conditions brought about by climate change. In some cases, disturbance increases their effectiveness because it motivates them to build larger dam structures that are more resistant to higher peak flows.

Restoration techniques are needed to address the disruption of processes occurring at large scales, thereby increasing ecosystem resilience. Although a number of such strategies may exist, facilitating the recovery of beaver throughout existing portions of their historic range is a viable climate adaptation and restoration strategy. Where beaver have been allowed to recolonize watersheds, they have been shown to strengthen and maintain overarching ecosystem functions necessary for the preservation of riparian systems and the species they contain.

Riparian restoration is effective at addressing lower level ecosystem properties, but these actions do little to buffer against large-scale climate-change impacts. Beaver present a low-cost restoration alternative. Policies are needed to promote beaver management and allow beaver to return to historical numbers where possible. Landowners need realistic and effective non-lethal strategies to manage potential nuisance beaver. Incentive programs are one possible option for

landowners to encourage beaver to remain on their property. In instances where on-site management is not feasible, relocating beaver to high priority restoration sites may be a tenable alternative. This requires the establishment of beaver relocation programs, whether they be by translocation or by attracting dispersing beaver using BDAs. Headway has been made in some states in encouraging relocation of nuisance animals. Other states have yet to adopt similar policies. With these policies in place, it may be possible to increase ecosystem function in riparian areas in the broader context of climate change and the increasing pressures of land use.

#### **5.4. References**

- Backhouse, F. 2019. Rethinking the beaver: Why beavers and humans have to learn to get along. <https://www.cbc.ca/radio/ideas/rethinking-the-beaver-why-beavers-and-humans-have-to-learn-to-get-along-1.4922662>.
- Beechie, T., and S. Bolton. 1999. An approach to restoring salmonid habitat-forming processes in Pacific Northwest watersheds. *Fisheries* 24:6–15.
- Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. Process-based principles for restoring river ecosystems. *BioScience* 60:209–222.
- Bergerud, A. T., and R. Miller. 1977. Population dynamics of Newfoundland beaver. *Canadian Journal of Zoology* 55:1480–1492.
- Correll, D. L., T. E. Jordan, and D. E. Weller. 2000. Beaver pond biogeochemical effects in the Maryland Coastal Plain. *Biogeochemistry* 49:217–239.
- DeVries, P., K. L. Fetherston, A. Vitale, and S. Madsen. 2012. Emulating riverine landscape controls of beaver in stream restoration. *Fisheries* 37:246–255.
- Frissell, C. a., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management* 10:199–214.
- Fuller, M. R., and B. L. Peckarsky. 2011. Ecosystem engineering by beavers affects mayfly life

- histories. *Freshwater Biology* 56:969–979.
- Grasse, J. E. 1951. Beaver ecology and management in the Rockies. *Journal of Forestry* 49:3–6.
- Hannah, L., G. F. Midgley, and D. Millar. 2002. Climate change-integrated conservation strategies. *Global Ecology and Biogeography* 11:485–495.
- Johnston, C. A., and R. J. Naiman. 1990. Aquatic patch creation in relation to beaver population trends. *Ecology* 71:1617–1621.
- Jones, C. G., J. H. Lawron, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.
- Julius, S. H., J. M. West, J. S. Baron, L. A. Joyce, P. Kareiva, B. D. Keller, M. Palmer, C. Peterson, and J. M. Scott. 2008. Preliminary review of adaptation options for climate-sensitive ecosystems and resources. *National Parks* 1.
- Lawler, J. J. 2009. Climate change adaptation strategies for resource management and conservation planning. *Annals of the New York Academy of Sciences* 1162:79–98.
- Liarsou, A. 2013. Interactions between the beaver (*Castor fiber L.*) and human societies: A long-term archaeological and historical approach. *Archaeological Review from Cambridge* 28:171–185.
- Mackie, R. S. 1997. *Trading Beyond the Mountains: The British Fur Trade on the Pacific, 1793-1843*. UBC Press, Vancouver, BC.
- McMaster, R. T., and N. D. McMaster. 2000. Vascular flora of beaver wetlands in western Massachusetts. *Rhodora*:175–197.
- Meentemeyer, R. K., and D. R. Butler. 1999. Hydrogeomorphic effects of beaver dams in glacier national park, Montana. *Physical Geography* 20:436–446.
- Naiman, J. R., J. M. Melillo, J. E. Hobbie, R. J. Naiman, J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67:1254–1269.
- Naiman, R. J. R., C. A. Johnston, and J. C. J. Kelley. 1988. Alteration of North American streams by beaver: The structure and dynamics of streams are changing as beaver recolonize their historic habitat. *BioScience* 38:753–762.
- Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes. 1984. Moose, microbes, and boreal forest 38:770–777.
- Peterson, R. P., and N. F. Payne. 1986. Productivity, size, age, and sex structure of nuisance

- beaver colonies in Wisconsin. *The Journal of Wildlife Management* 50:265–268.
- Petro, V. 2013. Evaluating “nuisance” beaver relocation as a tool to increase coho salmon habitat in the Alsea Basin of the central Oregon Coast Range. M.Sc. Thesis. Oregon State University, Corvallis, OR.
- Pollock, M. M., G. M. Lewallen, K. Woodruff, C. E. Jordan, and J. M. Castro. 2018. *The Beaver Restoration Guidebook: working with beaver to restore streams, wetlands, and floodplains*. Page United States Fish and Wildlife Service. V-2.01.
- Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1995. Beaver as engineers: Influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 in C. G. Lawton and J. J. H., editors. *Linking species to ecosystems*. Chapman & Hall, New York, NY, USA.
- Polvi, L. E., and E. Wohl. 2012. The beaver meadow complex revisited - the role of beavers in post-glacial floodplain development. *Earth Surface Processes and Landforms* 37:332–346.
- Roni, P., K. Hanson, and T. Beechie. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North American Journal of Fisheries Management* 28:856–890.
- Rosell, F., O. Bozsér, P. Collen, H. Parker, O. Bozser, P. Collen, and H. Parker. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* 35:248–276.
- Rybczynski, N. 2007. Castorid phylogenetics: Implications for the evolution of swimming and tree-exploitation in beavers. *Journal of Mammalian Evolution* 14:1–35.
- Rybczynski, N. 2008. Woodcutting behavior in beavers (Castoridae, Rodentia): estimating ecological performance in a modern and a fossil taxon. *Paleobiology* 34:389–402.
- Schlesinger, W. H., and J. S. Clark. 2001. Global environmental change; effects on biodiversity. Pages 175–223 in M. E. Soulé and G. H. Orians, editors. *Conservation Biology: Research Priorities for the Next Decade*. Island Press, Washington, DC, USA.
- Svendsen, E. 1989. Pair formation, duration of pair-bonds, and mate replacement in a population of beavers (*Castor canadensis*). *Canadian Journal of Zoology* 67:336–340.
- Welch, D. 2005. What should protected areas managers do in the face of climate change? *The George Wright Forum* 22:75–93.
- Woo, M.-K., and J. M. Waddington. 1990. Effects of beaver dams on subarctic wetland

hydrology. *Arctic* 43:223–230.

Wright, J., C. Jones, and A. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101.