DISSERTATION

THE EFFECTS OF BEAVER ENGINEERING ON DOWNSTREAM FLUXES IN COLORADO MOUNTAIN STREAMS

Submitted by

DeAnna J. Laurel

Department of Geosciences

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2019

Doctoral Committee:

Advisor: Ellen Wohl

Sara Rathburn
Tim Covino
Eugene Kelly

ABSTRACT

THE EFFECTS OF BEAVER ENGINEERING ON DOWNSTREAM FLUXES IN COLORADO MOUNTAIN STREAMS

Beaver meadows compose only a small fraction of catchment area in mountain watersheds, but they provide a potentially large role in retaining fluxes of water, sediment, and organic carbon (OC) in mountain meadows. Beaver (*Castor canadensis*) build dams and ponds that encourage overbank flows and deposition of fine sediment along with particulate OC that create an anastomosing stream channel and a geomorphically heterogeneous floodplain with high biodiversity. I combined geomorphic surveys, soil depth probing by rebar, and soil cores analyzed for carbon content to investigate the influence of beaver activity, geomorphic unit, soil depth, soil moisture, and drainage area on fluxes of fine sediment and organic carbon storage in 7 active and abandoned beaver meadows in Rocky Mountain National Park. I found that surface spatial heterogeneity and mean soil moisture differed significantly only between active and long abandoned meadows, indicating a nonlinear change through time. Soil depth and OC stock did not differ significantly between different levels of beaver activity, indicating that larger-scale geologic controls on valley sediment depth contribute to long-term storage of OC after beaver abandon a meadow. I examined the seasonal hydrologic flux between the inflow and outflow of 19 active and abandoned beaver meadows to determine the influence of beaver activity, valley geometry, elevation, drainage area, and meadow size relative to drainage area on the reduction of peak flow, enhancement of base flow, and lag of the recession curve of the meadow hydrographs during the Spring and Summer. I found that beaver activity, along with meadow size relative to drainage area, and valley geometry, influence peak flow attenuation. Predicting the flow attenuation is complicated by these additional factors, as well as the difficulty of quantifying subsurface processes that contribute to the lateral flow, storage, and release of water from the meadows. These results indicate that relatively wide meadows located in the upper reaches of channel networks are the best candidates among abandoned beaver meadows in mountain environments to store more organic carbon and attenuate peak flows if beaver are successfully reintroduced.

ACKNOWLEDGEMENTS

I am grateful for funding from the National Geographic Society and from NSF (EAR 1632798). I thank the National Park Service for permission to work in Rocky Mountain National Park. I also thank Heidi Anderson and Leland Dorchester for assistance with field data collection and laboratory analyses. I would like to thank and acknowledge the support from friends, my family, and my committee in completing this project. Dr. Sara Rathburn, Dr. Eugene Kelly, and Dr. Tim Covino provided valuable insight and suggestions that have infinitely improved my final dissertation. Finally, I would like to extend heartfelt thanks to my mentor and advisor Dr. Ellen Wohl for her friendship, patience, and support through this challenging and rewarding process.

TABLE OF CONTENTS

ABSTRACT ii

ACKNOWLEDGEMENTS iv

LIST OF TABLES........ vii

LIST OF FIGURES........ viii

1 Introduction 1

References 5

2 Chapter 2 – The Persistence of Beaver-Induced Geomorphic Heterogeneity and Organic Carbon Stock in River Corridors 7

- 2.1 Introduction 8
- 2.2 Study Area........ 13
- 2.3 Methods........ 16
  - 2.3.1 Field Methods and Laboratory Analyses........ 16
  - 2.3.2 Statistical Methods........ 19
- 2.4 Results 22
  - 2.4.1 Surface geomorphic heterogeneity 22
  - 2.4.2 Subsurface geomorphic heterogeneity........ 25
  - 2.4.3 Total floodplain soil organic carbon stock 26
- 2.5 Discussion and Conclusions 30

References 36

3 Chapter 3 – Attenuation of Seasonal Peak Flows by Beaver Meadows in the Southern Rockies of Colorado........ 42

3.1 Introduction 43

3.2 Study Area 48

3.3 Methods 53

3.4 Results 57

3.5 Discussion and Conclusions 79

References 85

4 Conclusion 90

References 95

APPENDIX – Supplemental Figures 96

LIST OF TABLES

Table 2.1 Summary characteristics for the meadow study sites 17

Table 2.2 Floodplain geomorphic units 18

Table 2.3 Metrics of geomorphic heterogeneity 25

Table 2.4 Summary of multiple linear regression model results 28

Table 2.5 Estimated values of total organic (<1.5 m depth) carbon stock in the upper portion of the meadows 30

Table 3.1 Summary of characteristics for the meadow study locations 50

Table 3.2 Summary of coefficients for stage-discharge relationships 55

Table 3.3 Summary of multiple linear regression model results for three models 61

LIST OF FIGURES

Figure 2.1 Conceptual model of feedbacks of river corridor configurations in the presence and absence of beaver 11

Figure 2.2 Location map of the study meadows within Rocky Mountain National Park 14

Figure 2.3 Visual representation of surface geomorphic heterogeneity in relation to level of beaver activity 23

Figure 2.4 Surface geomorphic heterogeneity as indicated by the Graf (2006) metric 24

Figure 2.5 Mean core soil moisture %, soil core depth, and mean organic carbon concentration by core 27

Figure 2.6 Mean organic carbon stock, by core 29

Figure 2.7 Schematic illustration of differences in relative importance of controls on OC storage in beaver meadows versus elk grasslands 32

Figure 3.1 Conceptual diagram 49

Figure 3.2 Map of study area in the Southern Rockies of Colorado 51

Figure 3.3 Google Earth view of inlet and outlet sites at North St. Vrain Creek 54

Figure 3.4 Boxplot of the difference in peak magnitude between the inflow and outflow .. 58

Figure 3.5 Boxplot of the baseflow enhancement 59

Figure 3.6 Boxplot of lag in recession curve 60

Figure 3.7a A selection of representative hydrographs for active meadows 63

Figure 3.7b A selection of representative hydrographs for partially active meadows 64

Figure 3.7c A selection of representative hydrographs for recently abandoned meadows 65

Figure 3.7d A selection of representative hydrographs for long abandoned meadows 66

Figure 3.8a Recession rate curves for active meadows 67

Figure 3.8b Recession rate curves for partially active meadows 69

Figure 3.8c Recession rate curves for recently abandoned meadows 70

Figure 3.8d Recession rate curves for long abandoned meadows 72

Figure 3.9a Hysteresis curves for active meadows 75

Figure 3.9b Hysteresis curves for partially active meadows 76

Figure 3.9c Hysteresis curves for recently abandoned meadows 77

Figure 3.9d Hysteresis curves for long abandoned meadows 78

Figure 3.10 Peak flow attenuation by the ratio of meadow area to drainage area 80

Figure S2.1 Median core soil moisture for 7 meadows 96

Figure S2.2 Core soil moisture by geomorphic unit 97

Figure S2.3 Soil core depth in relation to geomorphic unit 97

Figure S2.4 Soil core depth by meadow 98

Figure S2.5 Core OC concentration in relation to geomorphic unit 99

Figure S2.6 Core OC concentration in relation to meadow 100

Figure S2.7 Core OC stock in relation to geomorphic unit 101

Figure S2.8 Core OC stock in relation to meadow 102

Figure S2.9 Sample OC concentration by middle depth of each sample 103

Figure S3.1a Hydrographs for the remaining active meadows 104

Figure S3.1b Hydrographs for the remaining recently abandoned meadows 105

Figure S3.1c Hydrographs for the remaining long abandoned meadows 106

Figure S3.2 Baseflow augmentation plotted against the ratio of meadow area to drainage area 108

Figure S3.3 Recession curve lag plotted against the ratio of meadow area to drainage area 108

1 INTRODUCTION

Beaver (*Castor canadensis*) are engineers of their ecosystem (Rosell et al., 2005). Beavers can alter floodplain morphology through their construction activities, which include building dams across streams and digging ponds and escape channels. Their dams are capable of trapping sediment and nutrients, causing overbank flooding, raising the water table and altering riparian vegetation (Naiman et al., 1988; Pollock et al., 2003; Pollock et al., 2007; Westbrook et al., 2011; Polvi and Wohl, 2013;). Regular overbank flows on beaver-inhabited streams increase the deposition of fine sediment on the floodplain surface, fill floodplain ponds, and encourage the erosion and formation of secondary channels, which combined, create a geomorphically heterogeneous valley bottom meadow sometimes known as a beaver meadow (Morgan, 1868; Ruedemann and Schoonmaker, 1938; Ives, 1945) or beaver-meadow complex (Westbrook et al., 2011; Polvi and Wohl, 2012; Polvi and Wohl, 2013). Along with fine sediment, allochthonous particulate organic carbon can get deposited on the floodplain, or trapped behind dams and in ponds (Wohl, 2013). Beaver also encourage autochthonous carbon input to floodplains from the riparian vegetation such as willows that their engineering activities support. Beaver have likewise been shown to alter nitrogen and other nutrient dynamics in streams by affecting nitrogen retention time and storage, and affecting ecosystem productivity (Naiman and Melillo, 1984; Wegener et al., 2017). Naiman et al. (1988) describe the effect of beaver activity on stream ecosystems as a hierarchical process where beaver-induced changes to the hydrology in turn alter the morphology, then the sediment, followed by the nutrients, riparian vegetation, habitat and ultimately the species composition of ecosystems they inhabit.

Numerous previous studies have investigated the effects of beaver moving into a new environment, or the effects on the hydrology, geomorphology, and riparian community structure of removing beaver dams (Pollock et al., 2003; Green and Westbrook, 2009; Wright, 2009). Most studies that have looked at changes to hydrology and morphology after beaver abandon or are removed from a meadow have focused on single dams or ponds where the dam in question was removed. These smaller scale studies indicate that over a period of years, spatially heterogeneous meadows simplify and channels convert from multi-thread planforms to single-thread, commonly incised streams (Green and Westbrook, 2009). There is a lack of studies that look more broadly at the effects of beaver on meadows across a region or that have attempted to quantify changes to meadow morphology, sediment, hydrology, and nutrients in cases where the dams and other beaver structures were not directly removed by humans, but instead degraded naturally over time. Quantifying the changing morphology, hydrology, sediment, and carbon dynamics after the disappearance of beaver has implications for understanding the drivers behind the changes, the timelines over which they occur, and for assessing the potential for using beaver for floodplain restoration (Wohl, 2013).

The Southern Rockies in Colorado provide an ideal region to examine the consequences through time of beaver abandonment, as there are currently active beaver meadows as well as abandoned meadows of varying ages throughout the region. The diverse study area allows for an investigation of other factors aside from beaver that might influence fluxes of water, sediment, and organic carbon out of mountain catchments, such as contributing area, elevation, valley morphology, and geologic history, and how these factors may interact with beaver activity to shape channel and floodplain form and function. The widespread study area also allows for an investigation into what meadows might be better candidates than others for using beaver as a restoration tool for a variety of floodplain restoration goals, including riparian vegetation recovery and carbon sequestration.

In this study, I have quantified the magnitude in changes to morphology, carbon, sediment, and water, and investigate patterns or trends in the changes through time. Based on previous research (Burns and McDonnell, 1998; John and Klein, 2004; Lautz et al., 2006; Westbrook et al., 2006; Hood and Bayley, 2008; Westbrook et al., 2011; Briggs et al., 2012; Kramer et al., 2012; Gibson and Olden, 2014), I hypothesized that beaver meadows would be associated with greater geomorphologic heterogeneity, and greater storage of sediment, organic carbon, and water. I developed conceptual models to illustrate how these functions might change nonlinearly through time and tested those models with detailed studies of morphology, sediment, and carbon in 7 meadows in chapter 1, and then in chapter 2 added an additional 12 meadows for a larger scale investigation of the effects of beaver activity on hydrologic attenuation. Attenuation refers to the capture of flow by the meadow at peak flow magnitude, and then the slow release of that captured water later in the season. These detailed studies help build a picture of the changes that occur in river and floodplain form and process through time, the timing of the changes, and whether the changes in floodplain morphology that can be visually observed have an effect on river and floodplain function in terms of storage or export of organic carbon, sediment, and water.

Each of the next two chapters is a self-contained document that includes a review of the relevant literature, description of study area and methods, and presentation and interpretation of results. These chapters are written to be stand-alone journal articles. All the original data collected and analyzed for the two chapters can be accessed from the Colorado State University Mountain Scholar data repository.

REFERENCES

Briggs, M.A., Lautz, L.K., McKenzie, J.M., Gordon, R.P. and Hare, D.K. 2012. Using High-Resolution Distributed Temperature Sensing to Quantify Spatial and Temporal Variability in Vertical Hyporheic Flux. *Water Resources Research* 48.

Burns, D.A. and McDonnell, J.J. 1998. Effects of a Beaver Pond on Runoff Processes: Comparison of Two Headwater Catchments. *Journal of Hydrology* 205(3-4): 248-264.

Gibson, P.P. and Olden, J.D. 2014. Ecology, Management, and Conservation Implications of North American Beaver (Castor Canadensis) in Dryland Streams. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24: 391-409.

Green, K.C. and Westbrook, C.J. 2009. Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams. *BC Journal of Ecosystems and Management* 10(1): 68-79.

Hood, G.A. and Bayley, S.E. 2008. Beaver (Castor Canadensis) Mitigate the Effects of Climate on the Area of Open Water in Boreal Wetlands in Western Canada. *Biological Conservation* 141(2): 556-567.

Ives, R.L. 1945. The Beaver-Meadow Complex. *Journal of Geomorphology* 5: 191- 203.

John, S. and Klein, A. 2004. Hydrogeomorphic Effects of Beaver Dams on Floodplain Morphology: Avulsion Processes and Sediment Fluxes in Upland Valley Floors, Spessart, Germany. *Quaternaire* 15: 219-231.

Kramer, N., Wohl, E.E. and Harry, D.L. 2012. Using Ground Penetrating Radar to 'Unearth' Buried Beaver Dams. *Geology* 40(1): 43-46.

Lautz, L.K., Siegel, D.I. and Bauer, R.L. 2006. Impact of Debris Dams on Hyporheic Interaction Along a Semi-Arid Stream. *Hydrological Processes* 20(1): 183-196.

Morgan, L.H. 1868. *The American Beaver and His Works*. Philadelphia: J.B. Lippincott and Co.

Naiman, R.J. and Melillo, J.M. 1984. Nitrogen budget of a subarctic stream altered by beaver. *Oecologia* 62: 150-155.

Naiman, R.J., Johnston, C.A. and Kelley, J.C. 1988. Alteration of North American streams by beaver. *BioScience* 38: 753-762.

Pollock, M.M., Heim, M. and Werner, D. 2003. Hydrologic and geomorphic effects of beaver dams and their influence on fishes. In *Ecology And Management Of Wood In World Rivers*. American Fisheries Society: Bethesda; 213–233.

Pollock, M.M., Beechie, T.J. and Jordan, C.E. 2007. Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. *Earth Surface Processes and Landforms* 32: 1174-1185.

Polvi, L.E. and Wohl, E. 2012. The beaver meadow complex revisited – the role of beavers in post-glacial floodplain development. *Earth Surface Processes and Landforms* 37: 332-346.

Polvi, L.E. and Wohl, E. 2013. Biotic drivers of stream planform: Implications for understanding the past and restoring the future. *BioScience* 63: 439-452.

Rosell, F., Bozsér, O., Collen, P. and Parker, H. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* 35: 248–276

Ruedemann, R. and Schoonmaker, W.J. 1938. Beaver-Dams as Geologic Agents. *Science* 88: 523-535.

Westbrook, C.J., Cooper, D.J. and Baker, B.W. 2011. Beaver assisted river valley formation. *River Research and Applications* 27: 247-256.

Westbrook, C.J., Cooper, D.J. and Baker, B.W. 2006. Beaver Dams and Overbank Floods Influence Groundwater-Surface Water Interactions of a Rocky Mountain Riparian Area*.* *Water Resources Research* 42(6).

Wohl, E. 2013. Landscape-scale carbon storage associated with beaver dams. *Geophysical Research Letters* 40: 1-6.

Wright, J.P. 2009. Linking populations to landscapes: richness scenarios resulting from changes in the dynamics of an ecosystem engineer. *Ecology* 90(12): 3418-3429.

2 CHAPTER 2

THE PERSISTENCE OF BEAVER-INDUCED GEOMORPHIC HETEROGENEITY AND ORGANIC CARBON STOCK IN RIVER CORRIDORS

Chapter Summary

Beavers are widely recognized as ecosystem engineers for their ability to shape river corridors by building dams, digging small canals, and altering riparian vegetation. Through these activities, beavers create beaver meadows, which are segments of river corridor characterized by high geomorphic heterogeneity, attenuation of downstream fluxes, and biodiversity. We examine 7 beaver meadows on the eastern side of Rocky Mountain National Park, Colorado, USA with differing levels of beaver activity. We divide these sites into the four categories of active, partially active, recently abandoned (< 20 years), and long abandoned (> 30 years). We characterize geomorphic units within the river corridor and calculate metrics of surface geomorphic heterogeneity relative to category of beaver activity. We also use measures of subsurface geomorphic heterogeneity (soil moisture, soil depth, % clay content, organic carbon concentration) to compare heterogeneity across beaver meadow categories. Finally, we calculate organic carbon stock within the upper 1.5 m of each meadow and compare these values to category of beaver activity. We find that surface geomorphic heterogeneity and mean soil moisture differ significantly only between active and long abandoned meadows, suggesting a nonlinear decrease with time following beaver abandonment of a meadow. Soil depth and organic carbon stock do not differ consistently in relation to category of beaver meadow, suggesting that larger-scale geologic controls that foster deep floodplain soils can continue to maintain substantial organic

carbon stocks after beavers abandon a meadow. These results also indicate that the effects of beaver ecosystem engineering can persist for nearly three decades after the animals largely abandon a river corridor.

2.1 Introduction

Beavers – *Castor canadensis* in North America and *Castor fiber* in Eurasia – are commonly referred to as an ecosystem engineer because of their ability to shape the physical environment and associated hydrologic, geomorphic, biogeochemical, and ecological processes of river corridors (Ruedemann and Schoonmaker, 1938; Guegan et al., 1998; Beisel et al., 2000; Wright et al., 2002; Rosell et al., 2005; Wright, 2009). River corridors include the channel(s), floodplain and riparian zone, and underlying hyporheic zone (Harvey and Gooseff, 2015). Where beavers have modified the channel(s) and floodplain over a period of years to decades, a spatial mosaic of active and abandoned dams and ponds and secondary channels known as a beaver meadow (Polvi and Wohl, 2012) develops. Here, we examine correlations between beaver activity, geomorphic heterogeneity, and organic carbon storage in river corridors of the Southern Rocky Mountains. We define surface geomorphic heterogeneity as the spatial diversity of geomorphic units characterized via morphology, elevation, and vegetation. We define subsurface geomorphic heterogeneity as the spatial diversity of soil moisture, depth, % clay, and organic carbon concentration. Examining correlations between beaver activity and river corridor form and function is important to understanding how river corridors have changed during the past few centuries as human activities have significantly reduced beaver population densities throughout the northern hemisphere.

Beavers engage in three primary activities that influence geomorphic heterogeneity and retention of water, sediment, and organic matter in flux along river corridors: building dams, digging narrow canals to facilitate their movements, and altering riparian vegetation via herbivory. Beaver dams can cross a main channel, secondary channels, floodplain channels, tributaries, or valley-side seeps and springs (Olson and Hubert, 1994; Johnston, 2012). Dams create areas of ponded water and enhance lateral connectivity between the channel and floodplain by increasing overbank flow (Westbrook et al., 2006; Wegener et al., 2017). Increased water surface area and higher riparian water table can also increase the resilience of the river corridor to disturbances including flood, drought, and wildfire (Hood and Bayley, 2008). By creating pressure gradients within the flow, dams increase vertical connectivity between the channel and hyporheic zone (Lautz et al., 2006; Westbrook et al., 2013). Dams can also attenuate downstream fluxes of water, sediment, solutes, and particulate organic matter (Naiman et al., 1986, 1994; Butler and Malanson, 1995; Correll et al., 2000; Wegener et al., 2017). Canals dug by beaver can enlarge to become secondary channels and contribute to the formation of an anastomosing channel planform, which is commonly present where multiple beaver dams exist (John and Klein, 2004; Polvi and Wohl, 2012, 2013). Distribution of water among multiple channels reduces flow energy and enhances attenuation of flood peaks and retention of dissolved and particulate material. Finally, beavers herbivory can alter floodplain vegetation by favoring woody plants such as willows (*Salix* spp.) (Baker et al., 2005; Veraart et al., 2006). By facilitating the persistence of densely growing deciduous woody species in floodplains, beavers indirectly increase the hydraulic resistance of the floodplain by increasing overbank roughness and cohesion of floodplain sediment (Baker et al., 2005).

In summary, the net effects of beaver activities are to make river corridors more geomorphically heterogeneous (Gurnell, 1998; Westbrook et al., 2011; Polvi and Wohl, 2012; Westbrook et al., 2013). Geomorphic heterogeneity in turn correlates with greater retention of materials in flux (e.g., Wohl et al., 2012; Johnston, 2014; Wegener et al., 2017); greater lateral (channel-floodplain) (Westbrook et al., 2006) and vertical (channel-hyporheic) connectivity (Lautz et al., 2006); and greater resilience to natural and human disturbance (Hood and Bayley, 2008). This understanding is critical in the context of the massive historical declines in beaver populations and associated metamorphoses of river corridors (Naiman et al., 1988; Polvi and Wohl, 2013).

In regions such as some U.S. national parks, beavers were once actively trapped, then subsequently protected, but are still declining because of competition from native ungulates and removal of ungulate-predators such as wolves (Ripple and Beschta, 2003; Wolf et al., 2007; Beschta and Ripple, 2012). Loss of beavers and beaver dams commonly results in concentration of surface flow in a single channel, which is likely to incise. Overgrazing of deciduous woody species, abandonment of secondary channels, and incision of the main channel can lower the alluvial aquifer, transforming the river corridor into a so-called elk grassland (Peinetti et al., 2002; Wolf et al., 2007). An elk grassland is drier, less geomorphically heterogeneous, less retentive, and less resilient than a beaver meadow. We focus on Rocky Mountain National Park in Colorado, USA, where the scenario described above has changed most of the former beaver meadows to elk grasslands.

Figure 2.1 illustrates the conceptual model underlying our work. The alternative states of an active beaver meadow (upper feedback loop) and a long abandoned beaver meadow, also known as an elk grassland (lower feedback loop), exhibit substantial

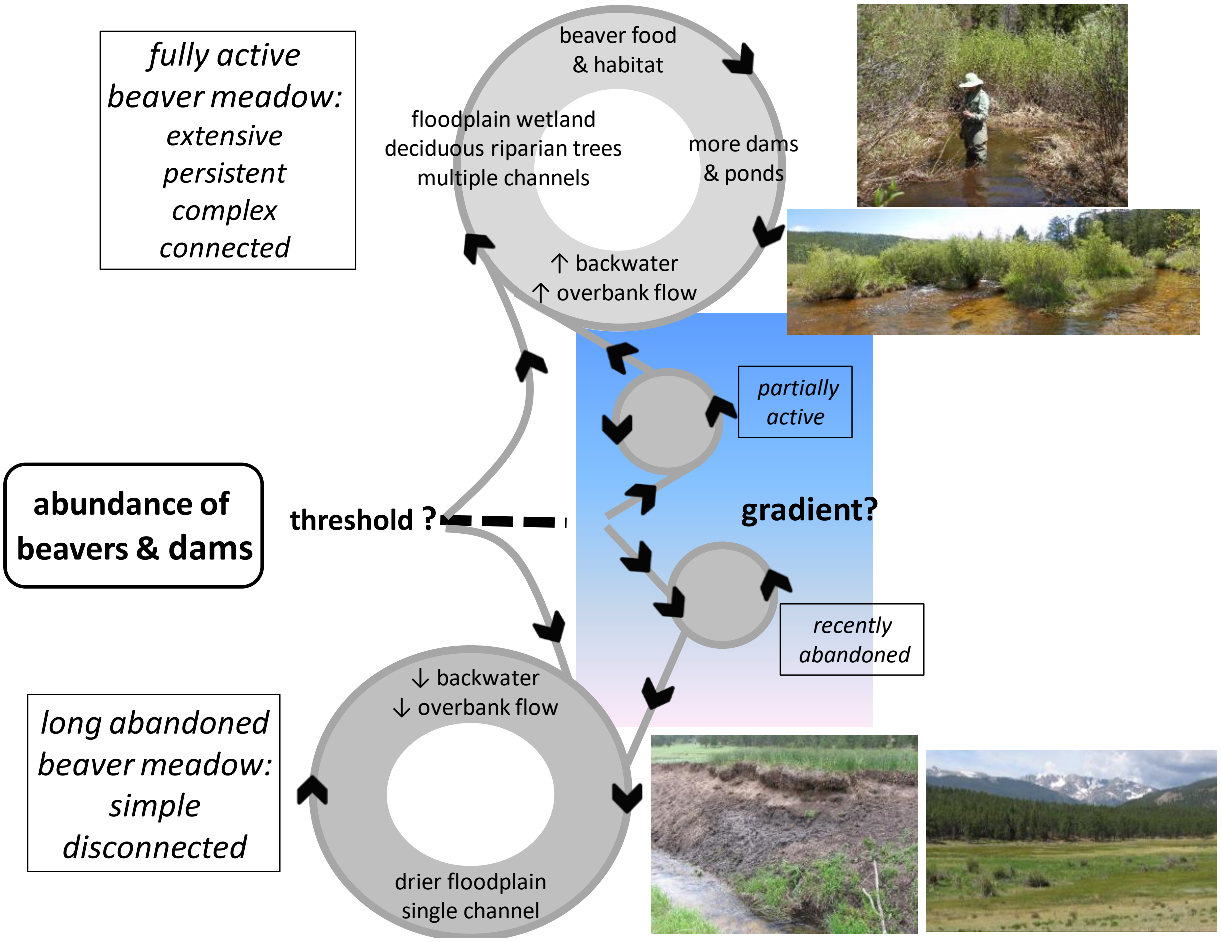


Figure 2.1. Conceptual model of feedbacks that maintain different configurations of a river corridor in the presence and absence of beaver.

differences in surface geomorphic heterogeneity. In this paper, we examine whether these two end-members are separated by an abrupt threshold, such that a beaver meadow rapidly becomes an elk grassland following beaver abandonment and the presence of beavers rapidly creates a beaver meadow. Alternatively, sites with differing levels of beaver activity and time since beaver abandonment could form a gradient with transitional levels of geomorphic heterogeneity, as indicated by the smaller feedback loops between the end-members. We focus on how beaver-induced geomorphic heterogeneity and retention of organic carbon decrease with time once beaver activity declines or ceases at a site.

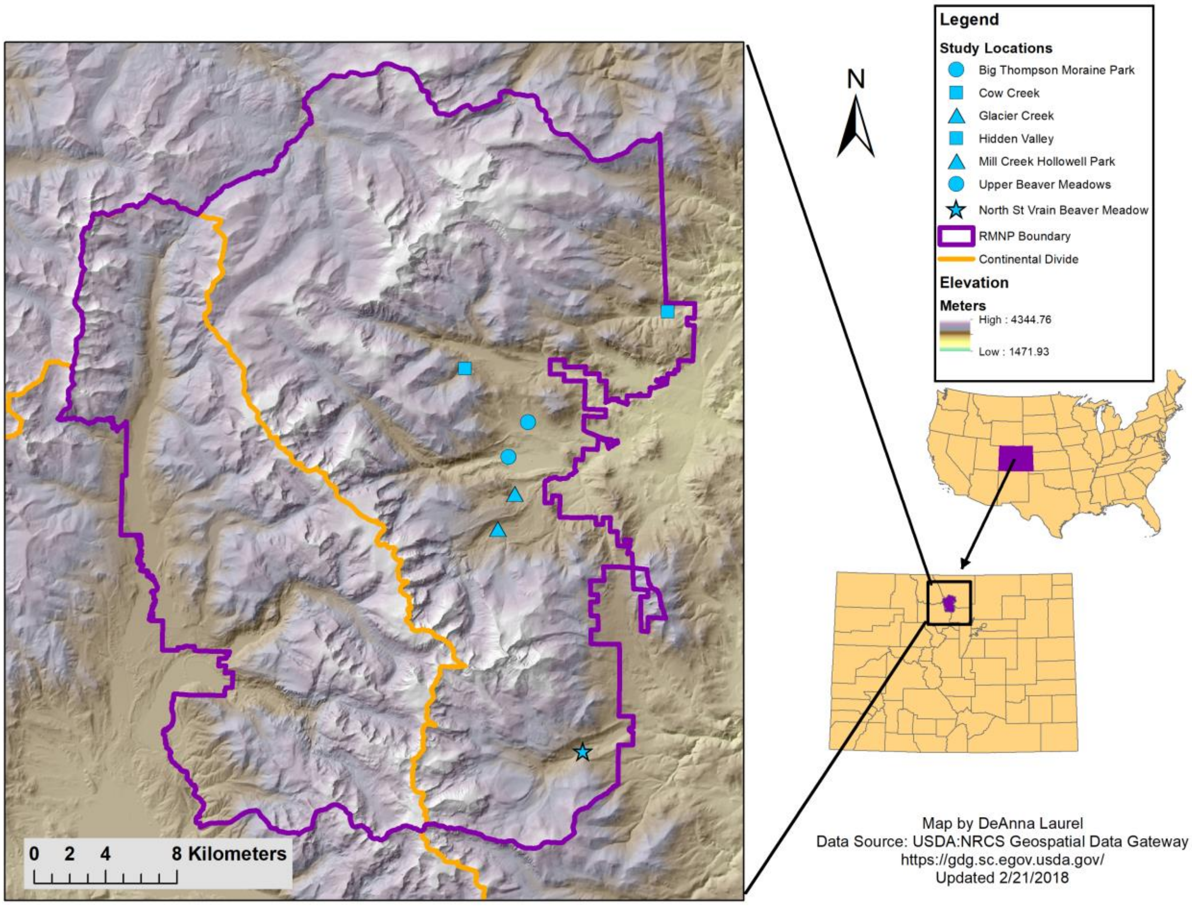
We hypothesize that geomorphic heterogeneity decreases nonlinearly with time since beaver abandonment (*H1*). Although observations from various river corridors clearly suggest loss of geomorphic heterogeneity following beaver abandonment (e.g. Green and Westbrook, 2009), we are not aware of any quantitative analyses of the relative rates at which these changes occur through time. We hypothesize a nonlinear decrease with time because observations suggest that willows and secondary channels disappear within two to three decades of beaver abandonment, but the meadow then appears to undergo little additional change.

We also hypothesize that organic carbon stock within floodplain soil declines nonlinearly with time following beaver abandonment of a river corridor, specifically, we hypothesize an initial decline and then relative stability (*H2*). We posit that the floodplain soils continue to store substantial quantities of organic carbon, although these may be lower than stocks in active beaver meadows (Wohl, 2013). This hypothesis is based on observations that channel-floodplain connectivity is reduced as beaver abandon a site. This results in a declining riparian water table, so that floodplain soils are less likely to be saturated and maintain the reducing conditions that favor high organic carbon concentrations (Trumbore and Czimczik, 2008). As riparian woody vegetation is replaced by herbaceous vegetation and grasses characteristic of shortgrass prairie, primary productivity and litterfall carbon inputs to the floodplain soil likely decline (Buell and Markewich, 2004). Peak flows are less likely to overtop the channel banks and add fluvially transported organic matter to the floodplain soil. All of these changes likely result in lower soil organic carbon concentrations in abandoned beaver meadows, but if these changes occur within one to two decades following beaver abandonment and the valley bottom then becomes relatively stable (i.e., incised channel with minimal lateral migration), we expect floodplain soil carbon stocks to initially decline and then remain stable with time.

2.2 Study Area

We collected data in 7 valley bottom meadows within Rocky Mountain National Park (RMNP) in north-central Colorado (Figure 2.2). RMNP is underlain by Precambrian crystalline rocks composed of granite, granodiorite, schist, and gneiss (Braddock and Cole, 1990), which produce sediment that is very low in $CaCO_3$ (Sutfin and Wohl, 2017). The eastern side of the park, where the meadows are located, is characterized by the high peaks of the continental divide, from which eastward-flowing streams descend along steep, narrow canyons that periodically open into wide, flat valley bottoms. The steep-sided valley walls and wide, flat valley bottoms are the result of the advance and retreat of alpine glaciers during the Pleistocene epoch (Anderson et al., 2006). The last glacial advance in the Rocky Mountain region, the Pinedale glaciation, extended down to ~ 2430 m and left a substantial terminal moraine that facilitated deposition of glacial outwash and formation of wide, flat valley segments that provide ideal habitat for beaver (Polvi and Wohl, 2012). The active and abandoned beaver meadows included in this study area are located above 2430 m, although Beaver and Cow Creeks did not have Pleistocene valley glaciers. In these unglaciated valleys, spatial variation in bedrock jointing causes longitudinal variation in valley geometry (Ehlen and Wohl, 2002; Wohl et al., 2017), but the beaver meadow sites are narrower than those in the glaciated valleys.

The mean annual precipitation for the eastern half of RMNP is between 30 and 80 cm, with the majority of the precipitation falling as snow, leading to a snowmelt-dominated



Map by DeAnna Laurel
Data Source: USDA:NRCS Geospatial Data Gateway
https://gdg.sc.egov.usda.gov/
Updated 2/21/2018

Figure 2.2. Location map of study meadows within Rocky Mountain National Park, Colorado, USA. The meadows are all east of the Continental Divide. Circles indicate long abandoned meadows, squares indicate recently abandoned meadows, triangles indicate partially active meadows and the star indicates the fully active meadow.

hydrograph for streams with headwaters in the park. These mountain streams seasonally flood during May or June at or exceeding bankfull stage in most years during the spring hydrograph snowmelt peak (Wohl et al., 2004). Upland forests in the subalpine and montane zones in which our study meadows lie are dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*) interspersed with aspen

(*Populus tremuloides*) (Veblen and Donnegan, 2005). The valley bottoms contain a combination of meadow and riparian species such as grasses and sedges (*Carex* spp.), blue spruce (*Picea pungens*), river birch (*Betula fontinalis*), and willow (*Salix* spp.). The valley bottom species composition is highly related to beaver activity, with increased density of willow and wetland riparian species occurring in valley bottoms that display beaver influence in the channel and floodplain morphology (Polvi et al., 2011).

Wolves were hunted to extinction in Rocky Mountain National Park during the 1920s and the numbers of elk and moose within the national park rose steadily during the 20th century (Hess, 1993; Andrews, 2015). Although numerous active beaver colonies were present along several drainages of the park during the 1950s, by the start of the 21st century only a single spatially extensive, active beaver meadow remained. This site along North St. Vrain Creek at the southeastern boundary of the national park is our reference site for understanding the form and function of other beaver meadows within the national park. We compare measures of surface and subsurface geomorphic heterogeneity (form) and organic carbon storage (function) among four categories of beaver meadows on the eastern side of Rocky Mountain National Park: active, partially active, recently abandoned, and long abandoned. Of our 7 study sites on the eastern side of the national park, North St. Vrain (NSV) is the active meadow, with at least three active beaver colonies currently present at the site and beaver dams spread across the entire valley bottom. Hollowell Park (Mill Creek) and Glacier Creeks are the partially active meadows. Each has limited beaver activity present along the main channel and laterally across the valley bottom, but no beaver activity that is longitudinally and laterally continuous along the entire valley bottom. Glacier Creek has relict beaver structures throughout the meadow; Hollowell Park appears relatively unaffected by beaver presence outside of the limited area of current beaver activity. Cow Creek and Hidden Valley are the recently abandoned sites. Cow Creek had beavers present up until the 2013 flood that affected the Front Range of Colorado. This flood removed the dams along Cow Creek and beavers were still absent from this meadow during the data collection for this project in 2015 and 2016, although they have recently started to re-colonize the valley. Hidden Valley definitively had beavers as recently as the late 1990s, and likely more recently than that. Although the beavers have been gone from this meadow for at least 10 years, there remain many intact dams off the main channel, as well as secondary channels, beaver runs, and a seasonally inundated and infilling pond. Moraine Park (Big Thompson River) and Upper Beaver Meadows (Beaver Brook) are the long abandoned sites. Although beavers were present at these sites into the 1970s, no dams remain on the channels and the valley bottom is largely grassland with a single, incised channel. Although there are no visible remnants of the beaver morphology on the stream or the floodplain, buried dams and ponded sediments are present beneath the surface (Kramer et al., 2012). Upper Beaver Meadows is included in the geomorphic heterogeneity analysis, but not the organic carbon (OC) analysis. Table 2.1 summarizes meadow characteristics, including estimates of the time of abandonment.

2.3 Methods

2.3.1 Field Methods and Laboratory Analyses

Fieldwork was conducted in the summers of 2015 and 2016. Geomorphic surveying involved walking transects perpendicular to the stream within each meadow, taking GPS coordinates in the center of each geomorphic unit along a transect, and measuring the

Table 2.1. Summary characteristics for the meadow study sites.

Meadow	Drainage Area (km^2)	Meadow Area (km^2)	Beaver Activity Level	Length Abandoned
NSV	89	0.42	Active	na
Glacier Creek	36.7	0.02	Partially Active	na
Hollowell Park	14.7	0.19	Partially Active	na
Hidden Valley	9.3	0.04	Recently Abandoned	< 20 yrs
Cow Creek	20.2	0.08	Recently Abandoned	5 yrs
Moraine Park	110	2.57	Long Abandoned	> 30 yrs
Upper Beaver Meadows	15	0.45	Long Abandoned	> 30 yrs

distance along the transect belonging to each geomorphic unit. Table 2.2 lists floodplain geomorphic units, which were distinguished by morphology, relative elevation above the main channel, and the vegetation community.

Sediment depth within geomorphic units was measured by pounding rebar into the ground until refusal by bedrock or cobble, or up to 1.5 m, the maximum length of the rebar probe. At each of 4 meadows (Hollowell Park, Hidden Valley, Cow Creek, Glacier Creek), 11 soil cores were collected for organic carbon analyses based on the sample size necessary to accurately estimate floodplain soil organic carbon storage in Front Range mountain streams (Sutfin and Wohl, 2017). Larger numbers of soil cores were collected at North St. Vrain (23 cores) and Moraine Park (19 cores) because these sites represent end-members in the continuum of beaver activity between the study locations. Soil samples were collected along transects perpendicular to the main channel, with attention paid to

Table 2.2. Floodplain geomorphic units.

Geomorphic unit	Description
Main channel	Primary active channel; perennial flow
Secondary channel	Secondary channels, with either perennial or ephemeral flow
Connected ponds	ponds frequently connected by surface flow to the main channel
Disconnected ponds	ponds without frequent connection to the main channel; secondary channels
Wetlands	wetlands where the ground was saturated to the surface even during the driest part of the year
Seasonally inundated	seasonally inundated higher floodplain surfaces that were saturated in the spring and early summer but dried later in the summer; common vegetation includes willows (Salix spp.), river birch (*Betula fontinalis*), grasses and sedges
Infrequently inundated	higher and drier floodplain surface that is rarely inundated; vegetation includes xeric, upland plant species such as juniper (*Juniperus scopulorum*) and conifers (*Pinus* spp.)

distributing samples among the different geomorphic units. At a sample location, ground vegetation was scraped clear to the surface of the mineral soil and samples were collected in 18 cm increments using a soil corer. Soils were sampled to the maximum corer depth (114 cm) or until the corer met with refusal. Refusal was primarily the result of encountering a gravel layer too coarse to sample or encountering a larger clast or buried piece of wood. A small number of samples from ponds were limited in collection depth because the soil was too saturated to be extracted with the soil corer. Soil moisture samples from all sites were collected over a 2-week period during base flow with no rainfall.

Samples were oven-dried for 24 hours at 105°C and soil moisture was calculated as the percent mass lost divided by the initial wet mass. The oven-dried mass of each sample, along with the volume of sediment collected in the soil corer, were used to calculate a bulk density for each sample. We assigned a texture class to the mineral soil in each sample following the USDA Natural Resources Conservation Service guidelines for hand texturing (NRCS, 1996).

Organic carbon concentration of the soil samples was measured at the Soil, Water, and Plant testing lab at Colorado State University. Samples were sieved to separate the < 2mm fraction, then the total carbon concentration (%) of the < 2 mm fraction was measured using a LECO TruSpec CN furnace (Nelson and Sommers, 1982). Inorganic carbon was measured by treating the sample with 0.4 HCl and measuring the CO_2 loss gravimetrically (NRCS, 1996). Subtracting the inorganic carbon from the total carbon concentration provided the OC concentration (%).

These field and laboratory data were used to quantify response variables that we related to the control variable, level of beaver activity. Response variables evaluated here are surface geomorphic heterogeneity, subsurface geomorphic heterogeneity (sediment depth, soil moisture, % clay content, organic carbon concentration), and total soil organic carbon stock of each meadow.

2.3.2. Statistical Methods

Surface geomorphic heterogeneity was quantified using several different metrics. First, we calculated the number of distinct geomorphic units per kilometer of valley width from the floodplain transect surveys, as a measure of spatial heterogeneity derived from

Graf (2006). These values were compared across the 7 study meadows using ANOVA and compared to each other with pairwise comparisons with a Tukey adjustment for multiple comparisons. Analyses were run in the statistical software R. We also characterized the meadow surface heterogeneity utilizing diversity metrics commonly used by ecologists that include how many different types of features (here, geomorphic units) are present in a beaver meadow, which is richness, and how evenly these features are distributed within the meadow (i.e., how many of each feature are present), which is evenness. We used the Shannon Diversity Index and Shannon Equitability, and the Simpson's Index of Diversity.

$$\text{Shannon Diversity Index} \quad H = -\sum_{i=1}^{S} p_i(\ln(p_i)) \tag{1}$$

$$\text{Shannon Equitability} \quad E_H = {}^{H}\!/_{\ln S} \tag{2}$$

$$\text{Simpson's Diversity Index} \quad D = 1 - \left(\frac{\sum n(n-1}{N(N-1}\right) \tag{3}$$

where n is number of individuals in each species (e.g., number of ponds within the geomorphic unit pond), N is the total number of individuals (i.e., total number of geomorphic units measured), p_i is the proportion n/N, and S is the number of species (i.e., number of types of geomorphic units), or the richness. Both the Shannon Diversity Index and the Simpson's Index combine the richness and the evenness of species into one value in order to make comparisons between sites. The Shannon Diversity Index places greater weight on the richness of features, whereas the Simpson Diversity Index prioritizes relative abundance of the different features in the calculation. Higher values of the Shannon and

Simpson's Diversity metrics indicate greater diversity, or in this case, greater geomorphic heterogeneity. The Shannon Equitability index is simply H divided by H_{max} (here, $ln\ S$), and assumes a value between 0 and 1, with 1 being complete evenness. Finally, we graphically displayed the proportion of surveyed meadow that falls into each geomorphic unit category with pie charts in order to visually compare the heterogeneity in these environments.

We characterized subsurface geomorphic heterogeneity for six of the meadows (Upper Beaver Meadows not included) based on four metrics: soil moisture, soil depth, % clay content (derived from hand texturing), and organic carbon concentration (% OC). We assessed soil moisture and % clay content because of their potential influence on plant growth and soil organic carbon content. We assessed soil depth and carbon concentration because of their influence on carbon stock. Comparisons of soil moisture, soil depth, % clay, % OC, and OC stock (Mg OC/ha) were made across geomorphic units, across study meadows, and across levels of beaver activity using the nonparametric Kruskal-Wallis test with a Bonferroni adjustment for multiple comparisons to assess whether beaver activity and the resulting geomorphic heterogeneity led to significantly different soil moisture, soil depth, % clay, or organic carbon content (% or stock).

A linear regression model was fit to the % OC and stock OC data to investigate correlations between predictor variables and OC content. Initially, a linear mixed effects model was chosen to account for potential random effects associated with the sampling design (along transects), but a comparison of models found that including a random effect was not necessary, so a simple multiple linear regression model was used instead. The predictor variables investigated included geomorphic unit, depth of sample (the middle value of each sample for % OC and the total core depth for OC stock), soil moisture, % clay content, drainage area, and geomorphic heterogeneity calculated as the number of distinct geomorphologic units per kilometer of valley width. OC content was modeled as the %OC in each sample, and as the OC stock aggregated over each core. The residuals of each model were checked to verify that the model assumptions were being met, including verifying the homoscedasticity of variance. In order to meet the model assumptions, the response variables were transformed: % OC was square root transformed and OC stock was natural log transformed. The significance of each predictor variable in the model was tested at alpha = 0.05 to determine which predictor variables have explanatory power, and hence influence the variability in OC concentration or stock. The linear regression models were run in R, utilizing the lm() function.

2.4 Results

2.4.1 Surface geomorphic heterogeneity

We characterized surface heterogeneity using the 7 geomorphic units described in the methods (Table 2.2). Simple visual comparison of the proportion of surface area in each geomorphic unit indicates that the long abandoned meadows (Upper Beaver Meadows and Moraine Park) have lower diversity of geomorphic units and less surface water than the active meadow (North St. Vrain) (Figure 2.3). The partially active meadows and recently abandoned meadows lie along a continuum between these end-members. Using the geomorphic heterogeneity metric derived from Graf (2006), the long abandoned meadow at Moraine Park differs significantly from all of the other sites (Figure 2.4). (The long abandoned meadow UBM does not differ significantly from recently abandoned sites.) All three ecological metrics of diversity, applied here to surface geomorphic heterogeneity,

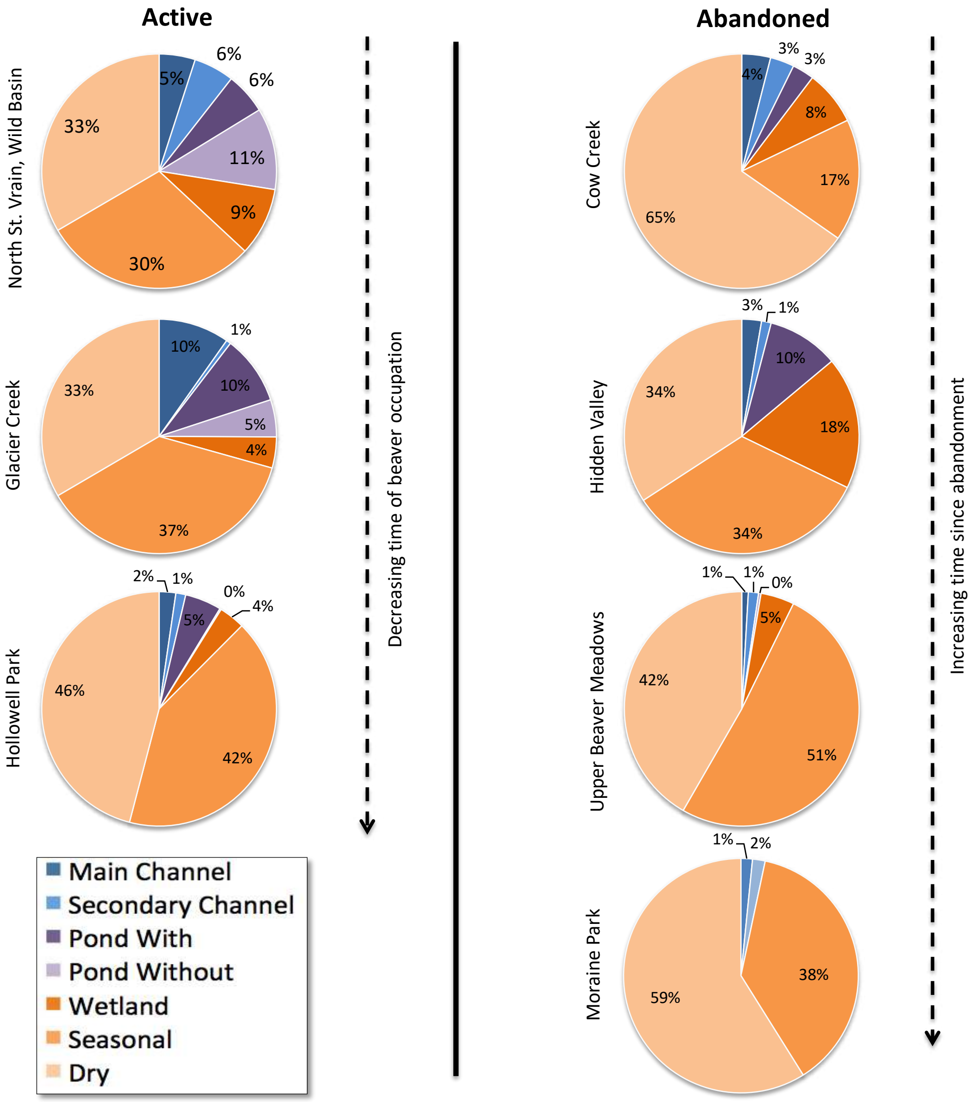


Figure 2.3. Visual representation of surface geomorphic heterogeneity in relation to level of beaver activity within a meadow. Total percent surface water is the sum of the percent channel and pond features for each meadow.

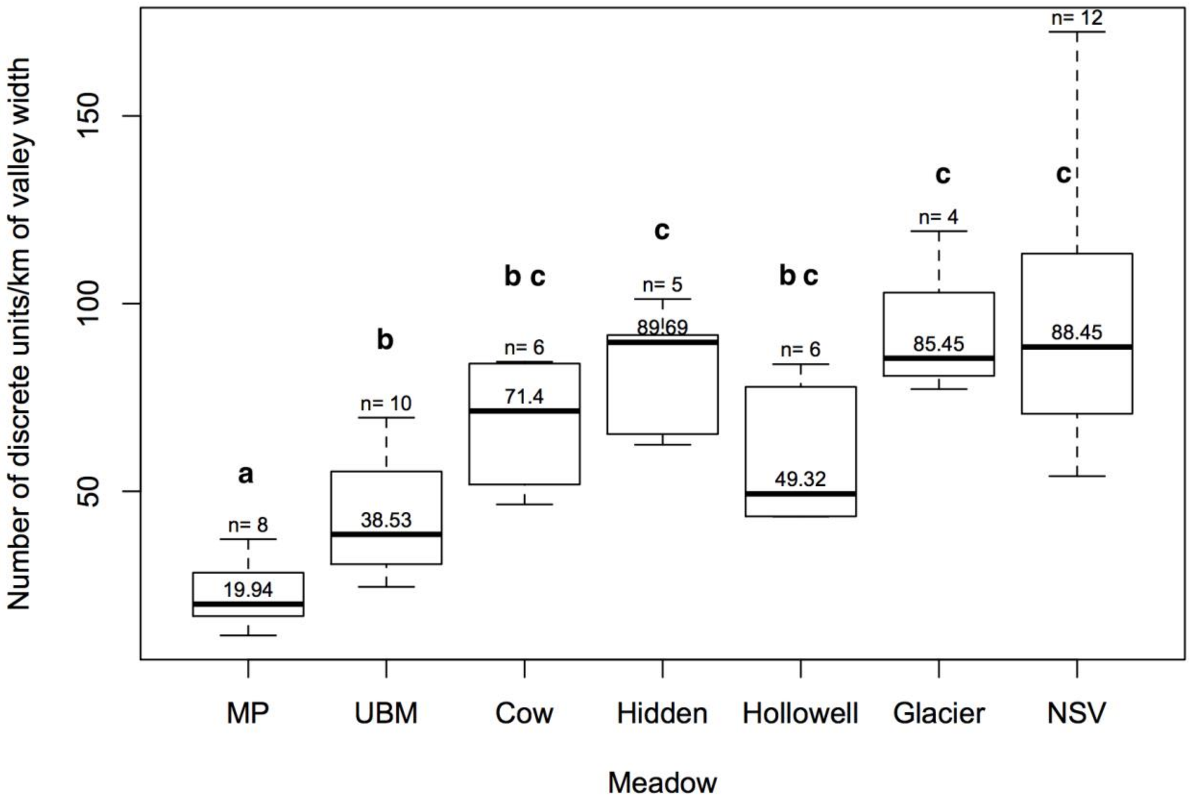


Figure 2.4. Surface geomorphic heterogeneity as indicated by the metric derived from Graf (2006) in relation to individual beaver meadows. Letters indicate significant differences between median values. Median value and sample size indicated for each meadow. In total, 51 transects were sampled.

indicate the highest heterogeneity in the active meadows. Heterogeneity decreases to the lowest level in the abandoned meadows with the exception of Hidden Valley, which has heterogeneity comparable to the active meadows (Table 2.3). Simpson's and Shannon's diversity indices are notably lower for the abandoned beaver meadows. Shannon's Equitability indicates greater evenness between geomorphic units in the active meadows than the abandoned meadows. Evenness also decreases with time since meadow abandonment (Table 2.3).

Table 2.3. Metrics of geomorphic heterogeneity.

Meadow	Average number of units per kilometer of valley width	Simpson's Index of Diversity (D)	Shannon Diversity Index	Shannon's Equitability (E_H)
NSV	95.268	0.779	1.639	0.915
Glacier Creek	91.856	0.742	1.495	0.835
Hollowell Park	57.821	0.713	1.448	0.808
Hidden Valley	82.037	0.765	1.535	0.857
Cow Creek	68.275	0.670	1.284	0.717
Upper Beaver Meadows	42.769	0.547	0.991	0.715
Moraine Park	22.359	0.475	0.816	0.589

These analyses support *H1.* Most indicators suggest that the geomorphic heterogeneity of the active beaver meadow mostly does not differ significantly from partially active and recently abandoned meadows (active NSV does differ significantly from partially active Hollowell). This suggests a nonlinear decrease in surface geomorphic heterogeneity with time since beaver abandonment.

2.4.2 Subsurface geomorphic heterogeneity

We examined soil moisture at the level of individual samples (vertical increments within a core) and the entire core. Soil moisture differs significantly at all scales considered. We focus on results at the core level because the trends and significance were the same for the sample level data. Mean core soil moisture differs significantly in the active meadow (NSV) and the long abandoned meadow (MP), but other meadows are gradational between these end-members (Figure 2.5, Figure S2.1). Mean core soil moisture shows few significant differences among geomorphic units (Figure S2.2).

Soil core depth does not differ significantly among geomorphic units (Figure S2.3), but does differ significantly among meadows (Figure S2.4). Soil core depth of partially active and recently abandoned meadows differs significantly from that of active and long abandoned meadows, which are similar to one another (Figure 2.5). Clay content does not differ significantly geomorphic units, with respect to level of beaver activity, or among sites.

Organic carbon concentration does not differ significantly between geomorphic units (Figure S2.5) but does differ significantly among meadows (Figure S2.6). Most importantly in the context of our hypotheses, organic carbon concentration does not differ significantly between meadow categories (Figure 2.5).

Thus, with respect to subsurface spatial heterogeneity, only soil moisture appears to decrease nonlinearly with time since beaver abandonment (*H1*).

We also modeled OC concentration at the level of individual samples (Table 2.4). Using a multiple linear regression model, geomorphic unit, soil moisture, clay content, depth, drainage area, and geomorphic surface heterogeneity are all significant predictor variables (Table 2.4).

2.4.3 Total floodplain soil organic carbon stock

Organic carbon stock does not differ significantly among geomorphic units (Figure S2.7). Organic carbon stock does differ significantly among meadows, although not in a

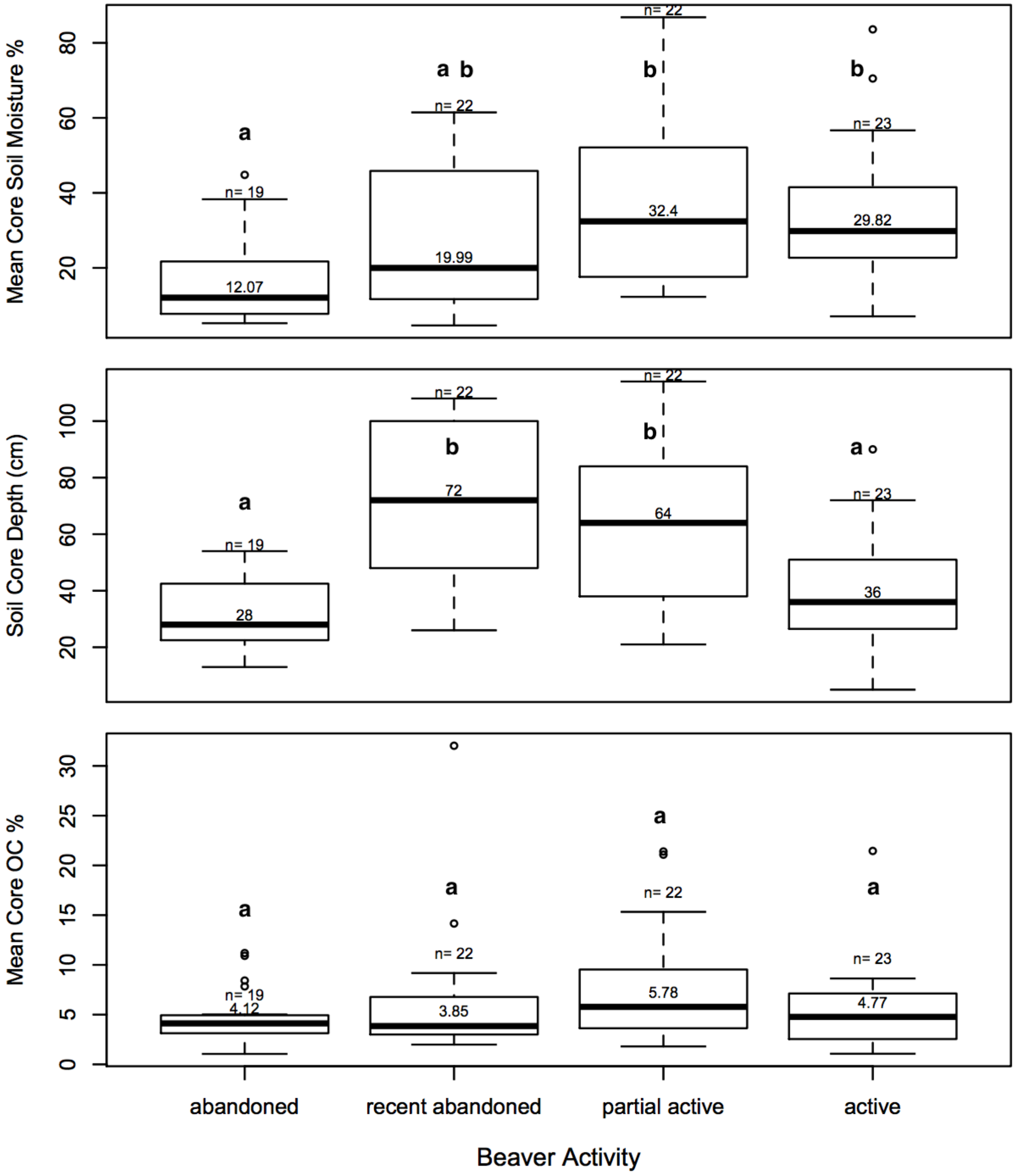


Figure 2.5. Mean core soil moisture %, soil core depth, and mean organic carbon concentration by core, in relation to beaver meadow categories. Letters indicate significance differences between mean values (comparisons made using nonparametric Kruskal-Wallis test with Bonferroni adjustment for multiple comparisons at the 0.05 significance level). Median value and sample size indicated for each meadow category.

Table 2.4. Summary of multiple linear regression model results for modeling OC (%) at the sample level, and OC Stock (MgC/ha) at the soil core level. Bolded values are significant at alpha = 0.05.

	OC (%)	OC stock (Mg C/ha)
Geomorphic unit	**<0.0001 (6.97)**[4]	**0.046 (2.50)**
Soil moisture[1] (%)	**<0.0001 (112.6) [0.0319]**[5]	0.671 (0.182) [-0.0026]
Clay content[3] (%)	**<0.0001 (114.6) [0.0201]**	**<0.001 (16.4) [0.0166]**
Depth[2] (cm)	**0.0015 (10.3) [-0.0109]**	**<0.0001 (121.0) [0.0215]**
Drainage area (km^2)	**0.0056 (7.80) [-0.00531]**	0.363 (0.839) [-0.00253]
Geomorphic surface heterogeneity	**<0.0001 (16.83) [-0.0099]**	**0.011 (6.71) [-0.00668]**

1. averaged over the core for the OC stock model
2. For the OC (%) model, the depth is the middle depth (cm) of the sample increment; for OC stock, it is the total depth of the soil core (cm).
3. averaged over the core for the OC stock model
4. *p* value (*F* statistic)
5. [coefficient β; effect of a unit increase of the predictor on the response]

manner that clearly relates to level of beaver activity (Figure S2.8). Similarly, the differences in organic carbon stock in relation to meadow category do not show a linear or nonlinear decrease with time (Figure 2.6) and thus do not support our hypothesis (*H2*).

We also modeled OC stock at the level of individual cores. Using a multiple linear regression model, geomorphic unit, clay content, soil moisture, the surface heterogeneity metric, and total depth of the core are all significant predictor variables (Table 2.4), but stepwise model progression indicates that clay content, total depth, and the surface geomorphic heterogeneity metric are the most important predictors of OC stock.

Finally, we estimated OC stock for each meadow. These estimations are a first-order approximation because we calculated volume of the upper meadow soil (≤ 1.5 m depth,

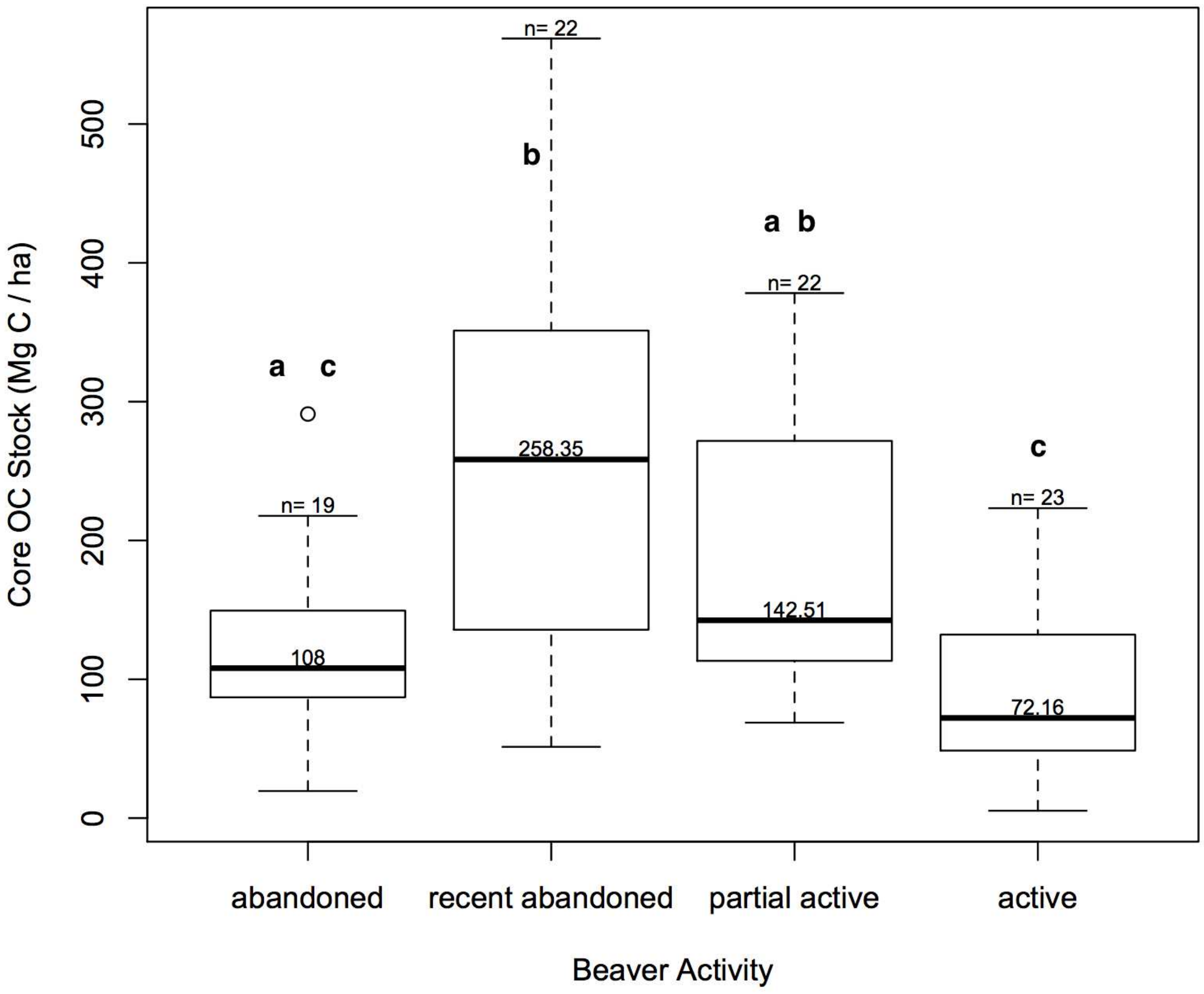


Figure 2.6. Mean organic carbon stock, by core, in relation to beaver meadow category. Letters indicate significance differences between mean values (comparisons made using nonparametric Kruskal-Wallis test with Bonferroni adjustment for multiple comparisons at the 0.05 significance level). Median value and sample size indicated for each meadow category.

depending on the average maximum depth reached within each meadow) and used the median soil bulk density and median OC concentration for each meadow to calculate stock. The results (Table 2.5) clearly indicate that level and timing of beaver activity are not the primary control on OC stock within a meadow and that OC stock does not differ between active and long abandoned meadows.

Table 2.5. Estimated values of total organic carbon stock in the upper portion (≤ 1.5 m depth) of each of the studied meadows, which are listed from active in the first row to long abandoned in the last row.

Meadow	Total OC (Mg C)	OC stock (Mg C/ha)
North St. Vrain	13166	313
Glacier	599	300
Hollowell	10175	536
Hidden Valley	2059	515
Cow Creek	15701	349
Upper Beaver Meadows	25272[1]	562[1]
Moraine Park	142445	554

[1] values based on data in Wohl (2013) for this site

2.5 Discussion and Conclusions

Measures of surface geomorphic heterogeneity support the first hypothesis, which is that geomorphic heterogeneity decreases nonlinearly with time since beaver abandonment. Partially active and recently abandoned meadows do not differ significantly from the active meadow, whereas the long abandoned meadows are significantly different. Among measures of subsurface geomorphic heterogeneity, only soil moisture varies in a manner that supports the first hypothesis. Soil depth appears to be controlled by other factors; clay content is likely similar between sites because of the consistent geology and very limited supply of clay in the study area; and soil organic carbon stock seems to be strongly influenced by soil depth.

The results generally do not support the second hypothesis, which is that floodplain soil organic carbon stock does not decline linearly with time following beaver abandonment of a river corridor. Floodplain soil organic carbon stock does not decline linearly with time (Figure 2.6), but the primary controls appear to be factors other than beaver activity. Soil depth appears to be particularly influential. The meadows with the greatest soil depths are those in the partially active and recently abandoned categories, and these categories also have the greatest carbon stock.

Geologic factors, rather than beaver activities, may exert the primary control on variations in soil depth among beaver meadows. The Hidden Valley meadow may have the greatest soil depth (Figure S2.4) and core-level organic carbon stock (Figure S2.8) because it is the only site studied here that has a base level above the Pleistocene terminal moraine. Hidden Valley Creek is tributary to the Fall River, which cuts through the terminal moraine. The small drainage area and stable, higher base level may facilitate sediment storage within the Hidden Valley beaver meadow. Conversely, the active North St. Vrain site and the long abandoned Moraine Park site may have the shallowest soil depths because these sites have the largest upstream drainage area, which may equate to greater transport capacity and lateral channel mobility in the beaver meadows. An important caveat to these interpretations is that we are only considering the upper 1.5 m of alluvium in each site. The large drainage area and multiple episodes of Pleistocene glaciation (Madole, 2012) in the Moraine Park drainage suggest that buried soils may be present beneath the cobble and boulder layer that limited our coring, but this deeper material is not considered in our analyses.

Soil organic carbon stock reflects the balance among (i) carbon inputs from autochthonous sources (riparian vegetation litterfall and stems cut by beavers) and allochthonous sources (overbank deposition of fluvially transported organic matter), (ii) carbon outputs via fluvial erosion of floodplain soil and organic matter, and (iii) carbon storage, which in turn reflects soil depth as well as sorption capacity and respiration rate (Figure 2.7). Sorption capacity and respiration rate reflect factors such as moisture content, temperature, and mineralogy (Scott and Wohl, in review). Although moisture content can reflect channel-floodplain connectivity as this influences riparian water table, moisture content can also reflect soil texture and groundwater inputs. The presence in Rocky Mountain National Park of fens and wet meadows not associated with valley bottoms indicates that the highly fractured crystalline bedrock of the region can support seeps and springs that create carbon-rich environments apart from beaver activity (Clow et al., 2003;

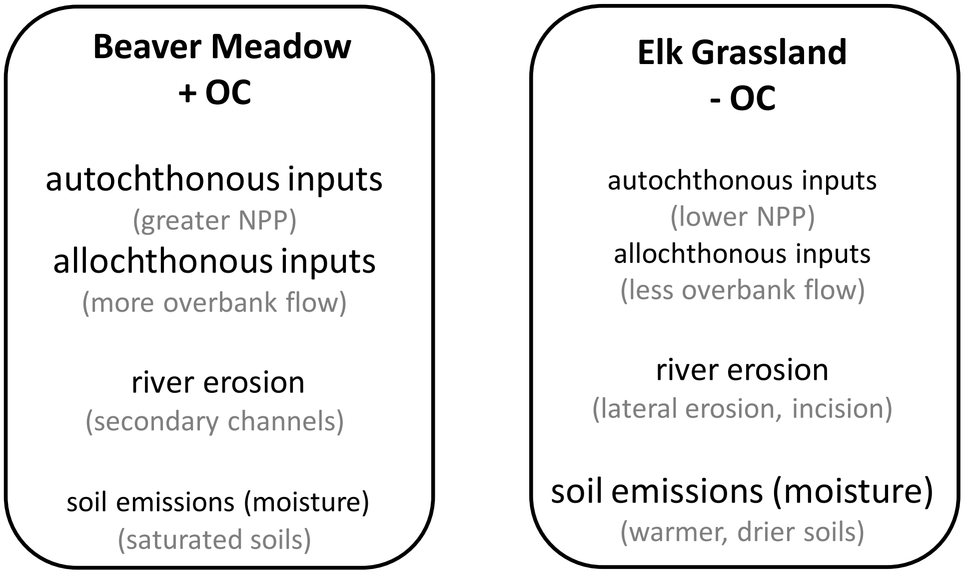


Figure 2.7. Schematic illustration of differences in the relative importance of diverse inputs, outputs, and controls on OC storage in beaver meadows versus elk grasslands. Relative size of black text within each box indicates relative importance of the process between the two scenarios (e.g., soil emissions of organic carbon are likely greater from elk grasslands).

Liu et al., 2004), and groundwater inputs to valley bottoms likely also influence carbon stock along some portions of the river network.

With respect to carbon inputs, recent work on other floodplains in the Rocky Mountains and elsewhere suggests that autochthonous inputs dominate (Lininger et al., 2018; Wohl and Scott, in review). The lack of buried, high OC concentrations at depth in the soil cores from the beaver meadows (Figure S2.9) suggests that authochthonous, rather than allochthonous, inputs also dominate these floodplains. While beavers are present in a meadow, their activities maintain high levels of autochthonous inputs via dense aquatic and riparian vegetation across floodplains and high levels of carbon storage via high riparian water tables. By creating an anastomosing channel planform, however, beavers may also increase carbon outputs via accelerated bank erosion and limited carbon deposition and storage in secondary channels except where beaver ponds are present on these channels (Sutfin, 2016). When beaver activity ceases as a result of competition from ungulates, the change in riparian vegetation toward bunchgrasses and small shrubs more characteristic of a semiarid steppe presumably reduces autochthonous carbon inputs (Buell and Markewich, 2004) and the incision of the main channel lowers the riparian water table and reduces carbon storage as floodplain soils dry (Trumbore and Czimczik, 2008), but the reversion to a single channel may reduce carbon outputs via fluvial erosion. If the single channel remains relatively stable, the abandoned beaver meadow may remain capable of storing substantial organic carbon stocks. This is particularly important in a management context because active or abandoned beaver meadows account for disproportionately large amounts of the organic carbon stored along valley bottoms in river networks (Wohl et al., 2012), so maintaining even abandoned beaver meadows in a stable (rather than actively eroding) state can foster carbon storage.

Fundamentally, soil organic carbon stock within a beaver meadow reflects soil depth, which is strongly influenced by geological factors of glacial history, bedrock geology, and drainage area. Beavers build on this geological template to create a heterogeneous environment that fosters high levels of soil moisture, finer textured floodplain soils, and higher inputs of autochthonous organic carbon, all of which enhance the organic carbon concentration and thus the overall stock. When beavers abandon a meadow, the persistence of stored organic carbon is governed by rates and magnitudes of change in sediment storage within the meadow, as well as organic carbon concentration within the floodplain soil.

Returning to the initial conceptual model (Figure 2.1), we do not see evidence for an abrupt threshold such that a beaver meadow changes significantly as soon as beavers abandon a site. Instead, several years are required before the effects of beaver ecosystem engineering are lost as dams disappear, secondary channels become inactive, and ponds are filled. In our study region on the eastern side of the Colorado Front Range, these changes seem to require circa 30 years to create significant differences in geomorphic heterogeneity and associated function. Storage of organic carbon in floodplain soils, however, may persist for much longer periods if the abandoned meadow remains stable (rather than subject to extensive lateral channel migration and fluvial erosion).

Our ability to quantify rates of change with beaver abandonment is limited by the fact that beaver have not abruptly left any of the sites that we studied. Instead, individual animals and colonies of beavers come and go through time. Since the field work described here, for example, beavers have recolonized the downstream portion of the Cow Creek site. At the North St. Vrain meadow, the location of individual dams and the status (filled or drained) of individual ponds changes each year. We used categories of beaver activity because of the difficulty in quantifying the number of beaver and active colonies within a meadow. With this caveat, however, our results indicate that the effect of beaver ecosystem engineering can persist for at least several years following a significant decline in beaver activity or abandonment of a site. This is important in the context of the increasing use of beaver reintroduction as part of river restoration (e.g., Burchsted et al., 2010; Pollock et al., 2014). Methylation of mercury, for example, occurs at much lower rates where beavers reoccupy historic beaver meadows than where the animals create new wetlands (Levanoni et al., 2015). This highlights the importance of either actively reintroducing beaver to abandoned sites or enhancing conditions at abandoned sites in a manner that facilitates recolonization by beaver.

REFERENCES

Anderson RS, Riihimaki CA, Safran EB, MacGregor KA. 2006. Facing reality: late Cenozoic evolution of smooth peaks, glacially ornamented valleys, and deep river gorges of Colorado's Front Range. In, SD Willett, N Hovius, MT Brandon, DM Fisher, eds, *Tectonics, Climate, and Landscape Evolution*. Geological Society of America Special Paper 398, Boulder, CO, 397-418.

Andrews TG. 2015. *Coyote Valley: Deep history in the high Rockies*. Harvard University Press, Cambridge, MA.

Baker BW, Ducharme HC, Mitchell DCS, Stanley TR, Peinetti HR. 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. *Ecological Applications* **15**: 110-118.

Baker BW, Hill EP. 2003. Beaver. In, GA Feldhamer, BC Thompson, JA Chapman, eds, *Wild Mammals of North America: Biology, Management, and Conservation*. The Johns Hopkins University Press, Baltimore, MD, 288-310.

Beisel JN, Usseglio-Polatera P, Moreteau JC. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia* **422/423**: 163-171.

Beschta RL, Ripple WJ. 2010. Recovering riparian plant communities with wolves in northern Yellowstone, USA. *Restoration Ecology* **18**: 380-389.

Beschta RL, Ripple WJ. 2012. The role of large predators in maintaining riparian plant communities and river morphology. *Geomorphology* **157-158**: 88-98.

Braddock WA, Cole JC. 1990. Geologic map of Rocky Mountain National Park and vicinity, Colorado. U.S. Geological Survey, Misc. Investigations Series I-1973, 1:50,000.

Buell GR, Markewich HW. 2004. Data compilation, synthesis, and calculations used for organic-carbon storage and inventory estimates for mineral soils of the Mississippi River basin. U.S. Geological Survey Professional Paper 1686-A, Reston, VA, 46 pp.

Burchsted D, Daniels MD, Thorson R, Vokoun J. 2010. The river discontinuum: applying beaver modifications to baseline conditions for restoration of forested headwaters. *BioScience* **60**: 908-922.

Butler DR, Malanson GP. 1995. Sedimentation rates and patterns in beaver ponds in a mountain environment. *Geomorphology* **13**: 255-269.

Butler DR, Malanson GP. 2005. The geomorphic influences of beaver dams and failures of beaver dams. *Geomorphology* **71**: 48-60.

Clow DW, Schrott L, Webb R, Campbell DH, Torrizo A, Dornblaser M. 2003. Ground water occurrence and contributions to streamflow in an alpine catchment, Colorado Front Range. *Ground Water* **41**: 937-950.

Correll DL, Jordan TE, Weller DE. 2000. Beaver pond biogeochemical effects in the Maryland coastal plain. *Biogeochemistry* **49**: 217–239.

Ehlen J, Wohl E. 2002. Joints and landform evolution in bedrock canyons. *Transactions of the Japanese Geomorphological Union* **23**: 237-255.

Graf WL. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. *Geomorphology* **79**: 336-360.

Green KC, Westbrook CJ. 2009. Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams. *BC Journal of Ecosystem Management* **10**: 68–79.

Guegan JF, Lek S, Oberdorff T. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature* **391**: 382-384.

Gurnell AM. 1998. The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography* **22**: 167-189.

Harvey J, Gooseff M. 2015. River corridor science: hydrologic exchange and ecological consequences from bedforms to basins. *Water Resources Research* **51**: 6893-6922.

Hess, K. 1993. *Rocky Times in Rocky Mountain National Park: An Unnatural History*. University Press of Colorado, Niwot.

Hood GA. 2011. *The Beaver Manifesto*. Rocky Mountain Books, Victoria, Canada.

Hood GA, Bayley SE. 2008. Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation* **141**: 556–567.

Hood GA, Larson DG 2014. Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal Canada. *Wetlands* **34**: 19-29.

John S, Klein A. 2004. Hydrogeomorphic effects of beaver dams on floodplain morphology: avulsion processes and sediment fluxes in upland valley floors (Spessart, Germany). *Quaternaire* **15**: 219–231.

Johnston CA. 2012. Beaver wetlands. In, DP Batzer, AH Baldwin, eds, *Wetland Habitats of North America: Ecology and Conservation Concerns*. University of California Press, Berkeley, 161-171.

Johnston CA. 2014. Beaver pond effects on carbon storage in soils. *Geoderma* **213**: 371-378.

Kramer N, Wohl EE, Harry DL. 2012. Using ground penetrating radar to 'unearth' buried beaver dams. *Geology* **40**: 43-46.

Lautz LK, Siegel DI, Bauer RL. 2006. Impact of debris dams on hyporheic interaction along a semi-arid stream. *Hydrological Processes* **20**: 183-196.

Levanoni O, Bishop K, Mckie BG, Hartman G, Eklof K, Ecke F. 2015. Impact of beaver pond colonization history on methylmercury concentrations in surface water. Environmental Science and Technology 49: 12,679-12,687.

Lininger KB, Wohl E, Rose JR. 2018. Geomorphic controls on floodplain soil organic carbon in the Yukon Flats, interior Alaska, from reach to river basin scales. *Water Resources Research* **54**: 1934-1951.

Liu F, Williams MW, Caine N. 2004. Source waters and flow paths in an alpine catchment, Colorado Front Range, United States. *Water Resources Research* **40**: W09401. doi: 10.1029/2004003076.

Madole RF. 2012. Holocene alluvial stratigraphy and response to climate change in the Roaring River valley, Front Range, Colorado, USA. *Quaternary Research* **78**: 197-208.

Naiman RJ, Melillo JM, Hobbie JE. 1986, Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* **67**: 1254–1269.

Naiman RJ, Johnston CA, Kelley JC. 1988, Alteration of North American streams by beaver. *Bioscience* **38**: 753–762.

Naiman RJ, Pinay G, Johnston CA, Pastor J. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* **75**: 905–921.
Nelson DW, Sommers LE. 1982. *Total carbon, organic carbon, and organic matter methods of soil analysis*. Part 2, Chemical and microbiological properties, 539-579.

NRCS. 1996. Method 6E1c. In Soil Survey Laboratory Methods. Soil Survey Investigations Report No. 42. Version 3.0. USDA, NRCS, National Soil Survey Center.

Olson R, Hubert WA. 1994. *Beaver: Water Resources and Riparian Habitat Manager*. University of Wyoming, Laramie, 48 pp.

Peinetti HR, Kalkhan MA, Coughenouri MB. 2002. Long-term changes in willow spatial distribution on the elk winter range of Rocky Mountain National Park (USA). *Landscape Ecology* **17**: 341-354.

Pollock MM, Beechie TJ, Wheaton JM, Jordan CE, Bouwes N, Weber N, Volk C. 2014. Using beaver dams to restore incised stream ecosystems. *BioScience* **64**: 279-290.

Pollock MM, Lewallen GM, Woodruff K, Jordan CE, Castro JM (Editors). 2017. *The Beaver Restoration Guidebook: Working with Beaver to Restore Streams, Wetlands, and Floodplains*. Version 2.0. United States Fish and Wildlife Service, Portland, Oregon. 219 pp. Online at: https://www.fws.gov/oregonfwo/promo.cfm?id=177175812

Polvi LE, Wohl EE, Merritt DM. 2011. Geomorphic and process domain controls on riparian zones in the Colorado Front Range. *Geomorphology* **125**: 504-516.

Polvi LE, Wohl E. 2012. The beaver meadow complex revisited – the role of beavers in post-glacial floodplain development. *Earth Surface Processes and Landforms* **37**: 332-346.

Polvi LE, Wohl E. 2013. Biotic drivers of stream planform: implications for understanding the past and restoring the future. *BioScience* **63**: 439-452.

Ripple WJ, Beschta RL. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* **184**: 299–313. DOI: 10.1016/S0378-1127(03) 00154-3.

Rosell F, Bozser O, Collen P, Parker H. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review* **35**: 248–276.

Ruedemann R, Schoonmaker WJ. 1938. Beaver-dams as geologic agents. *Science* **88**: 523-525.

Scott DN, Wohl EE. in review. Geomorphic regulation of soil organic carbon concentration in watersheds of the Rocky and Cascade Mountains, USA. *Earth Surface Dynamics*.

Shannon CE. 1948. A mathematical theory of communication. *The Bell System Technical Journal* **27**: 379-423 and 623-656.

Simpson EH. 1949. Measurement of diversity. *Nature* **163**: 688.

Sutfin NA. 2016. *Spatiotemporal variability of floodplain sediment and organic carbon retention in mountain streams of the Colorado Front Range*. PhD dissertation, Colorado State University, Fort Collins, CO, 331 pp.

Sutfin NA, Wohl E. 2017. Substantial soil organic carbon retention along floodplains of mountain streams. *Journal of Geophysical Research Earth Surface* **122**: 1325-1338.

Trumbore SE, Czimczik CI. 2008. An uncertain future for soil carbon. *Science* **321**: 1455-1456.

Veblen TT, Donnegan JA. 2005. *Historical Range of Variability for Forest Vegetation of the National Forests of the Colorado Front Range*. Final report, USDA Forest Service Agreement 1102-0001-99-033. Golden, CO 151 p.

Veraart AJ, Nolet BA, Rosell F, de Vries PP. 2006. Simulated winter browsing may lead to induced susceptibility of willows to beavers in spring. *Canadian Journal of Zoology* **84**: 1733-1742.

Wegener P, Covich T, Wohl E. 2017. Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism. *Water Resources Research* **53**: 4606-4623.

Westbrook CJ, Cooper DJ, Baker BW. 2006. Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. *Water Resources Research* **42**: W06404. DOI: 10.1029/2005WR004560.

Westbrook CJ, Cooper DJ, Baker BW. 2011. Beaver assisted river valley formation. *River Research and Applications* **27**: 247–256. DOI: 10.1002/rra.1359.

Westbrook CJ, Cooper DJ, Butler DR. 2013. Beaver hydrology and geomorphology. In, DR Butler, CR Hupp, eds, *Ecogeomorphology*. Academic Press, San Diego, CA, 293-306.
Wohl E. 2013. Landscape-scale carbon storage associated with beaver dams. *Geophysical Research Letters* **40**: 1-6.

Wohl E, Kuzma JN, Brown NE. 2004. Reach-scale channel geometry of a mountain river. *Earth Surface Processes and Landforms* **29**: 969-981.

Wohl E, Dwire K, Sutfin N, Polvi L, Bazan R. 2012. Mechanisms of carbon storage in mountainous headwater rivers. *Nature Communications* **3**: 1263, doi:10.1038/ncomms2274.

Wohl E, Rathburn S, Chignell S, Garrett K, Laurel D, Livers B, Patton A, Records R, Richards M, Schook DM, Sutfin NA, Wegener P. 2017. Mapping longitudinal stream connectivity in the North St. Vrain Creek watershed of Colorado. *Geomorphology* **277**: 171-181.

Wolf EC, Cooper DJ, Hobbs NT. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications* **17**: 1572–1587.

Wright JP. 2009. Linking populations to landscapes: richness scenarios resulting from changes in the dynamics of an ecosystem engineer. *Ecology* **90**: 3418-3429.

Wright JP, Jones CG, Flecker AS. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* **132**: 96-101.

3 CHAPTER 3

ATTENUATION OF SEASONAL PEAK FLOWS BY BEAVER MEADOWS IN THE SOUTHERN ROCKIES OF COLORADO

Chapter Summary

We use seasonal flow measurements from 19 beaver meadow sites with diverse drainage area, valley geometry, elevation, and levels of beaver activity to evaluate the effects of beaver engineering on stream flow. We measured stream flow at the inlet and outlet of each beaver meadow and used these paired hydrographs to evaluate attenuation of peak flow magnitude, enhancement of baseflow magnitude, and lag time of the recession curve. Our conceptual model and associated hypotheses propose that the level of beaver activity and the ratio of the meadow area relative to contributing drainage area influence the magnitude of hydrograph alteration. Potential control variables include drainage area, elevation, valley gradient, ratio of valley to channel width, ratio of beaver meadow area to drainage area, and categorical level of beaver activity (fully active, partially active, recently abandoned, long abandoned). We find that level of beaver activity significantly correlates with attenuation of peak flow, with other control variables adding explanatory power. The effect of beaver engineering on surface flow is not simple to predict, however, because of the control exerted by variables such as drainage area and the processes by which peak flow is retained and subsequently released from a beaver meadow.

3.1 Introduction

Beavers were once ubiquitous throughout forested environments of the northern hemisphere. In North America, *Castor canadensis* had a range that extended from northern Alaska to northern Mexico (Pollock et al., 2017). In Eurasia, *Castor fiber* extended from eastern Siberia west to Scandinavia and from the coast of the Arctic Ocean south to Spain, Iraq and Iran, as well as the Korean Peninsula and China (Rosell et al., 2005). Numerous studies document the diverse effects of ecosystem engineering by beavers, including increased habitat and biodiversity (Wright et al., 2002; Rosell et al., 2005) and attenuation of downstream fluxes of water (Woo and Waddington, 1990; Nyssen et al., 2011), sediment (Butler and Malanson, 1995; Westbrook et al., 2011), organic matter and carbon (Wohl, 2013; Johnston, 2014; Laurel and Wohl, 2019), and nutrients (Naiman et al., 1994). By changing the proportion of riparian areas occupied by standing and flowing water and diverse vegetation communities (Hood and Bayley, 2008; Green and Westbrook, 2009), beaver activity may also increase the resilience of river corridors to drought, wildfire, and changing climate (Baldwin, 2015).

An integral part of beaver ecosystem engineering is the construction of dams within river corridors, which include the active channel(s) and floodplain. In the simplest scenario, beavers build a single dam across a channel and the dam and backwater pond attenuate downstream fluxes by creating an obstacle and a storage feature, respectively. In narrow river corridors or where habitat is otherwise marginal, this may be the extent of beaver engineering. In wider river corridors with favorable habitat, beavers can occupy an area for decades to millennia (Kramer et al., 2012; Polvi and Wohl, 2012), building numerous dams across portions of the entire river corridor. This scenario, which is sometimes described as a beaver meadow complex (Ruedemann and Schoonmaker, 1938; Ives, 1942; Polvi and Wohl, 2012), results in a spatially heterogeneous river corridor, with dams and ponds in varying stages of activity or abandonment. Abandoned ponds gradually fill with sediment and host a succession of plant and animal species as the environment changes (e.g., Ray et al., 2001). Dams and associated ponds can be on secondary channels where a river has a multi-channel planform, and on tributaries or seeps and springs along the valley margins. The presence of beaver dams decreases longitudinal connectivity in river corridors (Burchsted et al., 2010), but greatly enhances vertical connectivity by promoting hyporheic exchange flows (Lautz et al., 2006) and lateral connectivity by promoting overbank flows (Westbrook et al., 2006) and channel avulsion and branching (John and Klein, 2004).

Retention of organic matter and greater lateral and vertical connectivity that promote an elevated riparian water table result in organic-rich soils in beaver meadows. These soils have long been recognized as valuable agricultural sites. Archeological evidence from Britain indicates that prehistoric peoples preferentially used beaver meadows for grazing and crops (Coles and Orme, 1983), and these practices continued in the New World, where European colonists sought the rich valley bottoms modified by beavers (Morgan, 1868; Mills, 1913; Cronon, 1983). Agriculturalists using beaver meadows commonly killed and drove off the beavers, a practice that continued well into the 20th century in portions of the western US (Andrews, 2015). Along with continuing expansion of land use, deforestation, and wetland and floodplain drainage, these activities have caused beaver populations to decline substantially and have made beaver meadows comparatively rare.

Since 2000, however, there has been a resurgence of interest in using beavers for river restoration both in Europe and the United States (e.g., Pollock et al., 2014). Beavers are being actively reintroduced in more than a dozen European countries (e.g., Rolauffs et al., 2001; Giriat et al., 2016) and, where beaver reintroduction is limited by suitable habitat or may no longer be feasible, beaver dam analogues are being created to mimic some of the effects of beaver ecosystem engineering (Pollock et al., 2017). Beaver restoration may be intended to serve multiple functions, but attenuation of downstream fluxes is a common objective. Consequently, understanding the magnitude and processes of attenuation under different scenarios is an important applied research goal, as well as being critical to understanding how river corridors functioned when abundant beavers and beaver meadows were present.

In arid to semiarid regions in which consumptive water use is carefully monitored, one of the questions associated with the presence of beavers is the cumulative effect of beaver engineering on water balance. The well-documented scenario is that the presence of a beaver dam and pond reduces peak flows downstream and increases base flows through the combined effects of surface and subsurface water storage (e.g., Woo and Waddington, 1990; Meentemeyer and Butler, 1999). Evapotranspiration from the ponded water and riparian plants in the river corridor also increase water loss to the atmosphere (Woo and Waddington, 1990), although quantitative estimates of the magnitude of evapotranspiration and surface and subsurface water storage in diverse environments await further research. There is also remarkably little knowledge of how the details of beaver engineering influence downstream fluxes and water storage. The most comprehensive study to date recorded stream and ground water levels above and below 54 single beaver dams over a summer, as well as flow at the outlet of two basins in subarctic wetlands in Canada (Woo and Waddington, 1990). Differentiating beaver dams based on how water passed the dam (overflow, throughflow, etc), Woo and Waddington found that each type of dam regulated flow differently. Other studies have primarily focused on a single dam-pond pair. These studies suggest limited attenuation at the watershed scale during large runoff periods such as snowmelt (e.g., Burns and McDonnell, 1998).

The scenario of a single dam-pond pair in a watershed is largely the product of centuries of human alteration of landscapes. Beavers live in family colonies and 2-year-olds leave the colony to establish new colonies within a few kilometers of their natal colony (Baker and Hill, 2003). In the absence of human-imposed limitations, numerous beaver colonies are present within a watershed, creating a stair-stepped configuration of successive dams on the main channel and across the floodplain, and multiple, spatially extensive beaver meadows along the length of a river (Naiman et al., 1986, 1988, 1994). Studies such as that by Nyssen et al. (2011), which examines the effects of six beaver dams along the Chevral River (14 km^2) in Belgium, are starting to demonstrate how multiple beaver dams can reduce even significant peak discharges and increase base flows, but there remains little quantification of the effects of a fully developed beaver meadow with the exception of Wegener et al. (2017). Working in a beaver meadow 1540 m long and averaging 254 m wide in the 84 km^2 catchment of North St. Vrain Creek in Colorado, USA, Wegener et al. quantitatively demonstrated a reduction of snowmelt peak flows and increase in base flows downstream from the beaver meadow. An otherwise comparable confined valley segment with no beaver activity exported more than six times as much surface flow as the beaver meadow during the snowmelt period of May to October.

The North St. Vrain beaver meadow does not include any beaver dams across the main channel but is actively occupied by beavers and includes multiple dams across secondary channels. This beaver meadow is located immediately upstream from a Pleistocene-age glacial terminal moraine in Rocky Mountain National Park. Many of the rivers draining eastward from the Continental Divide in the national park were occupied by valley glaciers during the Pleistocene, and the resulting glacial troughs create ideal beaver habitat. Prior to European settlement of the region, each of these rivers hosted large beaver meadows, most of which are now abandoned. When beavers abandon a site, their mainstem dams are gradually breached. Dams and ponds in other portions of the river corridor can persist for centuries, however, so that the river corridor retains relatively high geomorphic heterogeneity even in the absence of contemporary beaver activity (Laurel and Wohl, 2018). The presence of floodplain and beaver-pond alluvium, along with the continued presence of abandoned dams and ponds across the floodplain, allows these abandoned beaver meadows to continue to attenuate downstream fluxes, especially during peak flows that overtop the banks of the main channel. However, changes in the attenuation of surface flow in relation to characteristics such as level of beaver activity have not yet been investigated.

The primary objective of the research summarized here is to assess the degree to which beaver meadows attenuate downstream surface water fluxes in relation to four characteristics of the beaver meadow: relative size, absolute size, level of activity, and location of dams. Attenuation refers to a smoothing of the hydrograph where peak magnitude flow is decreased, and recession limb flow is increased as the meadow seasonally stores and later releases snowmelt peak flows. Relative size refers to the size of the beaver meadow relative to the contributing drainage area. A beaver meadow covering 10 hectares, to use a hypothetical example, might alter downstream fluxes to a different degree if it has a contributing drainage area of 1 km^2 versus a contributing area of 10 km^2. Absolute size refers to the area covered by a beaver meadow, regardless of contributing drainage area. Level of activity describes whether beavers are fully occupying a meadow and building dams across at least portions of the entire river corridor, or whether beaver activity is limited to a small portion of the river corridor, or absent entirely. Location of dams describes whether dams are present on the main channel or only on secondary channels or other portions of the floodplain (e.g., valley margin springs).

We initiated this research based on a conceptual model in which we proposed a nonlinear relationship between relative size of a beaver meadow and surface flow attenuation (Figure 3.1). We proposed in the model that the degree of attenuation would decline with declining levels of contemporary activity in the beaver meadow. The curves in Figure 3.1 represent hypothesized relationships that we test using data from 19 beaver meadows in the Colorado Front Range. Specifically, we hypothesize that: (*H1*) there is a significant difference in retention of surface flow between active and abandoned beaver meadows; (*H2*) retention decreases nonlinearly with time after beavers abandon a meadow; and (*H3*) additional parameters such as relative size contribute to retention in beaver meadows.

3.2 Study Area

The 19 watersheds included in this study all drain east from the Continental Divide in the Colorado Front Range and cover a range of elevation, drainage area, beaver meadow size, and levels of beaver activity (Table 3.1, Figure 3.2). All but 5 of the watersheds lie within or near Rocky Mountain National Park (RMNP), and are underlain by igneous and

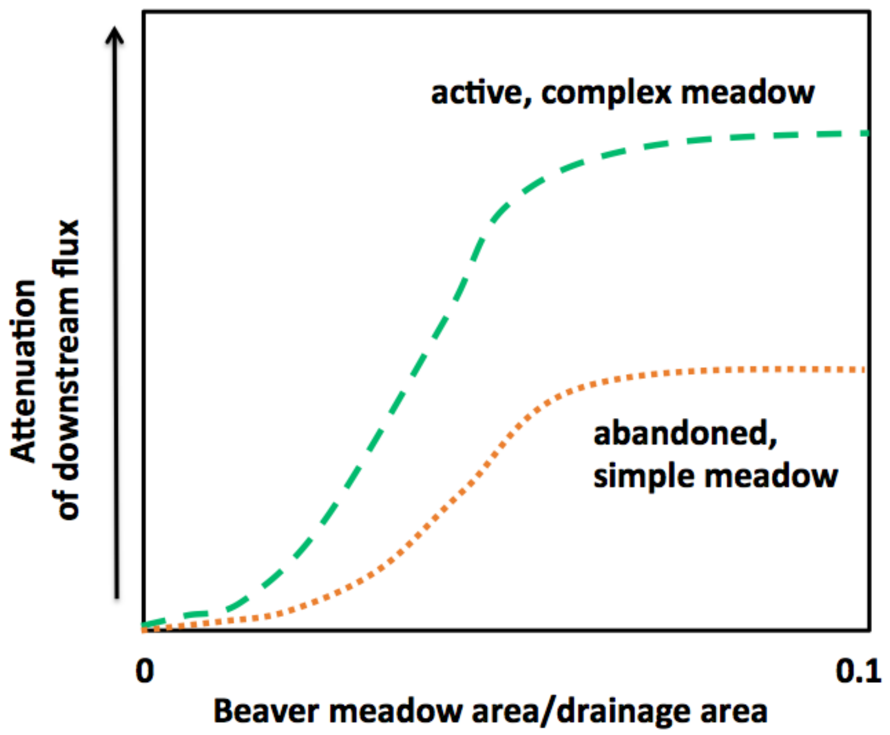


Figure 3.1. Conceptual diagram of a nonlinear relationship between attenuation of downstream flux and the meadow size relative to the drainage area. Active meadows are hypothesized to have greater attenuation across all meadow sizes than the abandoned meadows.

metamorphic Precambrian rocks including granite, granodiorite, schist, and gneiss (Braddock and Cole, 1990). The two lower elevation sites are located farther south near Sedalia, Colorado, where the geology is predominantly Eocene sedimentary bedrock overlain by Quaternary alluvium (Morgan et al., 2006). The highest elevation site is near the summit of Independence Pass, with similar Precambrian granitic and metamorphic rocks to those in RMNP (Bryant, 1979). The final two sites are located in the Fraser Experimental Forest, where the geology is crystalline gneiss and schist with the occasional granite outcrop and alluvium-filled valley bottoms (Alexander and Watkins, 1977). All sites except the two lowest elevation locations are within the mountains where the rugged

Table 3.1. Summary of characteristics for the meadow study locations.

Creek	Elevation (m)	Drainage Area (km²)	Meadow Area (km²)	Valley Slope	Ratio of Valley Width to Channel Width	Beaver Activity
Garber Creek	1913	27.2	0.04	0.027	30	Active
Lake Creek	3284	25.3	0.16	0.017	47	Active
N St Vrain Creek	2542	89	0.42	0.014	35	Active
Spruce Creek	2783	2.3	0.05	0.061	88	Active
W St Louis Creek	2768	14.2	0.01	0.019	12	Active
Glacier Creek	2691	36.7	0.02	0.025	10	Partial Active
Mill Creek	2559	14.7	0.19	0.012	34	Partial Active
Boulder Brook	2658	10.2	0.06	0.058	24	Recent Abandoned
Cow Creek	2404	20.2	0.08	0.04	19	Recent Abandoned
Hague Creek	3008	35	0.29	0.006	24	Recent Abandoned
Hidden Valley Creek	2797	9.3	0.04	0.014	39	Recent Abandoned
Unnamed Creek	2850	2.4	0.05	0.042	87	Recent Abandoned
Big Thompson River	2454	110	2.57	0.007	79	Abandoned
Corral Creek	3110	13.5	0.73	0.014	107	Abandoned
Fall Creek	2994	9.3	0.06	0.008	13	Abandoned
Jackson Creek	1902	64.2	0.02	0.032	12	Abandoned
SF Poudre River	2403	230.2	0.16	0.006	19	Abandoned
Trap Creek	3145	8.7	0.16	0.012	38	Abandoned
UBM Beaver Brook	2548	15	0.45	0.03	118	Abandoned

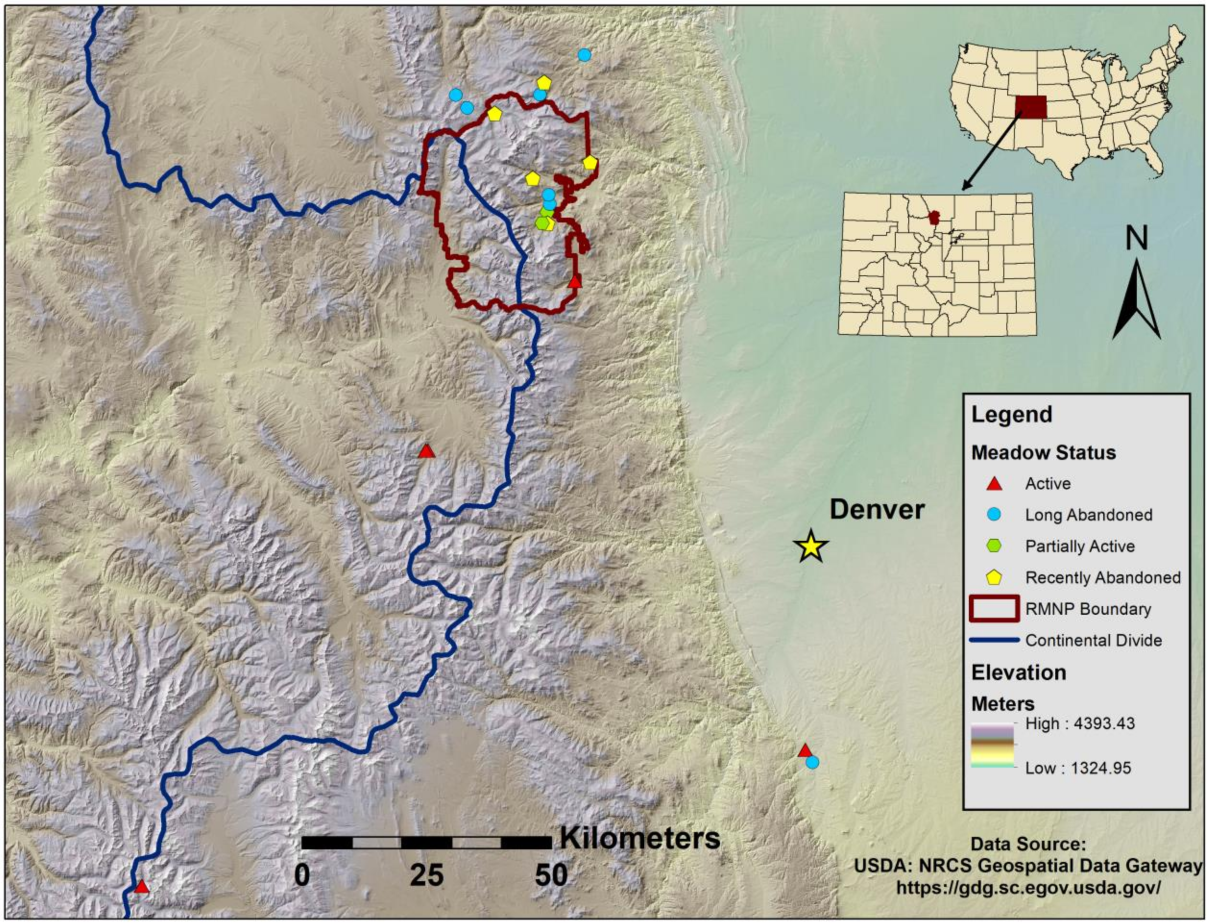


Figure 3.2. Map of study area in the Southern Rockies of Colorado. All but one location are east of the Continental Divide.

mountain peaks have been carved by the advance and retreat of glaciers, and subsequent fluvial erosion (Anderson et al., 2006). The generally steep, narrow streams open out periodically into wider, flatter valley bottoms carved by glaciers like "beads on a string" (Wohl et al., 2017). These wider, low gradient valleys are ideal habitat for beaver (Polvi and Wohl, 2012). The majority of the 19 study meadows lie above the 2300 m elevation of the last glacial terminal moraine (Pinedale, Pleistocene Epoch), although not all of the meadows were covered by glaciers in the last advance (Anderson et al., 2006). Generally, the un-glaciated meadows are narrower than nearby glaciated counterparts.

The mean annual precipitation across all the sites ranges from 30-80 cm, with greater precipitation falling in the higher elevation locations than the lower elevation. The majority of this precipitation falls in the winter months as snow and contributes to an annual snowmelt peak in the hydrograph, typically sometime in late May or June (Wohl et al., 2004). The subalpine and montane zone locations have upland forests comprised of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*) interspersed with aspen (*Populus tremuloides*) (Veblen and Donnegan, 2005). The two lowest elevation sites are drier and the forest stands are more sparse. They are primarily scrub oak (*Quercus gambelii*), juniper (*Juniperous* spp.) and open ponderosa pine woodland. Valley bottoms across all sites are dominated by willow (*Salix* spp.), grasses and sedges (*Carex* spp.), with a few sites also having river birch (*Betula fontinalis*) and blue spruce (*Picea pungens*).

Of the 19 sites, we classify 5 as active (Garber Creek, Lake Creek, N St. Vrain, Spruce Creek, W St. Louis Creek), 2 as partially active (Glacier Creek, Mill Creek), 5 as recently abandoned (Cow Creek, Hague Creek, Boulder Brook, Hidden Valley Creek, Unnamed Creek) and 7 as long abandoned (Big Thompson River, Corral Creek, Fall Creek, Jackson Creek, SF Poudre River, Trap Creek, UBM Beaver Brook). The abandoned meadows are predominantly in the north, while the southern locations are mostly active. Active meadows have beaver influence across the entire meadow extent, creating a complex of dams, ponds, secondary channels, and berms. Partially active meadows have beaver influence over less than half the meadow area, but the beavers are currently active and in residence. Recently abandoned meadows have no current resident beavers, but either still retain easily visible beaver structures like dams, ponds, and beaver runs (channels dug by beaver) or had verified beaver activity within the last decade. The long abandoned meadows lack any easily visible indication that beaver ever occupied the valley, although geophysical techniques such as GPR (Kramer et al., 2012), and historical documents such as beaver census records and aerial photographs have verified historical beaver presence.

3.3 Methods

We installed TruTrack capacitance rods at the inflow and outflow of each beaver meadow. Inflow and outflow sites were located on channel reaches with a single channel planform (rather than multi-channel) and a laterally confined valley relative to the beaver meadow (Figure 3.3). Capacitance units were programmed to record data at 15-minute intervals and remained in place from early May or June through September. Capacitance rod measurements of water depth were converted to discharge by developing stage-discharge curves for each measurement site based on multiple channel cross-sectional surveys and velocity measurements during the snowmelt hydrograph and base flow. Channels were surveyed with an auto level, stadia rod, and metric tape. Velocity was measured using a 1d Marsh-McBirney Flow Mate current meter. Rating curves based on cross-sectional surveys and velocity measurements were supplemented with modeling using WinXSPro (Hardy et al., 2005) (Table 3.2). WinXSPro utilizes the Jarrett (1984) equation, which was developed on streams in the study area, to develop a rating curve for a channel cross section based on channel roughness. Discharge in cubic meters per second was converted to millimeters per day by normalizing discharge by drainage area and then converting the units.

Statistical analyses focused on three hydrologic variables: attenuation of peak flow magnitude, enhancement of baseflow magnitude, and lag time of the recession curve. These metrics were all calculated as the difference in values between the inflow and outflow of each meadow. The three hydrograph metrics were analyzed with boxplots and non-parametric Kruskal-Wallis test with a Bonferroni adjustment for multiple comparisons between different beaver activity levels. In addition, multiple linear regression models were fit to these response variables to investigate the importance of other potential control variables aside from beaver activity. Potential predictor variables analyzed include beaver

Figure 3.3. Google Earth view of inlet and outlet sites of the North St. Vrain to demonstrate the study design at each meadow. Red line outlines the beaver meadow.

Table 3.2. Summary of coefficients for stage-discharge relationships.

		Stage-Discharge Coefficients ($Q = az^b$)	
Creek	Location	a	b
Garber Creek	Inflow	5.860	2.872
	Outflow	1.159	2.571
Lake Creek	Inflow	6.978	2.740
	Outflow	1.825	2.261
N St Vrain Creek*	Inflow	0.00000002	2.899
	Outflow	0.0056	1.017
Spruce Creek	Inflow	2.809	2.178
	Outflow	2.998	2.312
W St Louis Creek	Inflow	17.40	3.312
	Outflow	8.943	3.676
Glacier Creek	Inflow	8.999	2.523
	Outflow	5.879	2.661
Mill Creek	Inflow	10.81	5.980
	Outflow	0.7582	2.015
Boulder Brook	Inflow	14.39	3.209
	Outflow	5.322	2.248
Cow Creek	Inflow	10.82	4.831
	Outflow	181.5	7.809
Hague Creek	Inflow	9.601	2.188
	Outflow	2.765	3.730
Hidden Valley Creek	Inflow	5.318	3.11
	Outflow	0.7867	2.164
Unnamed Creek	Inflow	1.340	1.953
	Outflow	2.746	2.85
Big Thompson River	Inflow	8.984	3.952
	Outflow	10.82	1.870
Corral Creek	Inflow	2.031	1.939
	Outflow	0.2496	1.397
Fall Creek	Inflow	18.50	2.764
	Outflow	1.825	2.308
Jackson Creek	Inflow	40.06	3.015
	Outflow	7.891	2.881
SF Poudre River	Inflow	14.43	2.676
	Outflow	6.853	2.14
Trap Creek	Inflow	13.20	4.802
	Outflow	9.200	2.140
UBM Beaver Brook	Inflow	3.508	2.305
	Outflow	3.128	3.717

activity, valley slope (m/m), ratio of valley width to channel width, elevation (m), ratio of meadow area to drainage area, and drainage area (km^2). The additional variables were found using U.S. Geological Survey website StreamStats (drainage area, elevation), Google Earth imagery (valley width, valley area, and valley slope), and field surveys (channel width). As each model required, the response variable or predictor variables were log transformed in order to meet the model assumptions of normality and homoscedasticity of variance in the model residuals. The significance of potential predictor variables was assessed at the alpha = 0.05 and 0.1 levels to determine whether any of the potential variables have explanatory power for our response variables of hydrograph metrics. We also conducted a qualitative comparative analysis of the meadow hydrographs and plots of the inflow and outflow recession rates.

There is some inherent uncertainty in the use of rating curves to transform the stage data into discharge data stemming from the difficulty in measuring flow at high discharge. Therefore, we conducted additional analysis on the stage data to support the analyses on the discharge data. We analyzed stage data by converting the stage data to a “z-score”, i.e. normalizing the data by the mean and standard deviation for each location. We then plotted the inflow and outflow z-scores against each other in hysteresis plots to evaluate attenuation of flow over the snowmelt season. Hysteresis plots can show attenuation of the snowmelt flow by dual signature of deviation from the 1:1 line toward the inlet at peak flows, and deviation toward the outlet on the recession limb. Deviation toward the inlet at peak magnitudes indicates that the flow at the inlet was farther from the normalized flow than at the outlet; i.e., that there was greater magnitude flow at the inlet than at the outlet. This indicates a decrease in the peak flow magnitude between the inlet and the outlet.

Combined with an increase in recession limb flow magnitude at the outlet compared to the inlet, meadows with the dual signature show attenuation of the snowmelt peak flows.

3.4 Results

We compared hydrograph metrics across 4 different levels of beaver activity using boxplots and statistical comparison tests. Visual inspection of the boxplots shows slight trends in the three different metrics, although none of the groups are statistically different. Peak magnitude is attenuated at higher levels in the abandoned and recently abandoned meadows than in the partially and fully active meadows (Figure 3.4). Baseflow magnitude is enhanced in recently abandoned, partially and fully active meadows relative to abandoned meadows (Figure 3.5), and the lag time of the recession curve is higher in the active meadows relative to the abandoned, recently abandoned, and partially active meadows (Figure 3.6).

The multiple linear regression models investigated the potential for other predictor variables to explain the variation in the three hydrograph metrics. For the peak flow attenuation model, only beaver activity was significant at the alpha = 0.05 significance level. At the alpha = 0.1 significance level, three additional variables were significant in the model: valley slope, ratio of valley to channel width, and ratio of meadow area to drainage area (Table 3.3). For the base flow enhancement, none of the predictor variables were significant in the model, indicating that we have not captured the variables that could explain the variation in baseflow increase across meadows. In the model for lag in the recession curve, only the drainage area was a significant predictor variable, at the alpha = 0.1 level (Table 3.3). This indicates that contributing area is more important for explaining

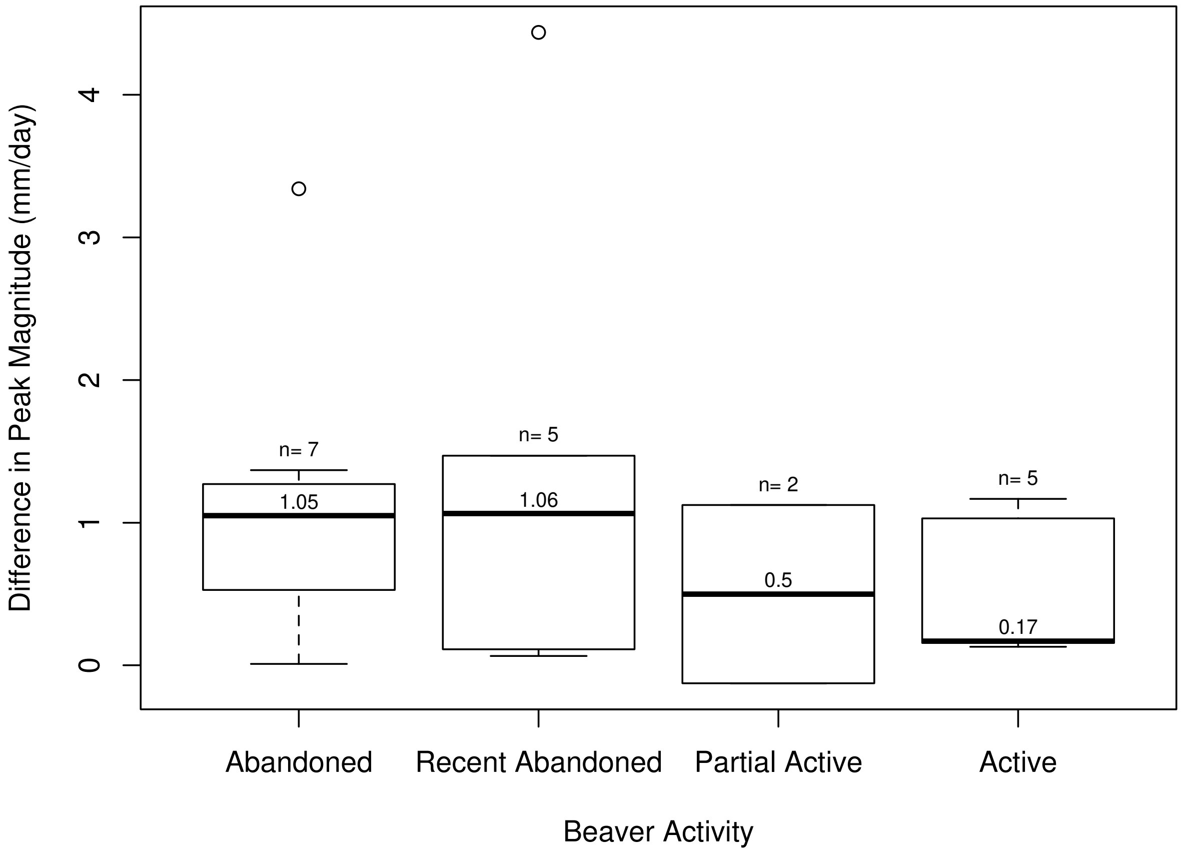


Figure 3.4. Boxplot of the difference in peak magnitude between the inflow and outflow across the four categories of beaver activity. There is no significant difference between the categories, although the trend indicates greater storage of peak flow in abandoned and recently abandoned meadows.

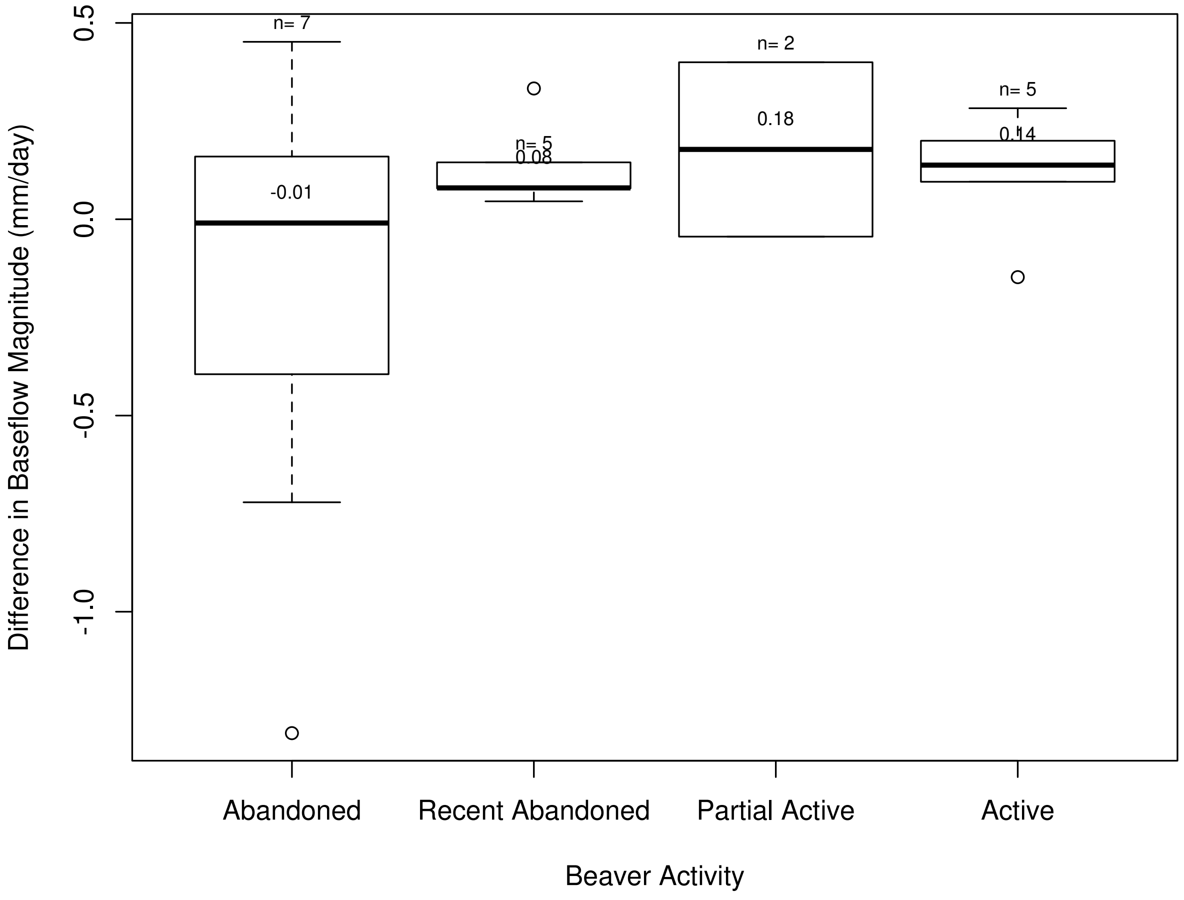


Figure 3.5. Boxplot of baseflow enhancement across the four categories of beaver activity. There is no significant difference between the categories, although the trend indicates greater augmentation of the base flow in active and partially active meadows.

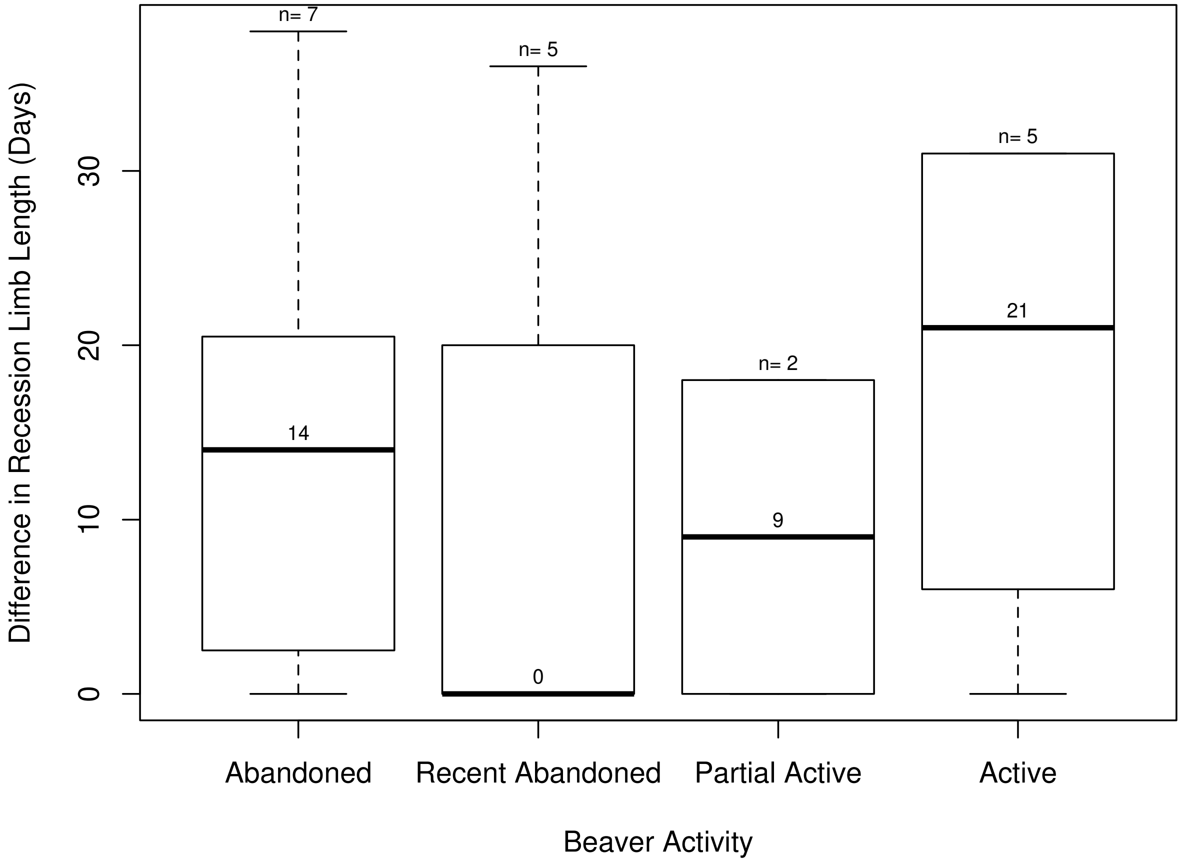


Figure 3.6. Boxplot of lag in recession curve across the four categories of beaver activity. There is no significant difference between the categories, although the trend indicates greater median lag time in active meadows.

Table 3.3. Summary of multiple linear regression model results for modeling peak flow attenuation, baseflow enhancement, and lag in the recession curve. As each model required, the response or predictor variables were log transformed to meet model assumptions. The table shows the *p* value (*F* statistic) [coefficient β; effect of a unit increase of the predictor on the response]. Bolded values are significant at alpha = 0.05. Italicized values are significant at alpha = 0.1.

	Difference in Peak Magnitude, Q (mm/day)	Difference in Base Flow Magnitude, Q (mm/day)	Difference in Recession Limb Length (days)
Beaver Activity	**0.035 (4.26)**	0.528 (0.7883)	0.840 (0.2776)
Valley Slope	*0.059 (4.53) [-2.190]*	0.964 (0.0021) [-7.059]	0.527 (0.4289) [-9.861]
Ratio of Valley to Channel Width	*0.058 (4.58) [0.000304]*	0.328 (1.0556) [0.00149]	0.551 (0.3804) [0.0353]
Elevation (m)	0.313 (1.13) [-0.00323]	0.520 (0.4437) [-0.000403]	0.345 (0.9806) [-0.0281]
Ratio of Meadow Area to Drainage Area	*0.073 (4.00) [0.617]*	0.510 (0.4662) [7.163]	0.343 (0.9899) [0.476]
Drainage Area (km^2)	0.114 (2.99) [-0.856]	0.391 (0.8047) [-0.00244]	*0.0744 (3.9671) [-10.258]*

the variation in recession lag than beaver activity. Additional information conveyed by the models relates to the direction of change in the response variable as the result of a change in the predictor variable. Of particular interest, the valley slope, the elevation, and the drainage area have a negative relationship with the three response variables, indicating that increasing any of these variables results in a decrease in peak attenuation, lower base flow augmentation, and decreased recession curve lag time.

We also visually, qualitatively compared the hydrographs and recession rate curves across the meadows. Visual comparison reveals that there is a large amount of variability between the relative inflow and outflow recession curves for every category of meadow, and the differences in the peak magnitude, baseflow magnitude, and recession lag are not parallel between individual sites within a category of beaver meadow activity. Some meadows may have peak magnitude loss, but not baseflow increase or recession lag and vice versa (Figure 3.7). There are active meadows that show large peak flow decrease, and little peak flow decrease, as well as sites that do and do not show end of summer baseflow increase among all the categories of beaver meadow activity (Figure 3.7).

Recession rate curves show the enhancement (or lack thereof) of baseflow during the end of summer, drier months. In the abandoned meadows, only two meadows show higher baseflow at the outlet than at the inlet (Corral Creek and Fall Creek). In the active meadows, two meadows show higher baseflow at the outflow than at the inflow (Figure 3.8). The other three active sites have higher baseflow at the inlet than the outlet. These dynamics reflect the magnitude of fluctuation in storage in the meadows during the summer flow season. The recently abandoned meadows have a gradient of base flow augmentation, from none to augmentation comparable to the highest values in active

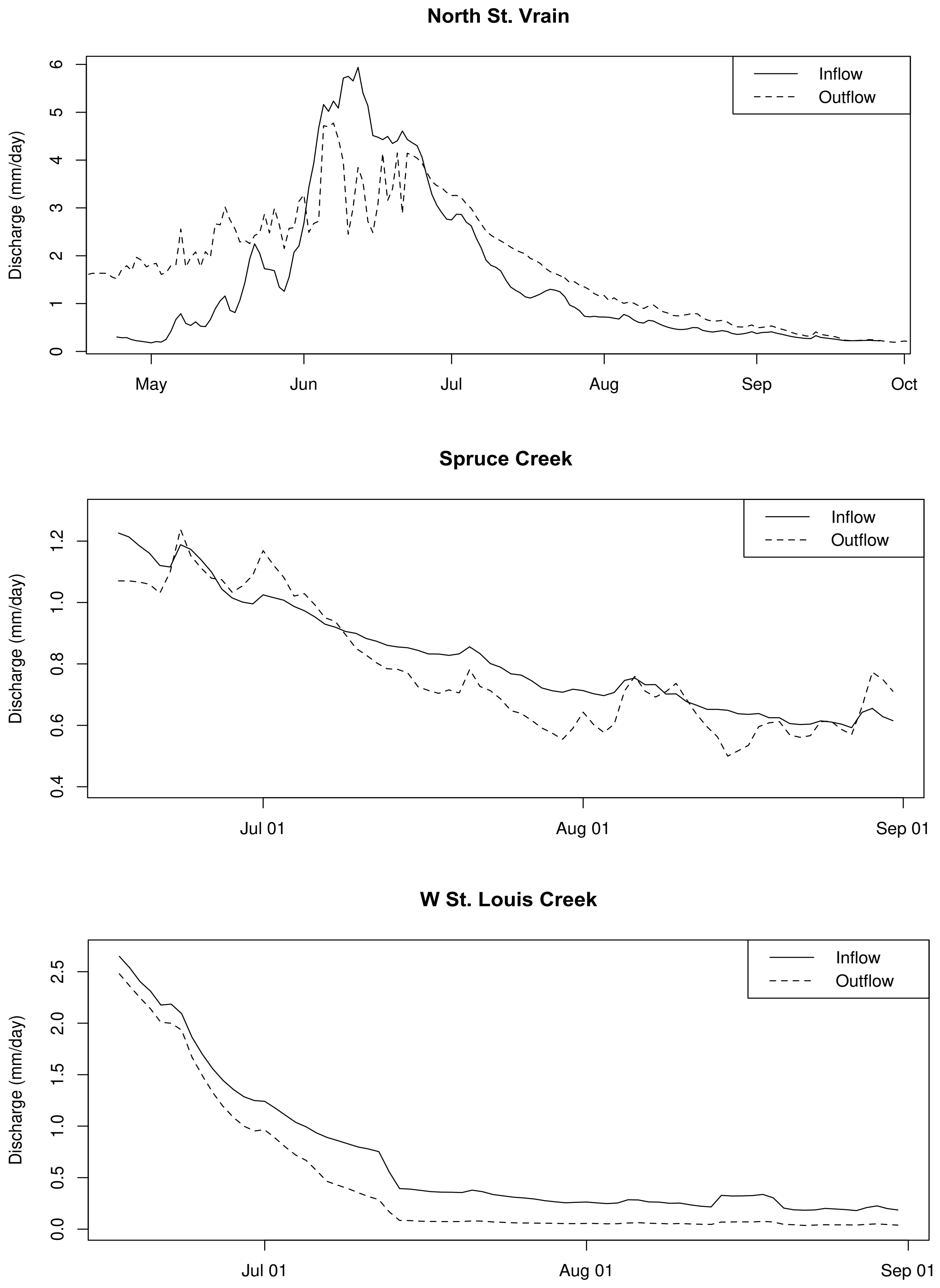


Figure 3.7a. A selection of representative hydrographs for active meadows.

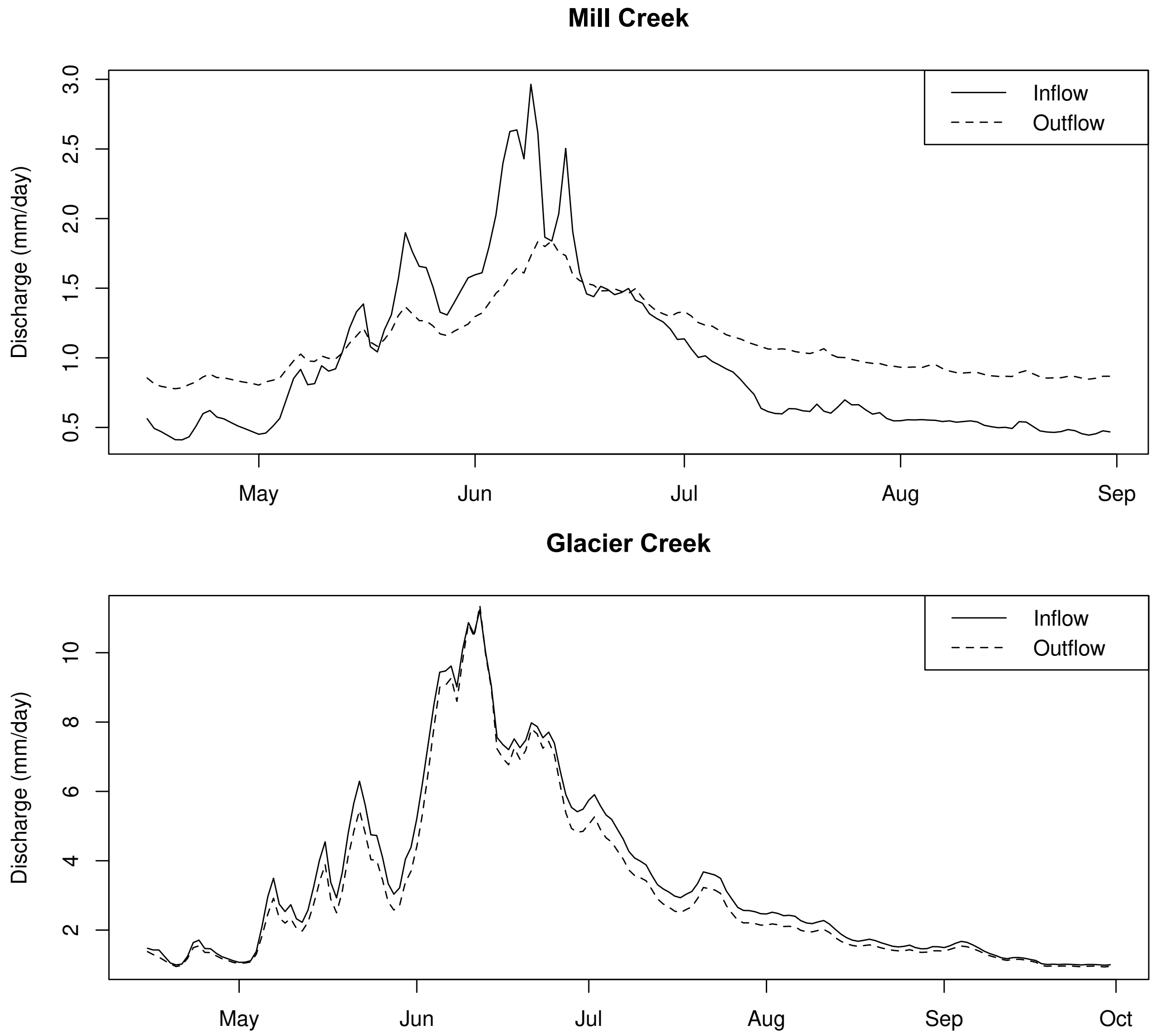
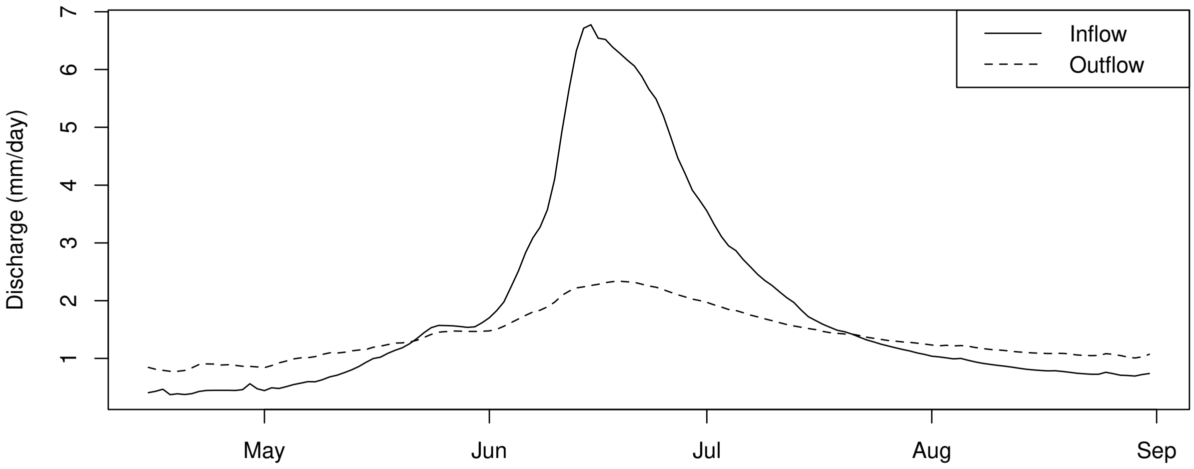


Figure 3.7b. A selection of representative hydrographs for partially active meadows.

Hidden Valley



Hague Creek

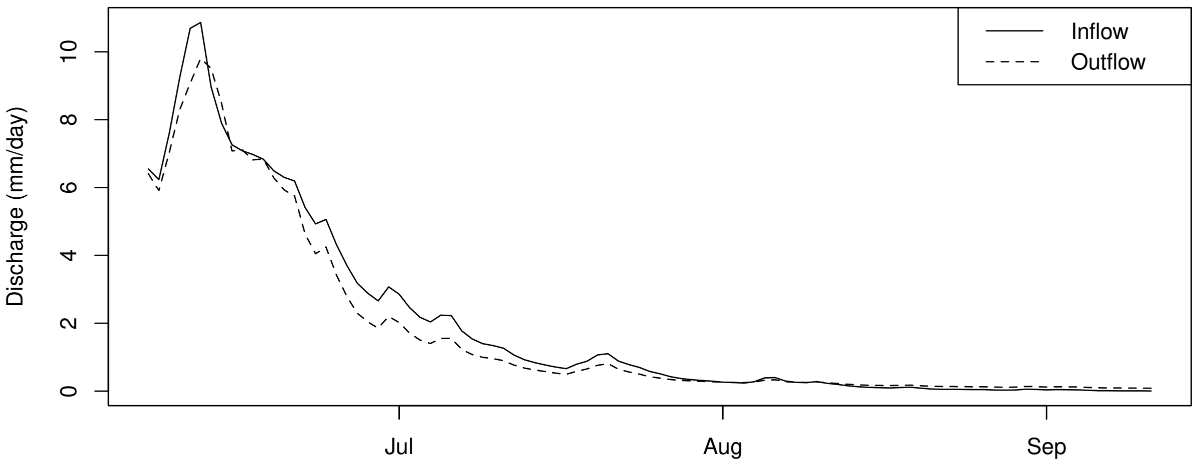


Figure 3.7c. A selection of representative hydrographs for recently abandoned meadows.

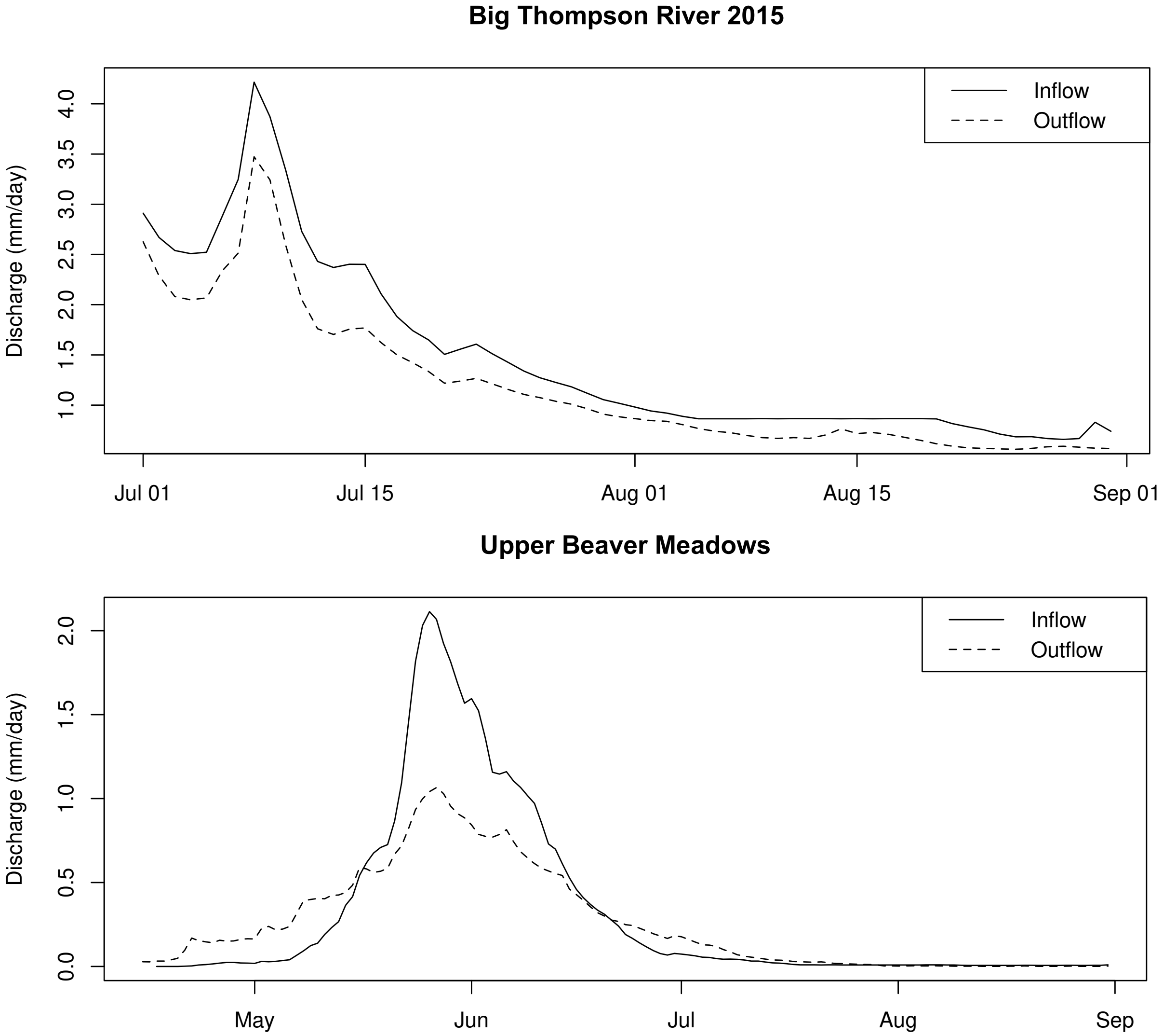


Figure 3.7d. A selection of representative hydrographs for long abandoned meadows. Hydrographs of the remaining 10 streams (all activity levels) can be found in the supplemental figures in the appendix.

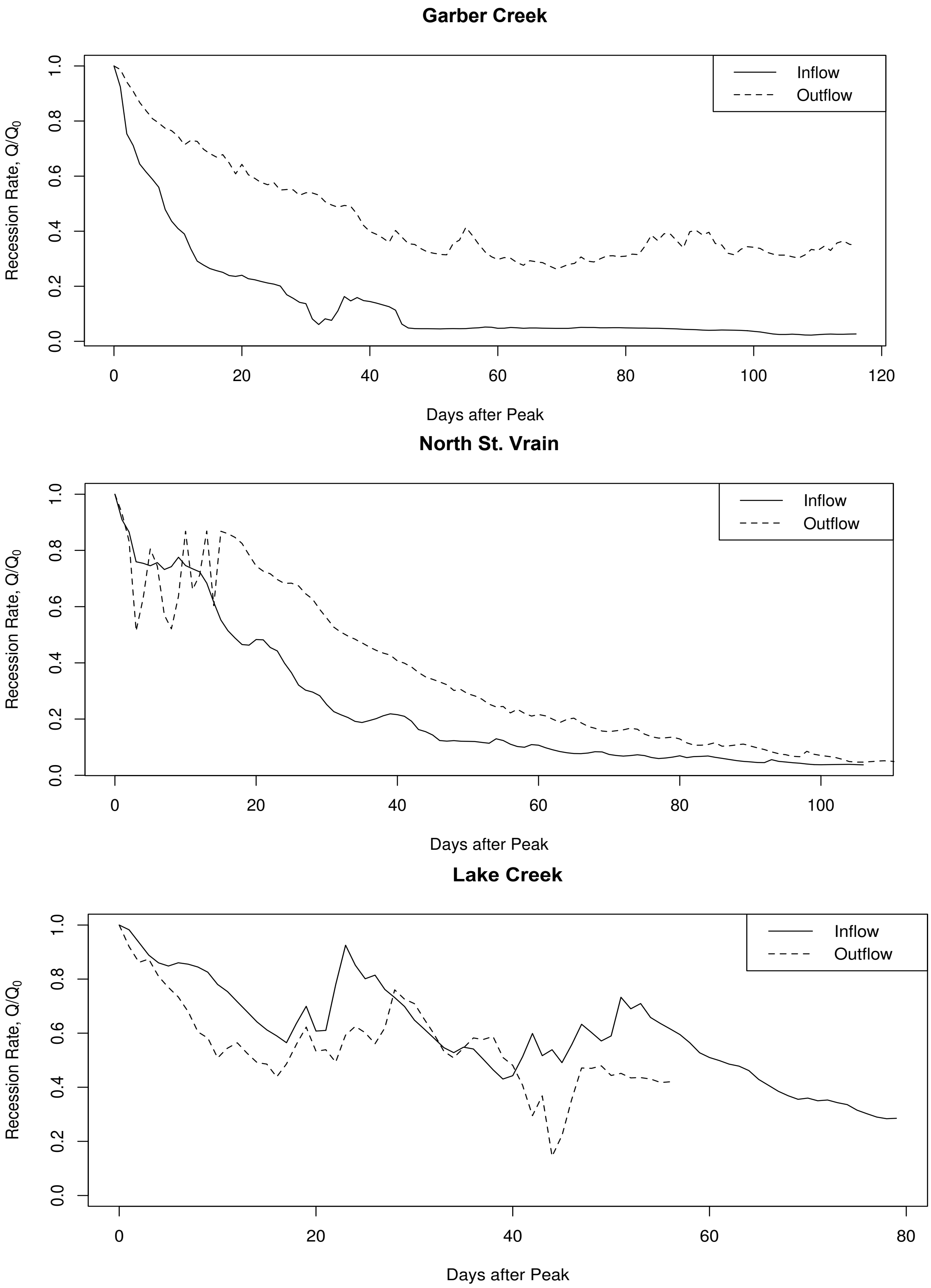
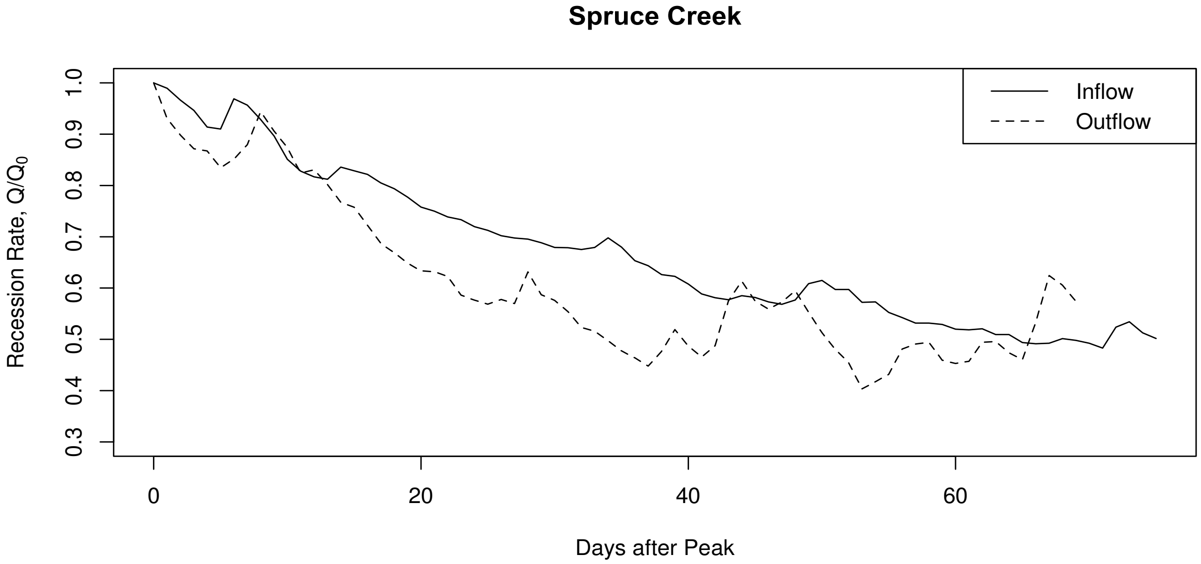


Figure 3.8a. Recession rate curves for active meadows. The recession curves show the rate at which the flow peak returns to base flow. In addition, they indicate augmentation of base flow in cases where the outflow has greater volume than the inflow.



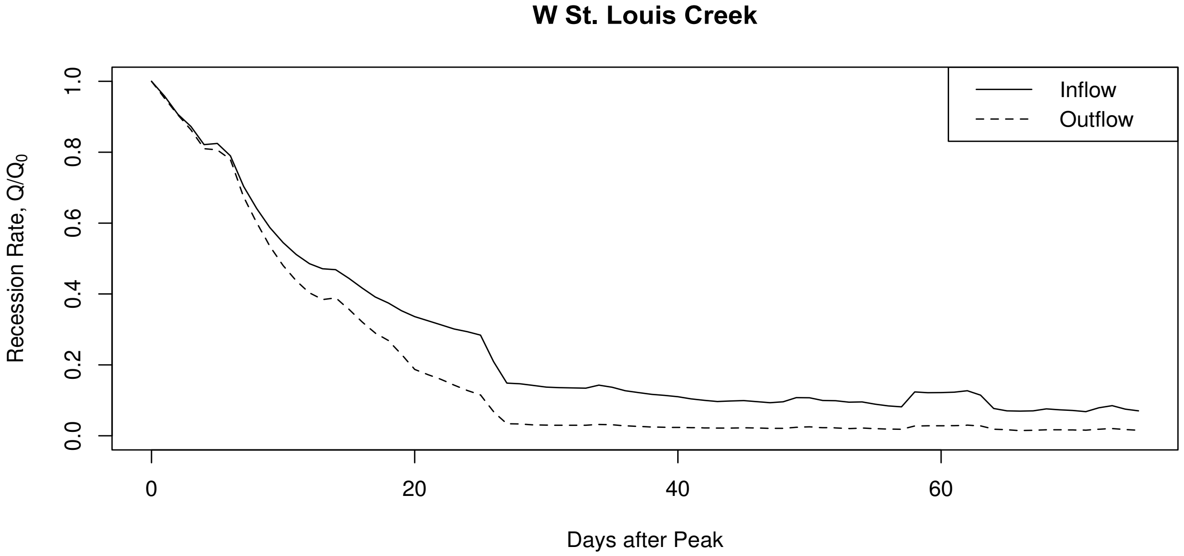


Figure 3.8a continued. Recession rate curves for active meadows.

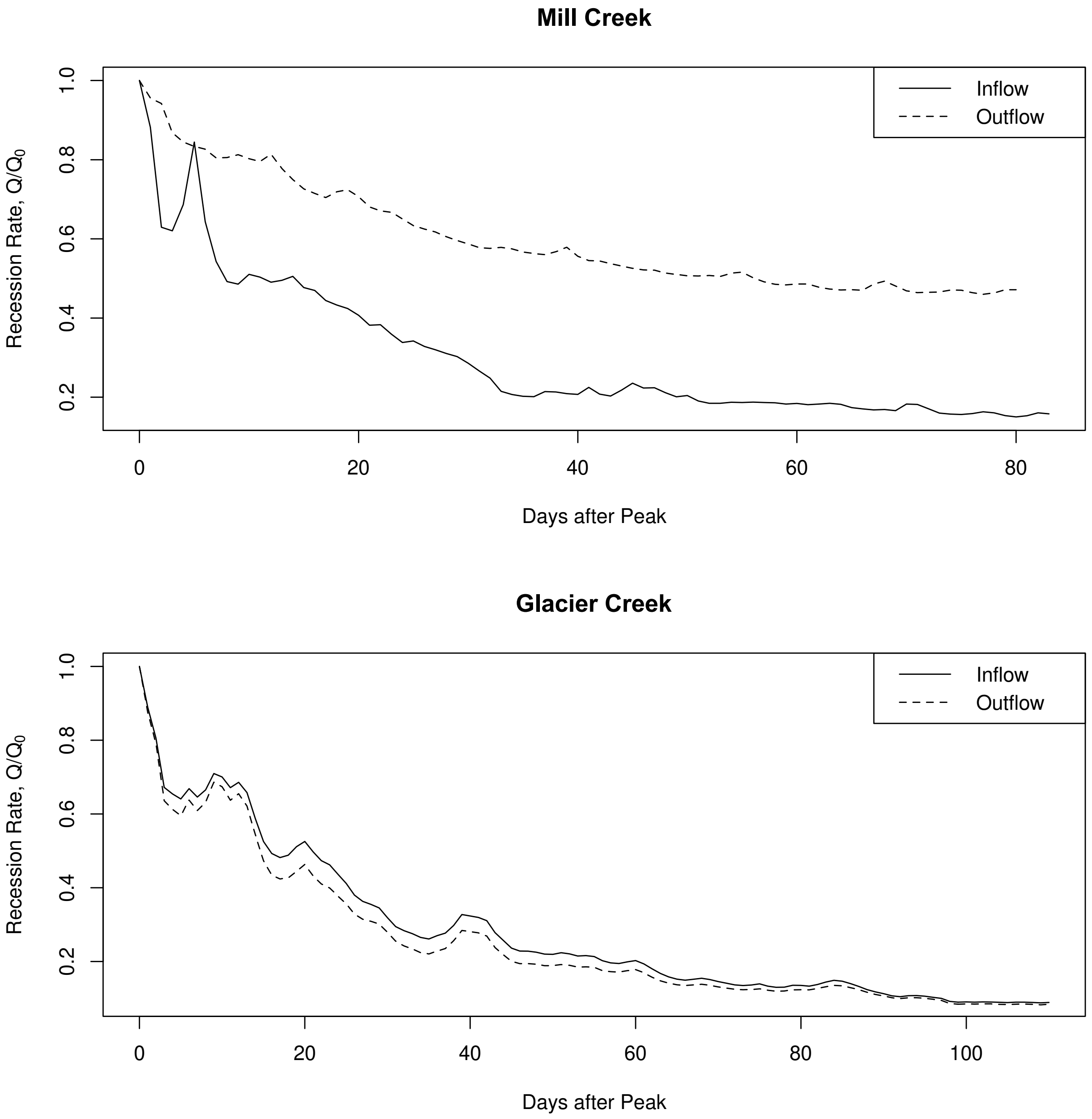


Figure 3.8b. Recession rate curves for partially active meadows.

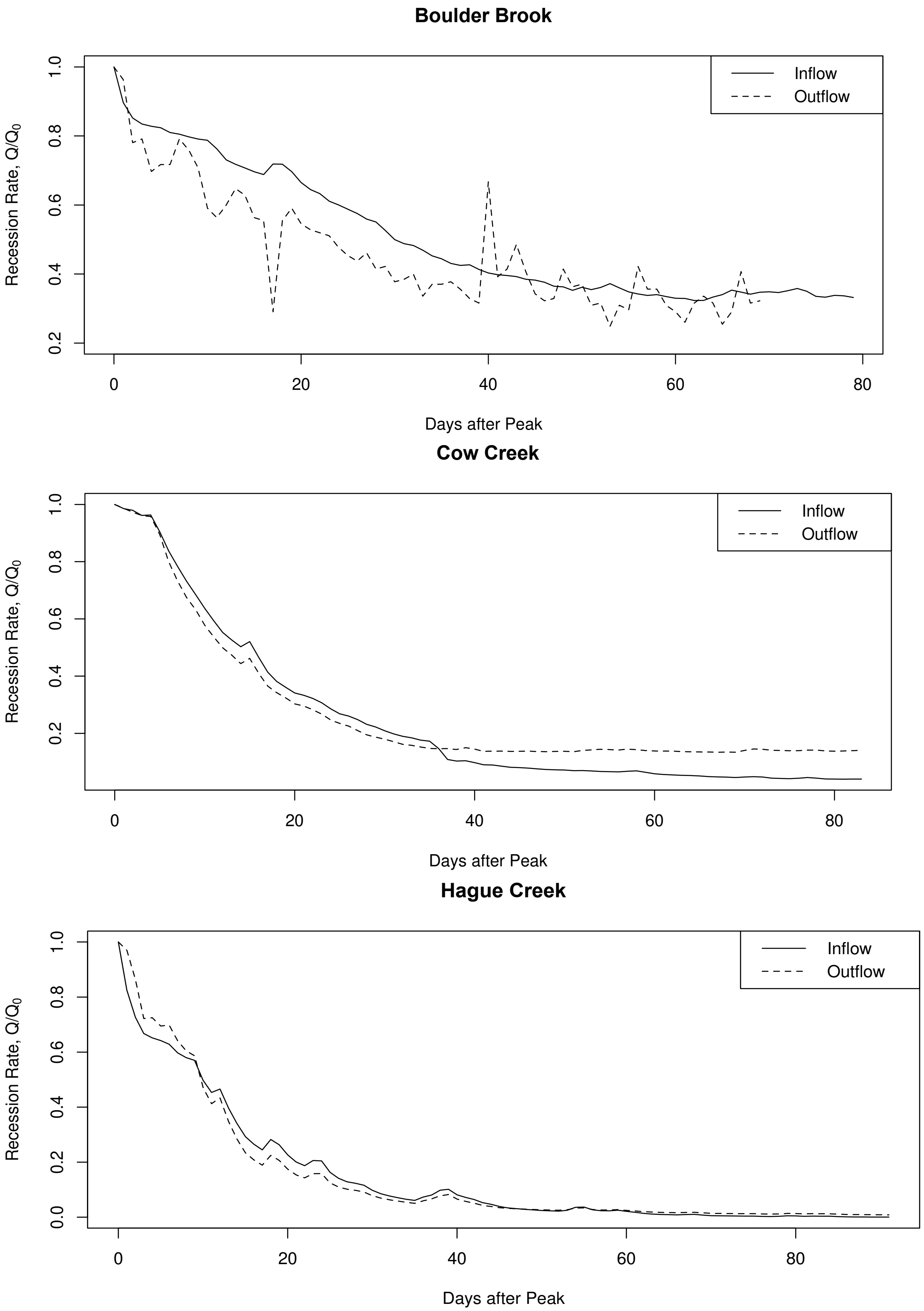


Figure 3.8c. Recession rate curves for recently abandoned meadows.

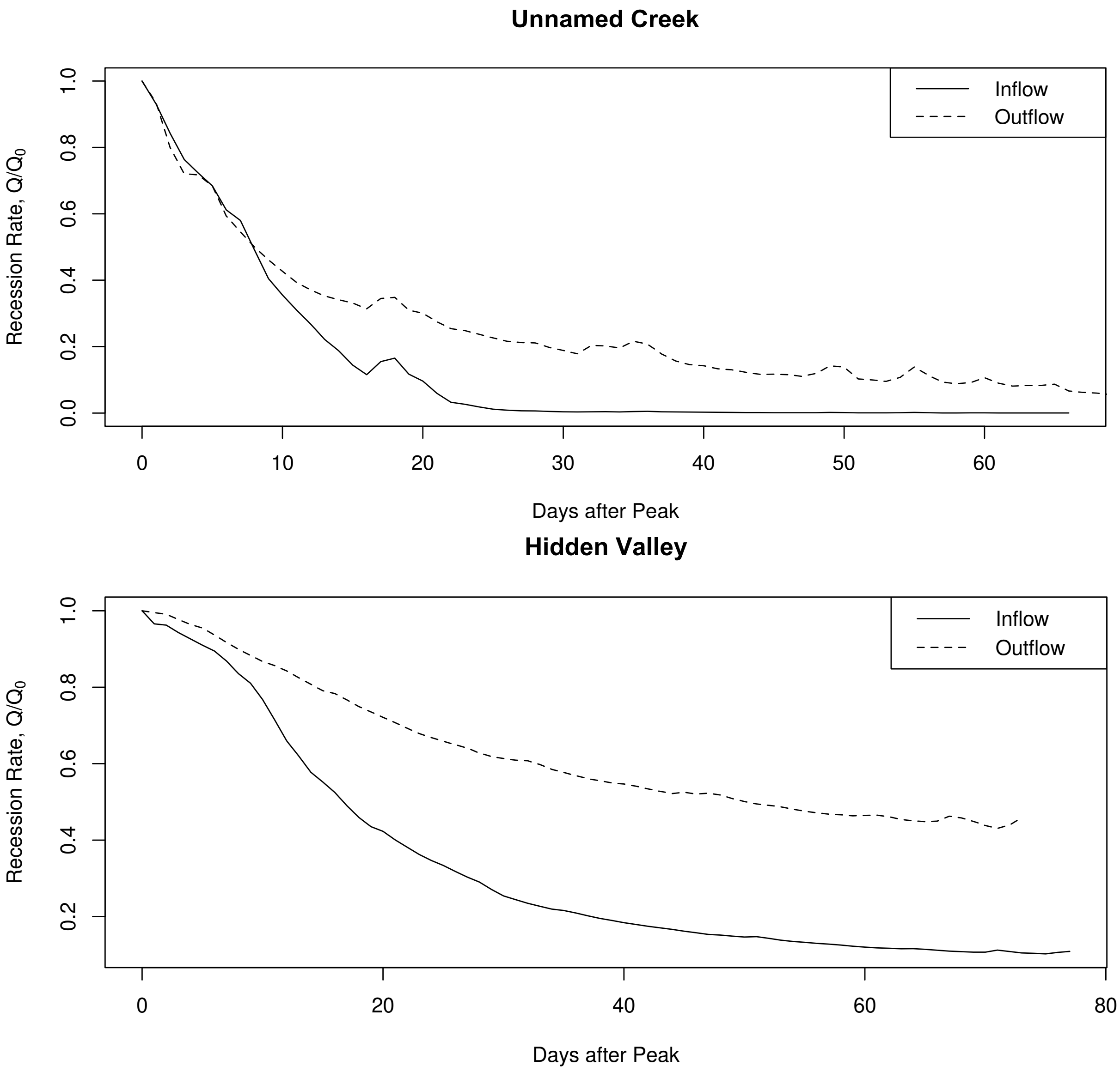


Figure 3.8c continued. Recession rate curves for recently abandoned meadows.

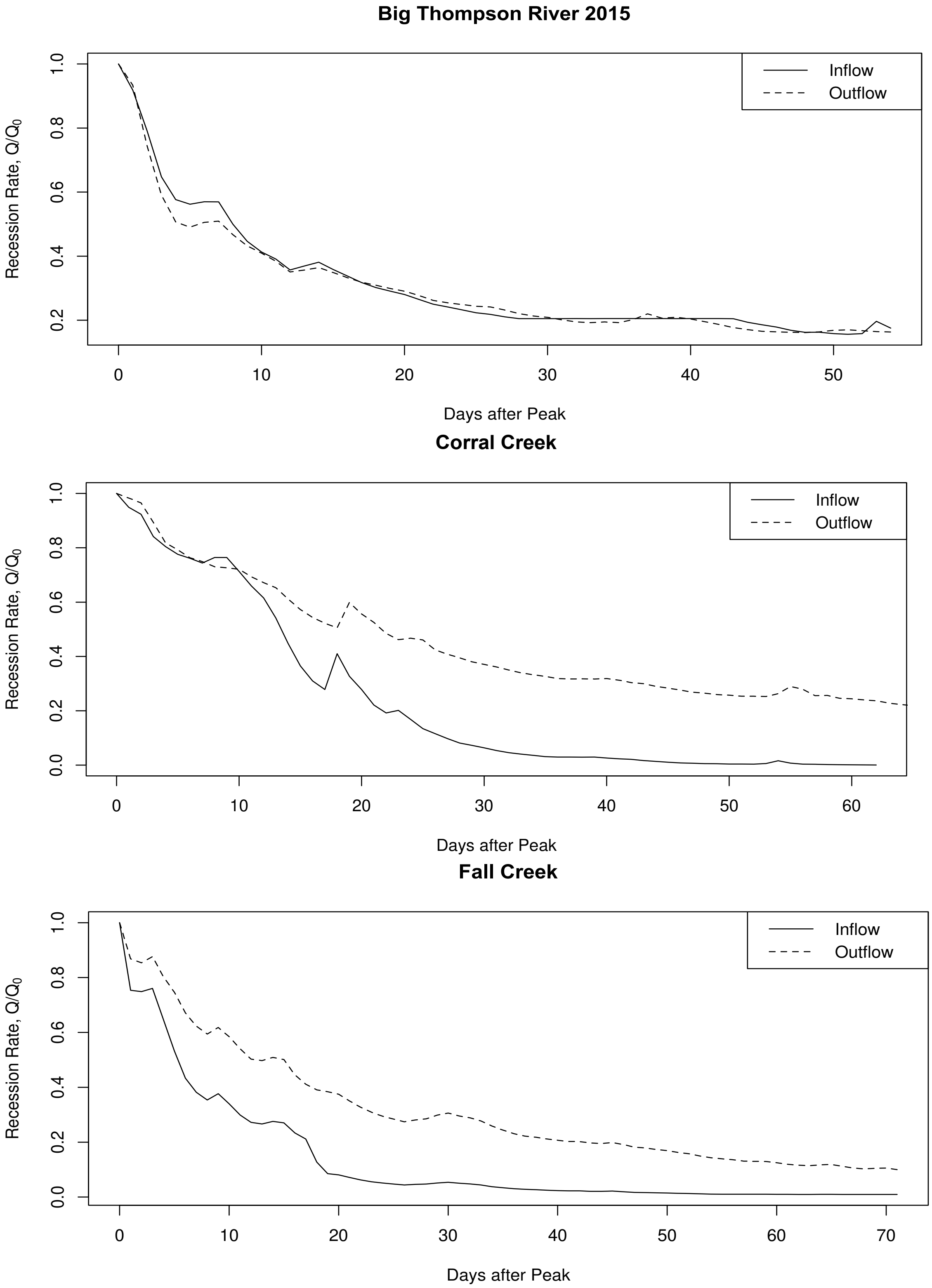


Figure 3.8d. Recession rate curves for long abandoned meadows.

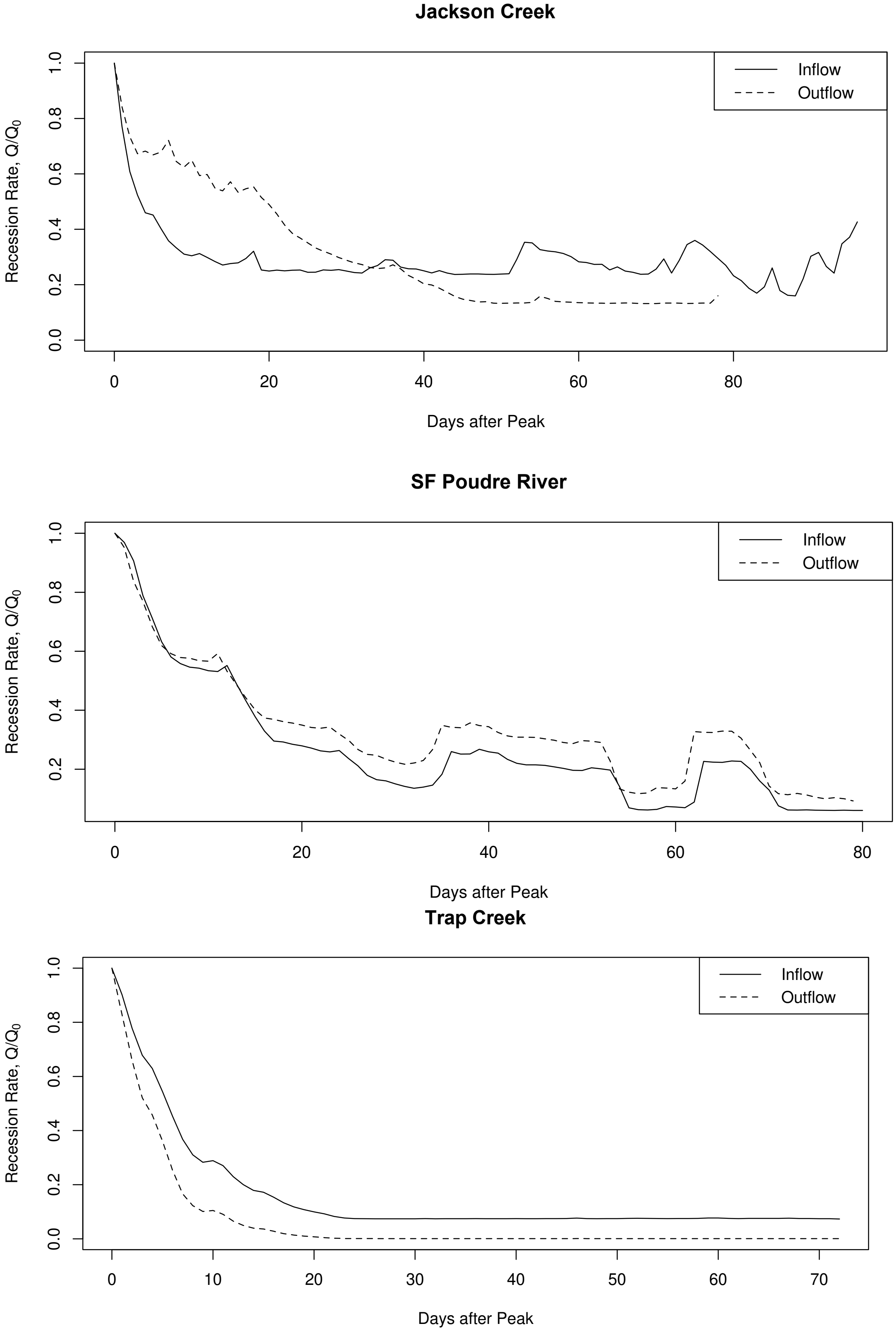


Figure 3.8d continued. Recession rate curves for long abandoned meadows.

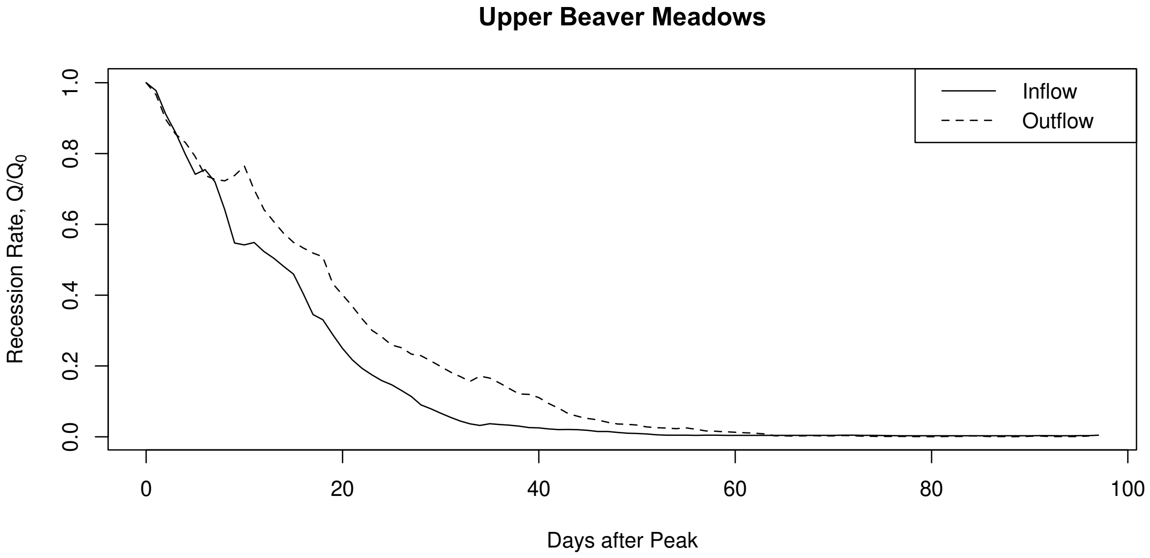


Figure 3.8d continued. Recession rate curves for long abandoned meadows.

meadows.

Analysis of the stage data using hysteresis curves supports the results of the quantitative and qualitative analyses of the discharge data. Hysteresis curves show some attenuation of peak flow in three of the four active sites (North St. Vrain, Spruce, and West St Louis Creeks), one of the two of the partially active sites (Mill Creek), three of the four recently active sites (Hidden Valley, Hague, and Unnamed Creeks), and only two of the five long abandoned sites (Upper Beaver Meadows) (Figure 3.9). Only 15 of the meadows were included in the hysteresis analysis – the other three sites had too much instrument error to see a clear signal in the data. There is variation in the degree of attenuation observed in every category of beaver activity, and some sites that show unexpected patterns of flow loss or gain at the outlet (e.g. Garber Creek, which is gaining flow at the outlet relative to the inlet for the entire snowmelt season) (Figure 3.9).

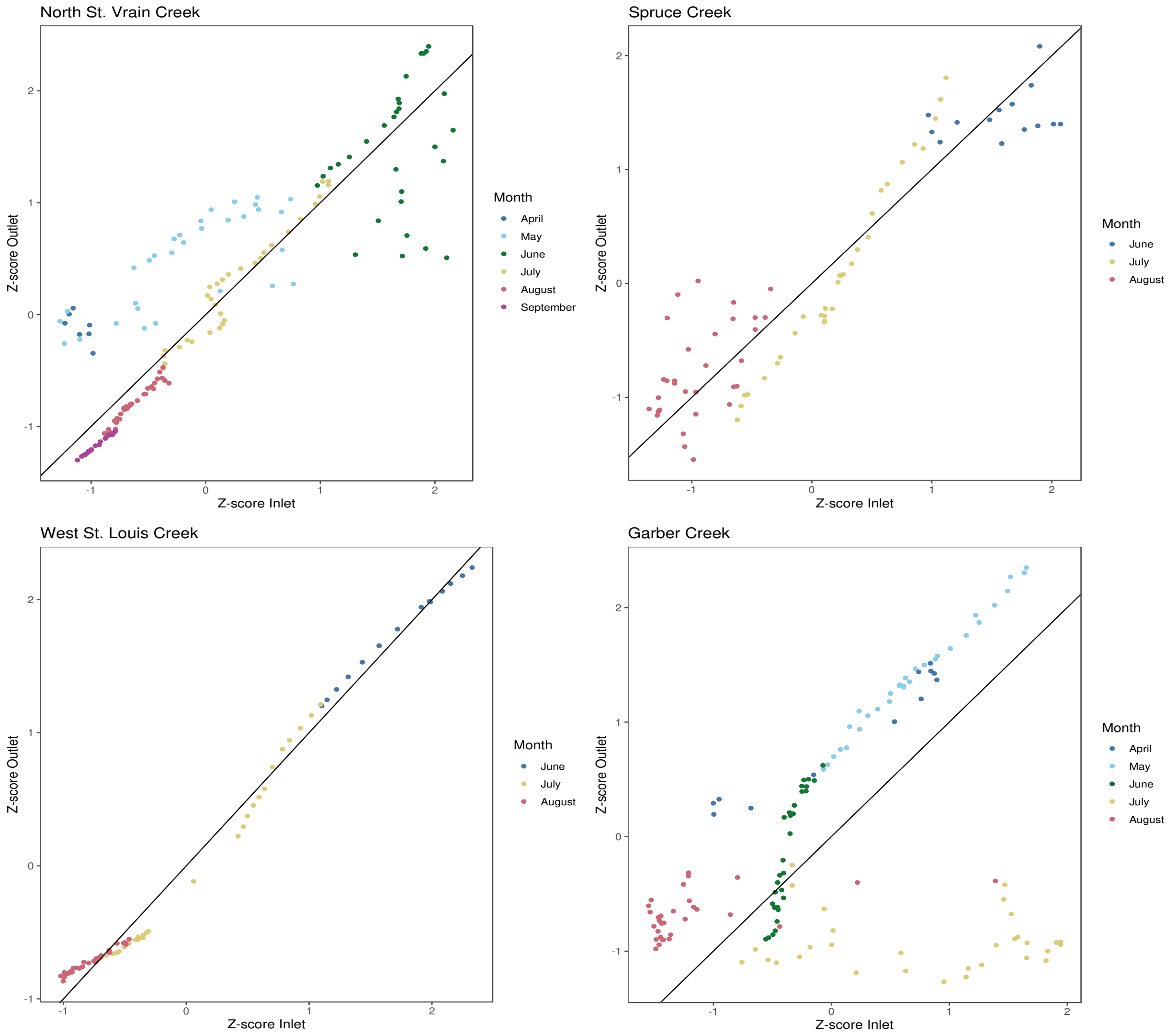


Figure 3.9a. Hysteresis curves of the normalized stage data ("z-score") at the outlet and inlet of each active meadow. Sites showing attenuation are listed first for each meadow type. Attenuation is visible in a deviation from the 1:1 line toward the inlet at peak flows, and toward the outlet during the recession limb (e.g. North St. Vrain Creek). Meadows that do not show attenuation lack this signature and may show an opposite trend.

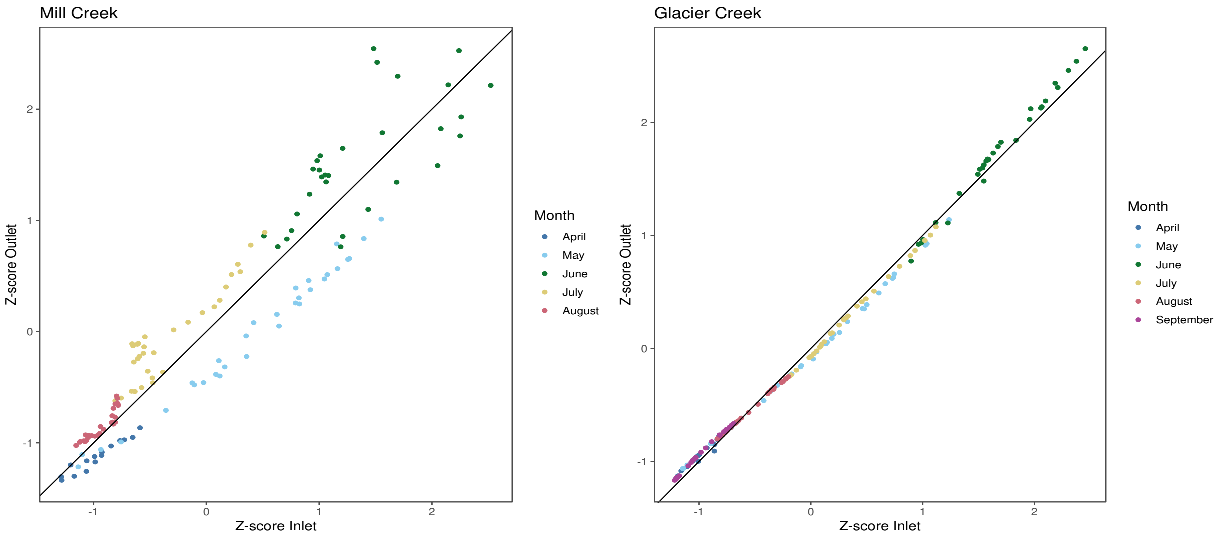


Figure 3.9b. Hysteresis curves of the normalized stage data ("z-score") at the outlet and inlet of each partially active meadow.

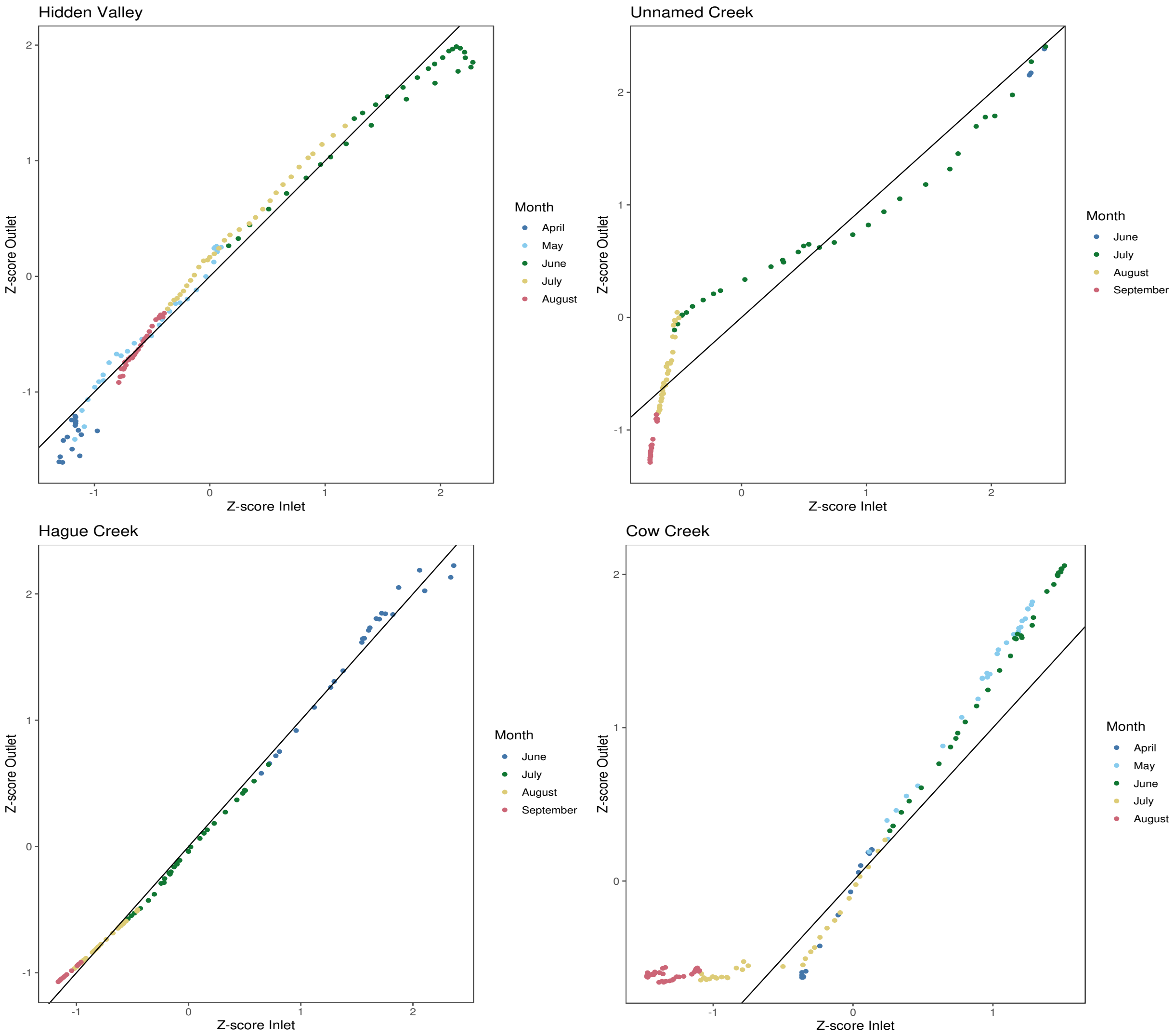


Figure 3.9c. Hysteresis curves of the normalized stage data (“z-score”) at the outlet and inlet of each recently abandoned meadow.

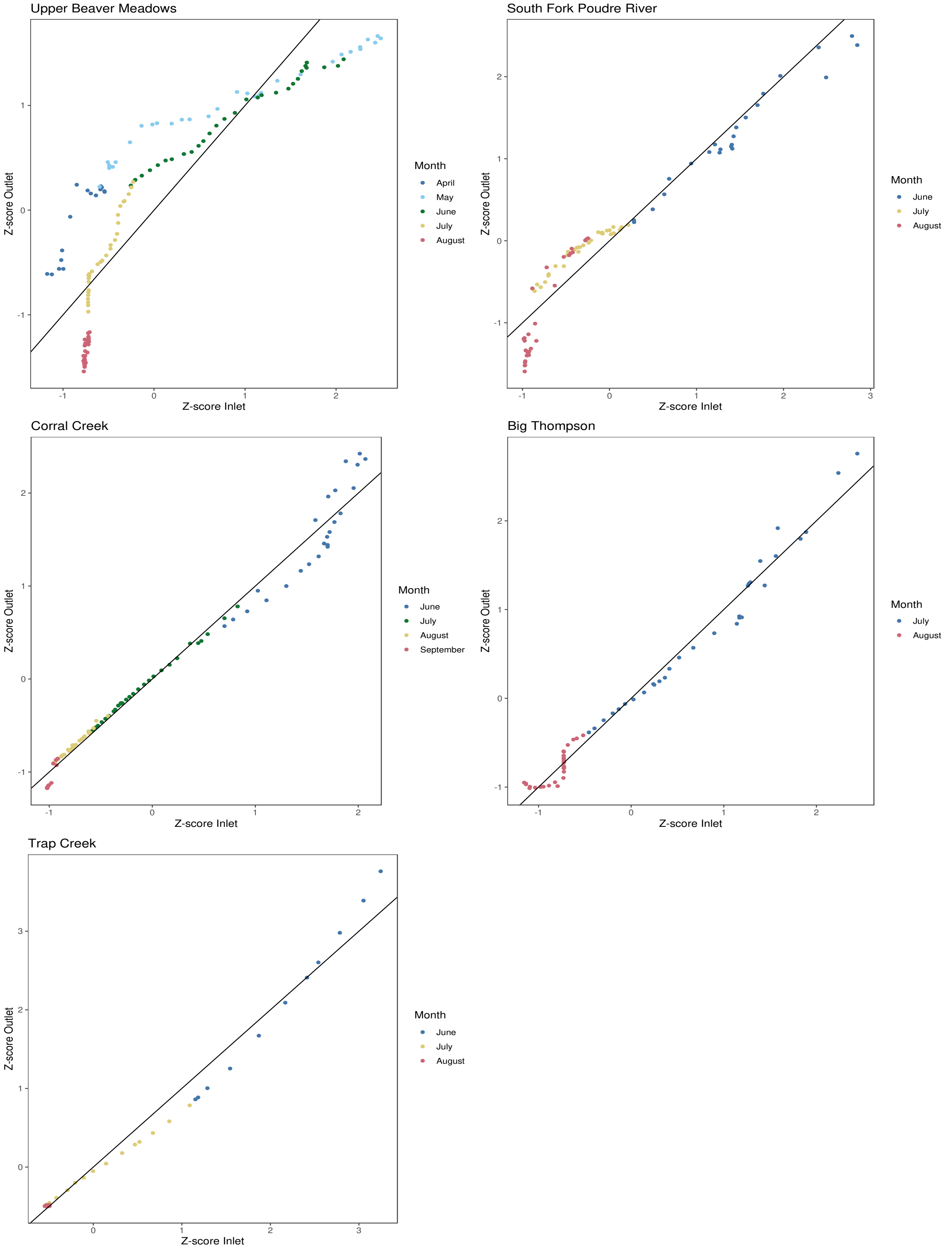


Figure 3.9d. Hysteresis curves of the normalized stage data ("z-score") at the outlet and inlet of each long abandoned meadow.

3.5 Discussion and Conclusions

The effects of beaver ecosystem engineering on stream flow are not as straightforward as originally envisioned in our conceptual model (Figure 3.1). Although multiple linear regression analysis indicates that beaver activity significantly influences the magnitude of peak flow attenuation, our analyses suggest that additional factors influence how beaver engineering decreases peak flow magnitudes, augments base flow in the drier months, and increases lag time of the recession curve (attenuation) (Figure 3.10). Evaluation of the seasonal hydrograph at individual beaver meadows provides insight into the complexities that govern the effects of beaver activities on hydrologic response.

The lack of peak flow decrease and lack of base flow enhancement in the active meadows at Spruce Creek and West St. Louis Creek (Figure 3.7), for example, may reflect the presence of multiple channel-spanning dams in these meadows, with terraced ponds that extend across the entire valley width. In the early part of the summer, these ponds are full to the brim with snowmelt and the meadow does not have much room for additional storage, so the hydrograph peak is translated downstream. Later in the summer, evaporation from the ponds and groundwater recharge may create additional storage, resulting in decreased base flow at the meadow outflow compared to the meadow inflow as the ponds store surface flow. In the stage analysis, these meadows do show some attenuation, but it is minor compared to North St. Vrain Creek. In contrast, the meadow on North St. Vrain Creek is also fully active, with multiple secondary channels, but does not include any dams spanning the main channel. The North St. Vrain meadow has large peak flow decrease and augmentation of base flow later in the summer. Work by Wegener et al. (2017) at this site indicates that increased lateral connectivity allows the meadow to

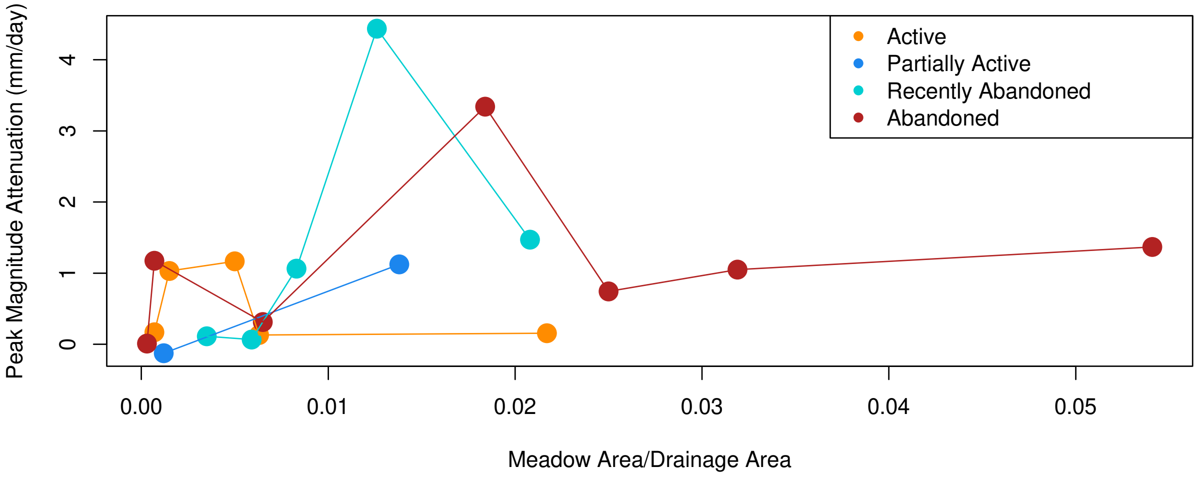


Figure 3.10. Peak flow attenuation plotted against the ratio of meadow area to drainage area in the style of the conceptual diagram. The measured data are not as straightforward as the conceptual diagram. The data show a peak in attenuation at moderate meadow to drainage area ratios, and suggest that partially and fully abandoned meadows have greater overall peak attenuation.

function as a sink for water during high flow and a source during base flow. The hysteresis plot indicates strong attenuation for this meadow. The manner in which longitudinal and lateral connectivity change in the different beaver meadows likely exerts a strong influence on hydrologic response. Longitudinal connectivity is high in all three meadows during peak flow but declines during base flow at the Spruce and West St. Louis sites. Lateral connectivity is likely relatively constant at the Spruce and West St. Louis sites, but increases substantially during peak flow at North St. Vrain. Declining longitudinal connectivity at Spruce and West St. Louis may cause the decreased base flow. Increased lateral connectivity during peak flow and decreased lateral connectivity during base flow may explain the increased base flow below the North St. Vrain site.

Hidden Valley Creek is a recently abandoned site, but like Spruce Creek and W St. Louis Creek, it retains at least one channel-spanning dam at the downstream end of the meadow. This dam increases the lateral connectivity of the meadow during high flow, leading to significant attenuation of the peak snowmelt flow. The lateral connectivity decreases during lower flow and the water that laterally moved into floodplain at high flow returns to the channel, augmenting the base flow late in the summer. The partially active meadow on Mill Creek behaves similarly as the result of dams that create secondary channels in the upstream half of the meadow. Glacier Creek, in contrast, is a partially active meadow but has no dams on the main stem and has less beaver influence over the extent of the meadow than a fully active meadow. As a result, the lateral and longitudinal connectivity does not alter substantially through the season and there is virtually no attenuation of peak flow or augmentation of base flow (Figure 3.7, 3.9).

These observations suggest that simply categorizing beaver meadows with respect to level of beaver activity does not adequately characterize the effects of beaver engineering on stream flow. Two additional approaches should be evaluated in future studies. When developing a dataset evaluating trends across numerous beaver meadows, as in our study, insights could be enhanced by creating more detailed metrics of beaver engineering, such as number of cross-channel dams per unit length of channel, proportion of the meadow area occupied by surface water, or storage capacity of ponds. When working with a smaller number of study sites, taking a more process-based approach that quantifies surface and subsurface flow paths could provide useful insight into the site-specific effects of beaver engineering.

Multiple linear regression analyses also suggest that other physical characteristics of beaver meadows, beyond level of beaver activity, influence the alteration of stream flow by meadows. Valley slope, valley width, and ratio of meadow area to drainage area are additional explanatory factors from the models for the peak magnitude attenuation. Across different beaver activity in the meadows, lower valley slope, smaller drainage area, and lower elevation are associated with greater attenuation. Lower valley slope may correspond to greater extent of overbank flow, as these sites have a broader valley floor and more of a trapezoidal valley cross section, relative to sites with a steeper valley slopes and a more V-shaped valley cross section. A smaller drainage area may equate to more attenuation of the seasonal flow peak entering the beaver meadow. Larger drainage area commonly equates to greater peak flow attenuation in the absence of beaver activity (e.g., Menabde et al., 2001) but the effect of a single beaver meadow on attenuation may be greatest in a small watershed. Lower elevation may correspond to greater attenuation because of the greater potential for evapotranspiration from beaver ponds and riparian vegetation in the warmer, drier conditions at lower elevations in the study area, or because of greater groundwater recharge at lower elevations.

Similarly, larger ratio of valley to channel width and larger ratio of meadow area to drainage area are associated with greater peak flow attenuation. These correlations are intuitive: a wider beaver meadow relative to the main channel and a larger meadow size for a given drainage area should facilitate greater overbank flow and peak magnitude attenuation.

Returning to our original conceptual model, we find that the model does not accurately reflect our observations. Instead, the curve for attenuation of peak flow magnitude peaks at a relatively small ratio of meadow area to drainage area and the attenuation is greater at abandoned meadows (Figure 3.10), suggesting that factors other than area ratio most strongly influence the magnitude of peak flow attenuation. With respect to the hypotheses, there is no significant difference in retention of surface flow between active and abandoned meadows (Figures 3.4 to 3.6), so we reject *H1*. Retention does not necessarily decrease with time after beavers abandon a meadow, when assessed across multiple meadows with differing histories of abandonment, so we reject *H2*. The most rigorous test of *H2* would be to evaluate hydrologic characteristics of a particular beaver meadow(s) before and after abandonment, but this has not yet been done. Additional parameters do help to explain observed flow retention in beaver meadows, which supports *H3*.

Recently (Pollock et al., 2014), and at varying times in the past (e.g., Scheffer, 1938; Albert and Trimble, 2000), beaver reintroduction has been suggested as a tool for restoring riparian zones altered by overgrazing or channel incision. Beaver dams demonstrably increase the retention of water in a river network, but our comparison of seasonal hydrographs across 19 beaver meadows with diverse characteristics indicates that predicting the magnitude of hydrograph change associated with beaver engineering is not straightforward. Changes in peak and base flow downstream from a meadow occupied by beavers depend on the level of physical alteration in the river corridor caused by beaver activities, but also on such basic physical characteristics as contributing drainage area, downstream gradient of the beaver meadow, size of the beaver meadow relative to contributing drainage area, and width of the meadow relative to the main channel. These and other physical characteristics may be particularly important in governing the distribution of stored peak flow into evapotranspiration, subsurface storage, and stream flow via mechanisms that are not adequately captured in our analyses. The results summarized here, combined with more detailed, site-specific investigations such as that of

Wegener et al. (2017), suggest that conceptually or quantitatively characterizing the three-dimensional (longitudinal, lateral, vertical) connectivity of each beaver meadow may be necessary to predict the specific effects of beaver engineering on different components of the seasonal hydrograph.

REFERENCES

Albert S, T Trimble. 2000. Beavers are partners in riparian restoration on the Zuni Indian Reservation. Ecological Restoration 18: 87-92.

Alexander RR, RK Watkins. 1977. The Fraser Experimental Forest, Colorado. General Technical Report RM-40. USDA Forest Service. 39 p.

Anderson RS, Riihimaki CA, Safran EB, MacGregor KA. 2006. Facing reality: late Cenozoic evolution of smooth peaks, glacially ornamented valleys, and deep river gorges of Colorado's Front Range. In, SD Willett, N Hovius, MT Brandon, DM Fisher, eds. Tectonics, Climate, and Landscape Evolution. Geological Society of America Special Paper 398, Boulder, CO, 397-418.

Andrews TG. 2015. Coyote Valley: Deep history in the high Rockies. Harvard University Press, Cambridge, MA.

Baker BW, EP Hill. 2003. Beaver. In, GA Feldhammer, BC Thompson and JA Chapman, editors, Wild mammals of North America: biology, management, and conservation, 2nd edition. The Johns Hopkins University Press, Baltimore, Maryland, 288-310.

J. Baldwin J. 2015. Potential mitigation of and adaptation to climate-driven changes in California's highlands through increased beaver populations. California Fish and Game 101: 218-240.

Bryant B. 1979. Geology of the Aspen 15-minute Quadrangle, Pitkin and Gunnison Counties, Colorado. Geological Survey Professional Paper 1073. US Geological Survey. United States Government Printing Office, Washington. 153 p.

Burchsted B, MD Daniels, R Thorson, J Vokoun. 2010. The river discontinuum: applying beaver modifications to baseline conditions for restoration of forested headwaters. BioScience 60: 908-922.

Burns DA, JJ McDonnell. 1998. Effects of a beaver pond on runoff processes: comparison of two headwater catchments. Journal of Hydrology 205: 248-264.

Butler DR, GP Malanson. 1995. Sedimentation rates and patterns in beaver ponds in a mountain environment. Geomorphology 13: 255-269.

Coles JM, BJ Orme. 1983. *Homo sapiens* or *Castor fiber*? Antiquity LVII: 95-102.

Cronon W. 1983. Changes in the Land: Indians, Colonists, and the Ecology of New England. Hill and Wang, New York.

Giriat D, E Gorczyca, M Sobucki. 2016. Beaver ponds' impact on fluvial processes (Beskid Niski Mts., SE Poland). Science of the Total Environment 544: 339-353.

Green KC, CJ Westbrook. 2009. Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams. BC Journal of Ecosystems and Management 10: 68-79.

Hardy T, P Panja, D Mathias. 2005 WinXSPRO, A Channel Cross Section Analyzer, User's Manual, Version 3.0. Gen. Tech. Rep. RMRS-GTR-147. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 94 p.

Hood GA, SE Bayley. 2008. Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. Biological Conservation 141: 556-567.

Ives RL. 1942. The beaver-meadow complex. Journal of Geomorphology 5: 191-203.

Jarrett RD. 1984. Hydraulics of high-gradient streams. Journal of Hydraulic Engineering 110: 1519-1539.

John S, A Klein. 2004. Hydrogeomorphic effects of beaver dams on floodplain morphology: avulsion processes and sediment fluxes in upland valley floors (Spessart, Germany). Quaternaire, 15: 219-231.

Johnston CA. 2014. Beaver pond effects on carbon storage in soils. Geoderma 213: 371-378.

Kramer N, EE Wohl, DL Harry. 2012. Using ground penetrating radar to 'unearth' buried beaver dams. Geology 40: 43-46.

Laurel D, E Wohl. 2019. The persistence of beaver-induced geomorphic heterogeneity and organic carbon stock in river corridors. Earth Surface Processes and Landforms 44: 342-353.

Lautz LK, DI Siegel, RL Bauer. 2006. Impact of debris dams on hyporheic interaction along a semi-arid stream. Hydrological Processes 20: 183-196.

Meentemeyer RK, DR Butler. 1999. Hydrogeomorphic effects of beaver ponds in Glacier National Park, Montana. Physical Geography 20: 436-446.

Menabde M, S Veitzer, V Gupta, M Sivapalan. 2001. Tests of peak flow scaling in simulated self-similar river networks. Advances in Water Resources 24: 991-999.

Mills EA. 1913. In beaver world. Houghton Mifflin, Boston.

Morgan LH. 1868. The American beaver and his works. J.B. Lippincott & Co., Philadelphia.

Morgan ML, J McHarge, PE Barkmann. 2006. OF-05-06 Geologic Map of the Sedalia Quadrangle, Douglas County, Colorado. Geology. Open File Reports. Denver, CO: Colorado Geological Survey, Division of Minerals and Geology. Department of Natural Resources.
Naiman RJ, JM Melillo, JE Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67: 1254-1269.

Naiman RJ, CA Johnston, JC Kelley. 1988. Alteration of North American streams by beaver. BioScience 38: 753-762.

Naiman RJ, G Pinay, CA Johnston, J Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75: 905-921.

Nyssen J, J Pontzeele, 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.

Pollock MM, TJ Beechie, JM Wheaton, CE Jordan, N Bouwes, N Weber, C Volk. 2014. Using beaver dams to restore incised stream ecosystems. BioScience 64: 279-290.

Pollock MM, Lewallen GM, Woodruff K, Jordan CE, Castro JM (Editors). 2017. *The Beaver Restoration Guidebook: Working with Beaver to Restore Streams, Wetlands, and Floodplains*. Version 2.0. United States Fish and Wildlife Service, Portland, Oregon. 219 pp. Online at: https://www.fws.gov/oregonfwo/promo.cfm?id=177175812

Polvi LE, 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.
Ray AM, AJ Rebertus, HL Ray. 2001. Macrophyte succession in Minnesota beaver ponds. Canadian Journal of Botany 79: 487-499.

Rolauffs P, D Hering, S Lohse. 2001. Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. Hydrobiologia 459: 201-212.

Rosell F, O Bozser, P Collen, H Parker. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Review 35: 248-276.

Ruedemann R, WJ Schoonmaker. 1938. Beaver-dams as geologic agents. Science 88: 523-525.

Scheffer PM. 1938. The beaver as an upstream engineer. Soil Conservation 3: 178-181.

U.S. Geological Survey, 2016, The StreamStats program, online at http://streamstats.usgs.gov, accessed on (3/10/2018).

Veblen TT, JA Donnegan. 2005. Historical range of variability for forest vegetation of the national forests of the Colorado Front Range. Final report, USDA Forest Service, agreement no. 1102-0001-99-033.

Wegener P, T Covino, E Wohl. 2017. Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism. Water Resources Research 53: 4606-4623.

Westbrook CJ, DJ Cooper, BW Baker. 2006. Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. Water Resources Research 42: W06404, 12 pp.

Westbrook CJ, DJ Cooper, BW Baker. 2011. Beaver assisted river valley formation. River Research and Applications 27: 257-256.

Wohl E. 2013. Landscape-scale carbon storage associated with beaver dams. Geophysical Research Letters 40: 1-6.

Wohl E, JN Kuzma, NE Brown. 2004. Reach-scale channel geometry of a mountain river. Earth Surface Processes and Landforms 29: 969-981.

Wohl E, KB Lininger, DN Scott. 2017. River beads as a conceptual framework for building carbon storage and resilience to extreme climate events into river management. Biogeochemistry. DOI 10.1007/s10533-017-0397-7.

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

Wright JP, CG Jones, AS Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132: 96-101.

4 CONCLUSION

Studies of beaver influence on stream and meadow hydrology, sediment, carbon, and other nutrient dynamics have tended to focus on single ponds or meadows and have looked predominantly at the alterations that occur when beaver move into an environment. These existing studies agree that beavers exert a strong control on the fluxes of water, sediment, carbon, and nutrients, leading to the creation of heterogeneous wetland ecosystems. The altered environment provides rich habitat that leads to increased biodiversity over time, making beavers historically a keystone species in river ecosystems throughout North America (*Castor canadensis*) and much of Europe (*Castor fiber*). In the Colorado mountains, beaver now occupy a fraction of the unconfined valley bottom meadows that they did historically, and there have been few studies that look at how beaver-altered ecosystems change over time after beaver have disappeared from their historic habitats. My study aimed to investigate the alteration in hydrology, geomorphology, and carbon fluxes of beaver meadow environments after the beaver disappear. I proposed conceptual models for nonlinear changes in the geomorphology, organic carbon storage and hydrologic storage of current and former beaver meadows and tested these models with investigations of the geomorphic heterogeneity in the morphology, the soil organic carbon content, and the meadow effect on stream flow.

I investigated beaver influence on meadow floodplain morphology and soil organic carbon in 7 active and abandoned beaver meadows in the Colorado mountains. I found evidence to support the idea that the morphology of the meadows changes nonlinearly with time; the geomorphic heterogeneity in floodplain features was similar between active, partially active, and recent abandoned meadows. Only long abandoned meadows differed significantly from the rest and had much less spatially heterogeneous morphology, with simplified channel planform and less floodplain variation. I investigated additional controls on soil organic carbon stock and found that beaver activity and geomorphic heterogeneity are not the primary influence on OC stock. Soil depth is a strong influence on the total soil organic carbon stock, and the meadows with the greatest soil depth were the recently abandoned and partially active meadows. The meadow with the deepest measured soil depth had characteristics that contribute to soil aggradation, including being located above the Pleistocene terminal moraine, having a small drainage area, and having an intact beaver dam at the downstream outlet from the meadow. In contrast, shallower soils and lower soil organic carbon stock were found in the active and abandoned meadows with the largest drainage areas, perhaps because of greater sediment transport capacity and lateral channel migration in the larger catchments. The storage of organic carbon stocks through time after beaver abandon a meadow is a balance between decreased autochthonous inputs from the changing riparian vegetation supported by beaver alterations and the export of soil organic carbon along with sediment via fluvial erosion. Transition to a simplified planform may reduce the export of sediment and result in longer-term storage of existing meadow carbon stocks.

Beaver effect on stream flow was examined over a larger sample size of 19 meadows in the Southern Rockies of Colorado. Across the study locations, beaver activity alone was insufficient to explain peak flow decrease, base flow augmentation, or lag in the recession curve of the stream hydrograph (attenuation) between the meadow inlets and outlets. There was no significant difference in these metrics between the different categories of beaver activity, also indicating that differences between meadows are not the result of changes through time, nonlinear or otherwise. Rather, I found that other characteristics of each meadow, such as the drainage area, longitudinal valley slope, ratio of meadow area to drainage area, and valley width contribute to explaining the variation in peak flow attenuation, likely because they contribute to the changing dynamics of lateral, vertical, and longitudinal connectivity throughout the summer season, and to partitioning of water between the channel, surface floodplain storage, subsurface storage, and evapotranspiration.

Overall, it appears the easily perceived changes to the floodplain and channel morphology occur over a period of several years to decades after beaver abandon a meadow, and the changes do occur nonlinearly through time and may exhibit a threshold. This change in the geomorphology does not, however, appear to have a strong relationship to the function of the meadow floodplain in terms of its storage of organic carbon or its attenuation and release of hydrologic fluxes. Even after beaver disappear, they may have a legacy effect on the function of a meadow as a retention feature in mountain catchments, and other factors may be more important than the presence of beaver modifications for meadow function as a retention feature.

Beaver meadows along mountain streams act like beads along the string of a river, as described by Wohl et al. (2017). Beads store organic carbon and attenuate peak flows. The degree to which beaver activities enhance the existing properties of these beads depends both on the details of the beaver engineering (how many dams and ponds, where they are located), but also on the geomorphic context of the bead itself (position in network, valley geometry, elevation). My results indicate that beaver meadows higher in the network, having smaller drainage areas and on smaller streams may maximize the retention properties of "bead" meadows. These locations may have less lateral channel migration, and slower floodplain turnover, resulting in greater OC storage and, perhaps, greater flow attenuation. These meadows may be good candidates to reintroduce beaver for maximum effect in the catchment.

At several times in the past, and at the present, beaver have been proposed as a tool for restoring channel and floodplain form and function. In the past, restoration has included introducing beaver to incised channels to encourage sediment retention and aggradation, or returning beaver to meadows to enhance wetland restoration and regrowth of riparian vegetation. Recently, beaver have been proposed as a potential tool to aid in increasing carbon sequestration in river corridors to aid in addressing climate change, and as a tool for increasing the resilience of floodplain ecosystems to disturbances like drought and fire (Baldwin, 2015). Studies such as mine are essential for understanding the potential beavers have to meet these and other restoration goals, and to understand the confounding factors that limit or contribute to the potential success of beavers as a restoration tool.

Future work that will move our understanding along in pursuit of these goals includes developing a remote sensing method to characterize floodplain and beaver meadow geomorphic heterogeneity. LiDAR could potentially provide the level of topographic detail necessary to distinguish floodplain morphologic features, but a future study of this method compared to on-the-ground surveys will be necessary to verify its usefulness for this application. Our understanding of soil organic carbon stocks in stream meadows would benefit from dating the carbon and sediment in meadows to quantify not just the volume of carbon stored, but also the storage time and may help elucidate the difference in carbon stocks I found between currently active and long abandoned beaver meadows. Finally, fully understanding the effects that beaver engineering have on stream flow will require continued study of more detailed environmental changes caused by beaver activities, such as number and location of beaver dams, dams per unit of channel length, storage capacity of beaver ponds, and perhaps additional detailed study of the longitudinal, lateral, and vertical flow connectivity in these meadows throughout the snowmelt season. Multi-year studies that capture the inter-annual variability in stream flow, and comparison with channel segments on confined reaches adjacent to the meadow reaches may aid in understanding the confounding variables that currently limit our understanding of beaver effect on stream hydrographs.

REFERENCES

Baldwin J. 2015. Potential mitigation of and adaptation to climate-driven changes in California’s highlands through increased beaver populations. California Fish and Game 101: 218-240.

Wohl E, KB Lininger, DN Scott. 2017. River beads as a conceptual framework for building carbon storage and resilience to extreme climate events into river management. Biogeochemistry. DOI 10.1007/s10533-017-0397-7.

APPENDIX

SUPPLEMENTAL FIGURES

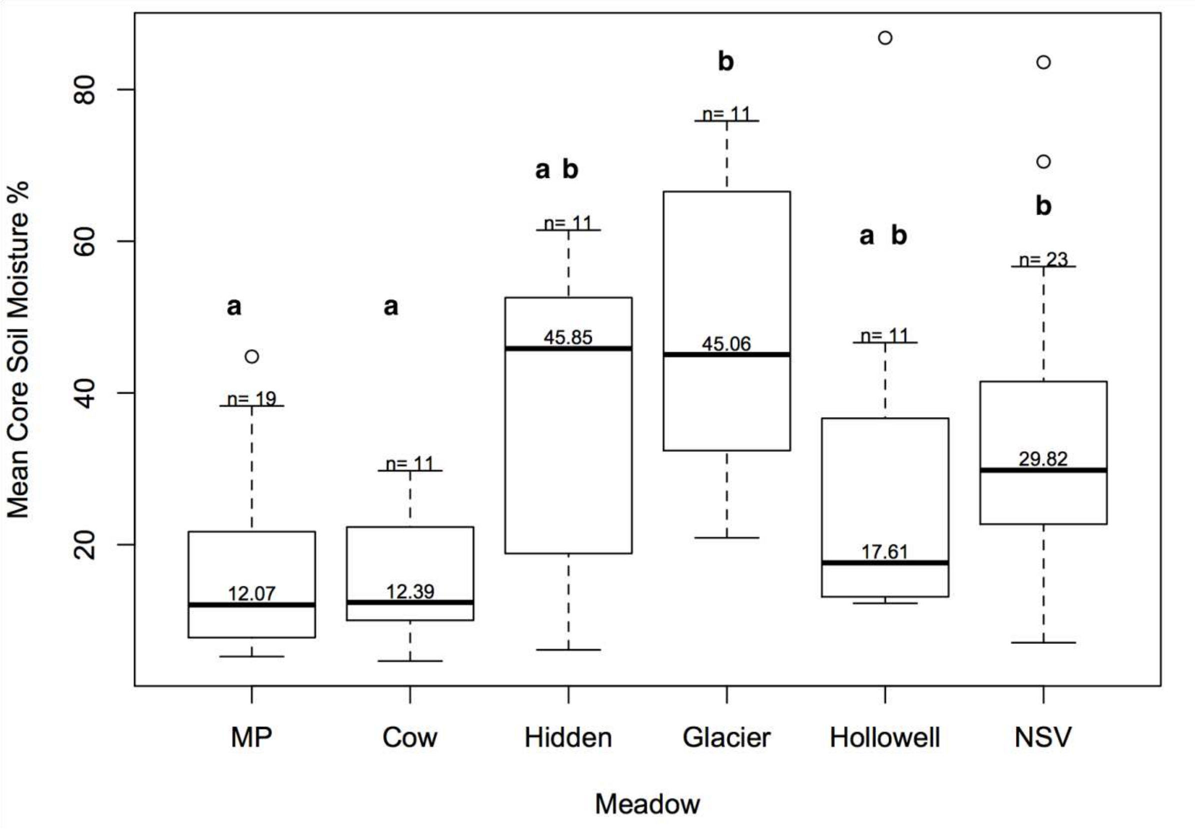


Figure S2.1. Median core soil moisture differs significantly in the active meadow (NSV) and the long abandoned meadow (MP), but other meadows are gradational between these end-members. Letters indicate significant differences. Median values and sample size are listed for each meadow.

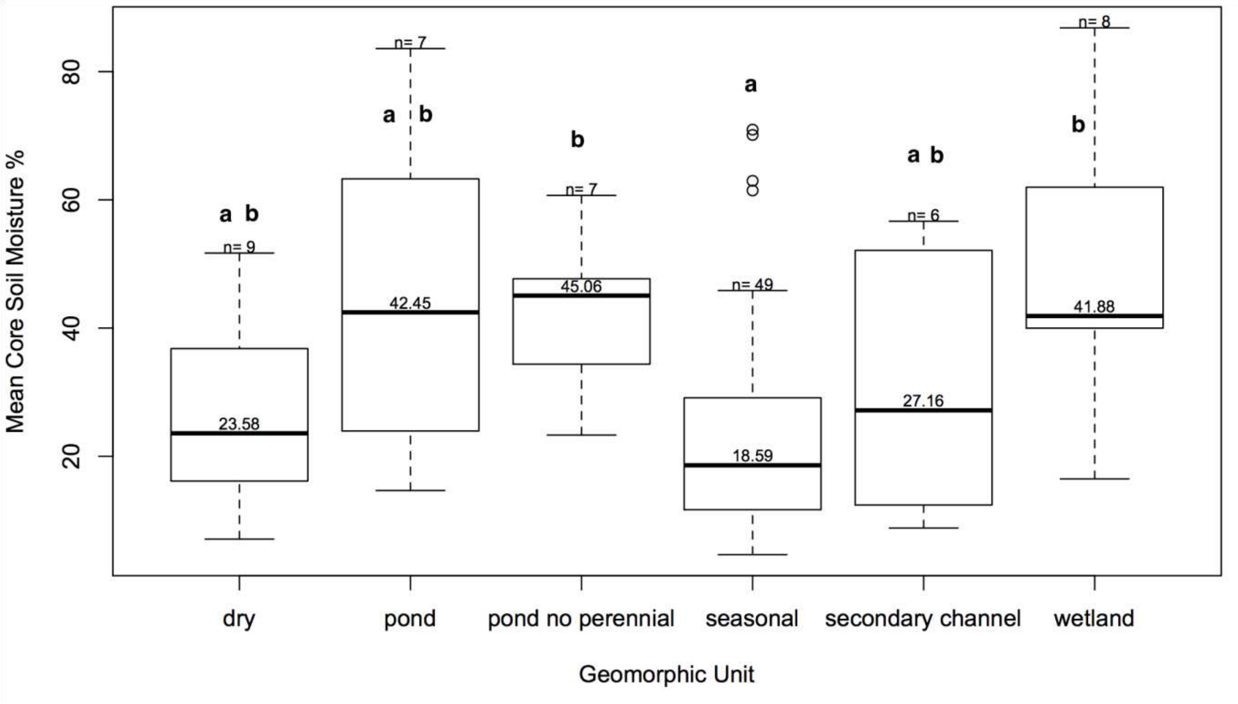


Figure S2.2. Core soil moisture by geomorphic unit. Letters indicate significant differences. Median values and sample size are listed for each floodplain geomorphic unit.

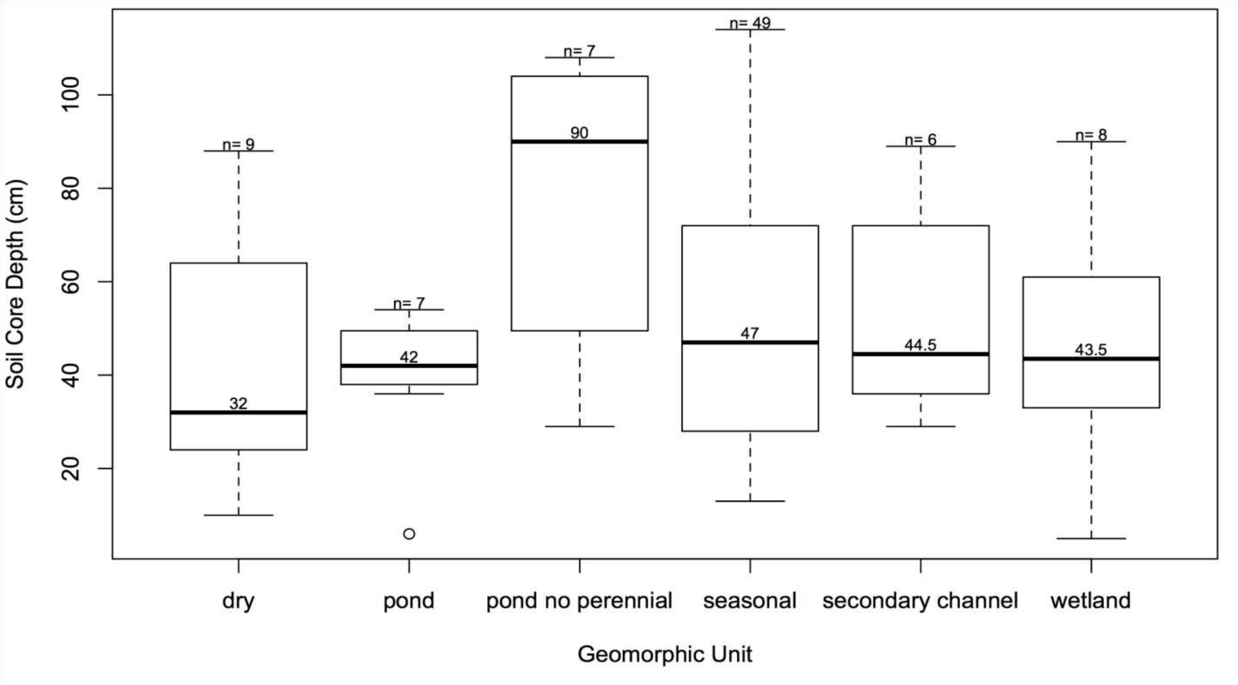


Figure S2.3. Soil core depth in relation to geomorphic unit. No significant differences in median soil core depth among geomorphic units. Median values and sample size are listed for each floodplain geomorphic unit.

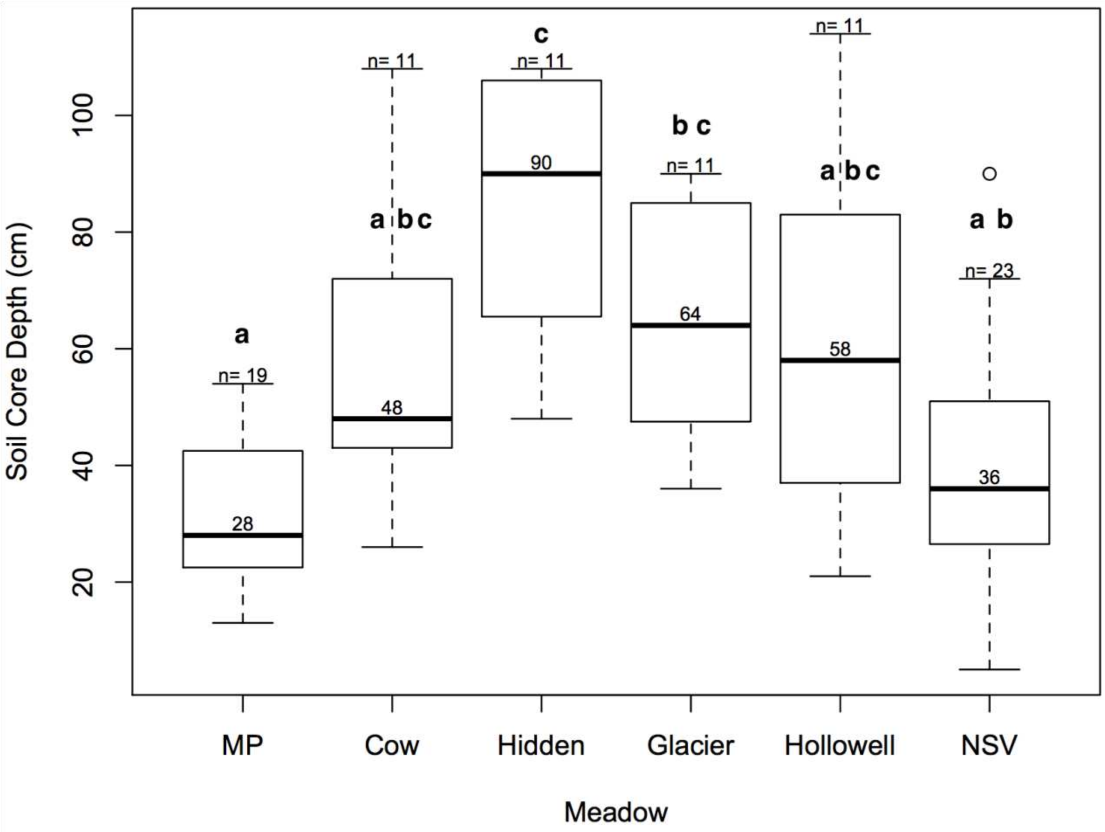


Figure S2.4. Soil core depth by meadow. Letters indicate significant differences. Median values and sample size are listed for each meadow.

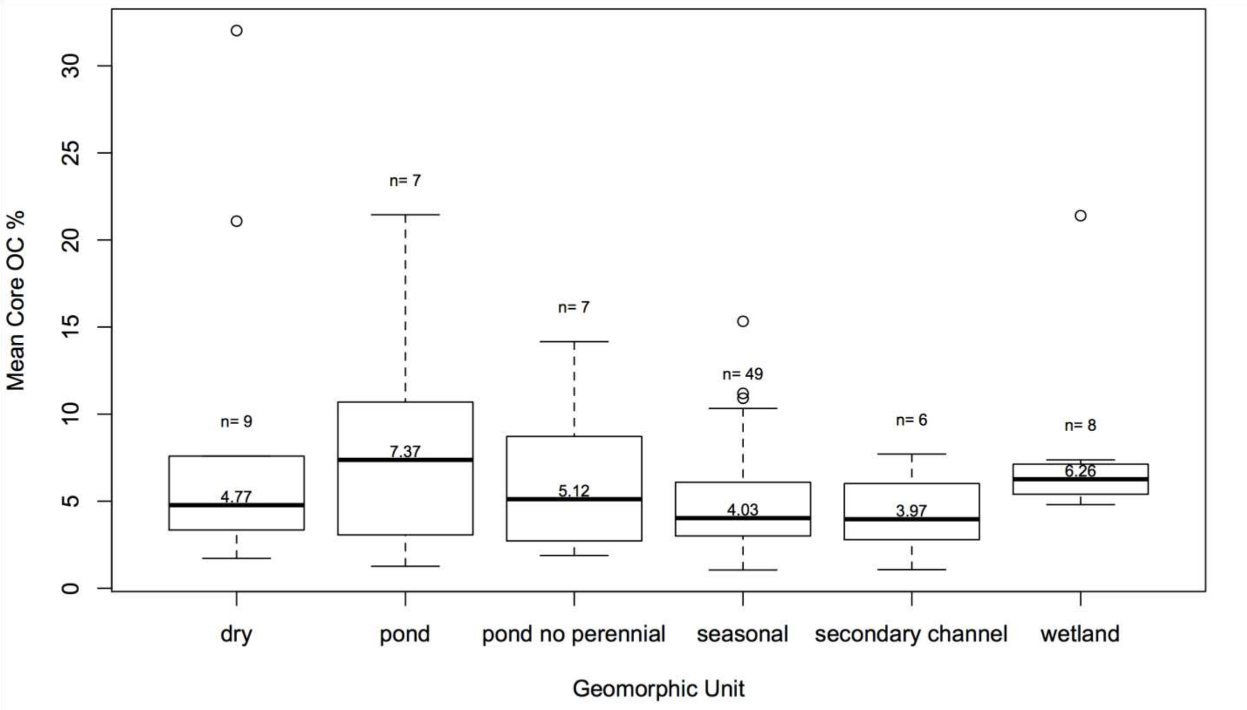


Figure S2.5. Core organic carbon concentration in relation to geomorphic unit. No significant differences in median core OC concentration among geomorphic units. Median values and sample size are listed for each floodplain geomorphic unit.

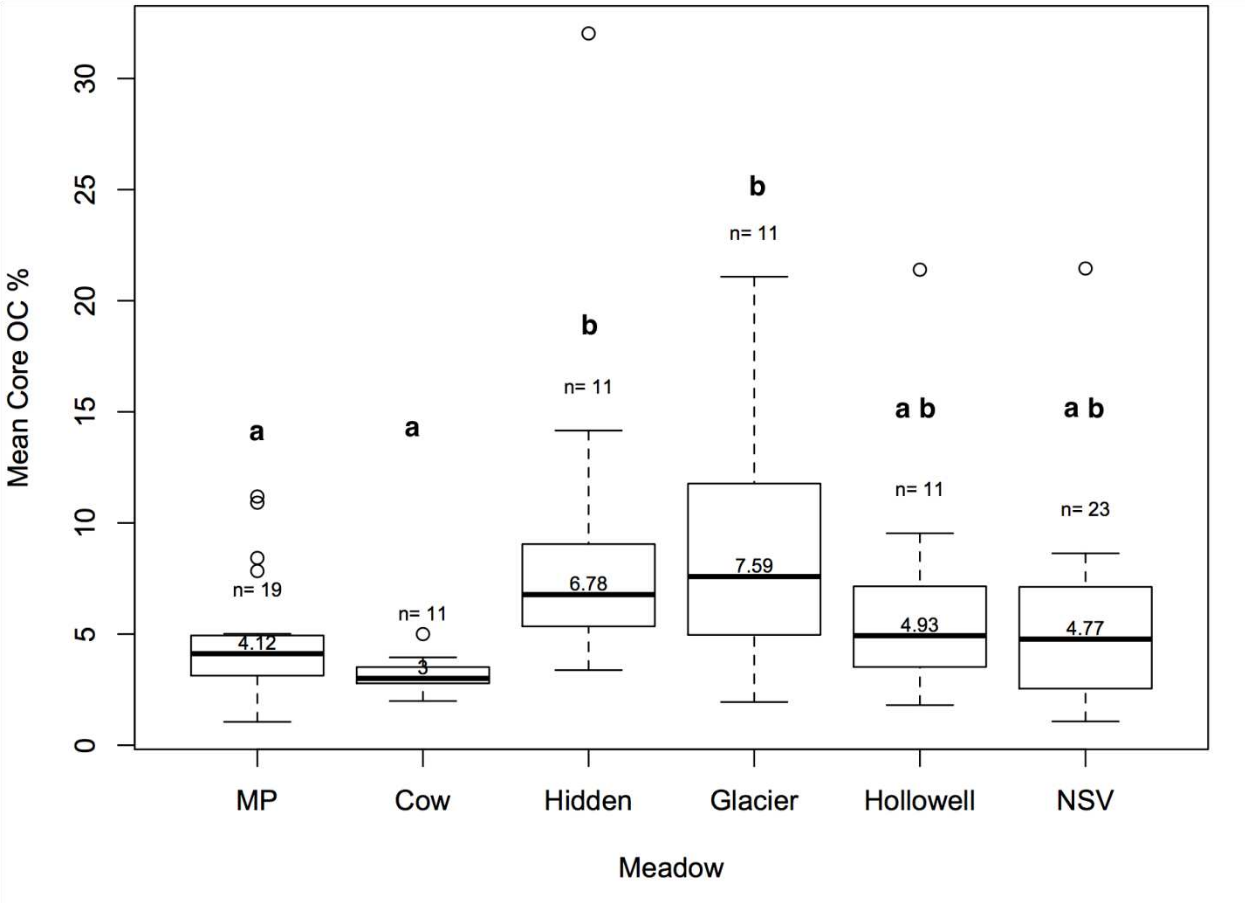


Figure S2.6. Core organic carbon concentration in relation to meadow. Letters indicate significant differences. Median values and sample size are listed for each meadow.

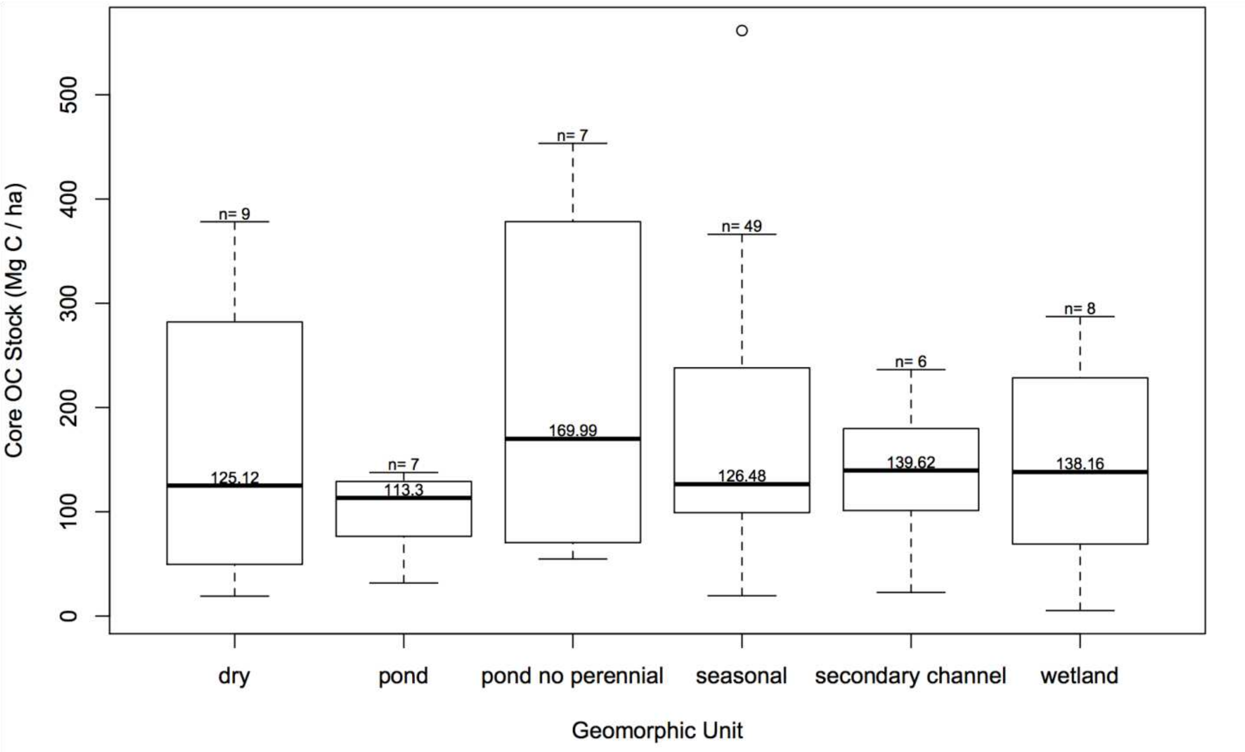


Figure S2.7. Core organic carbon stock in relation to geomorphic unit. No significant differences in median core OC stock among geomorphic units. Median values and sample size are listed for each floodplain geomorphic unit.

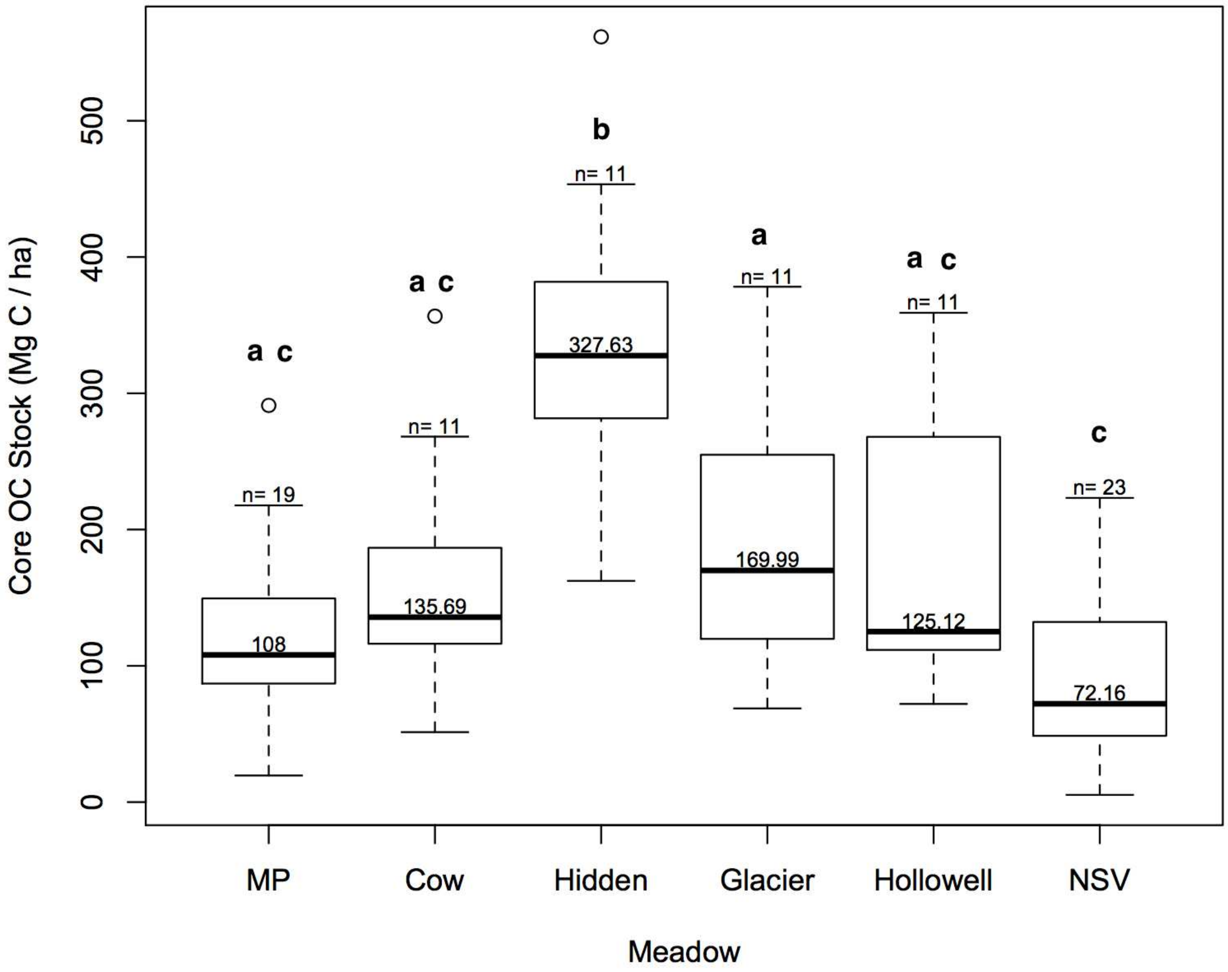


Figure S2.8. Core organic carbon stock in relation to meadow. Letters indicate significant differences. Median value and sample size are listed for each meadow.

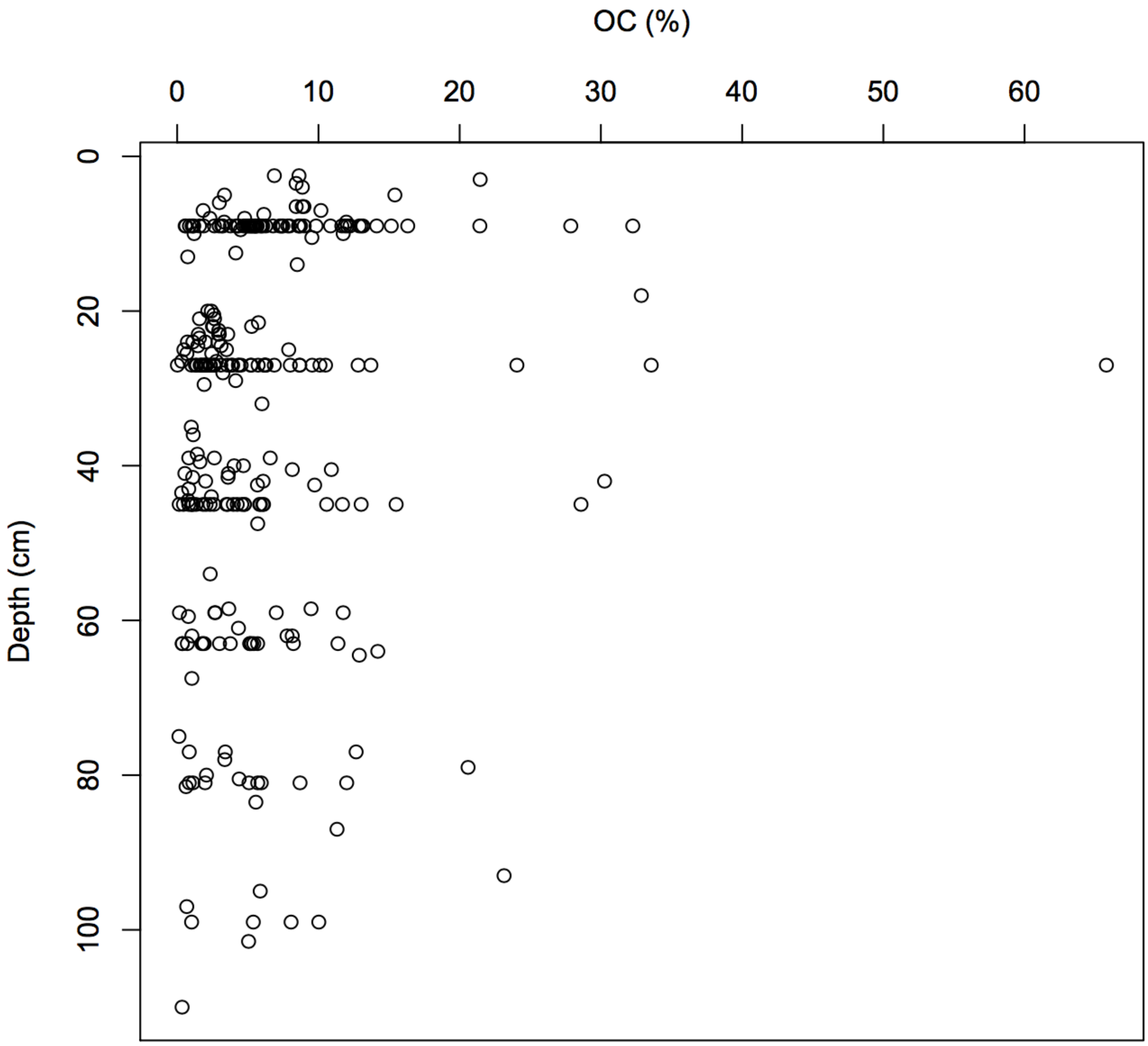
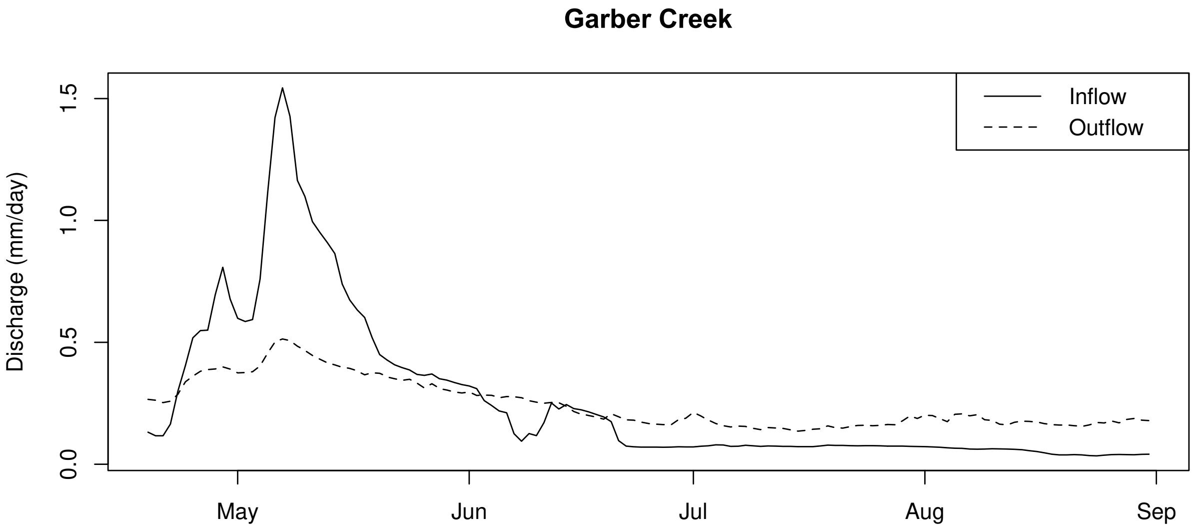


Figure S2.9. Sample organic carbon concentration (%) plotted against the middle depth (cm) of each sample.



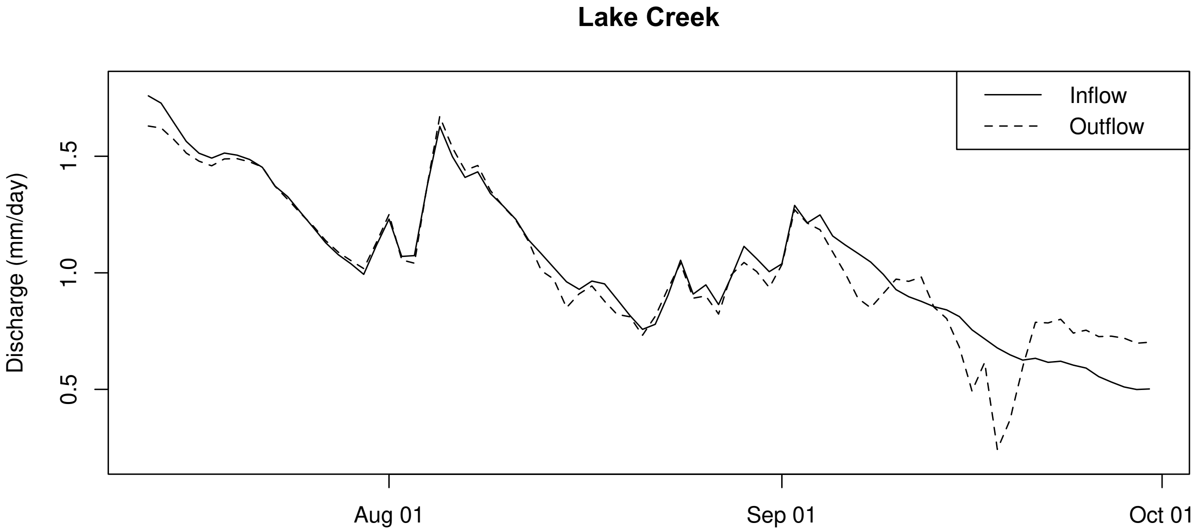


Figure S3.1a. Stream hydrographs for the remaining active meadows.

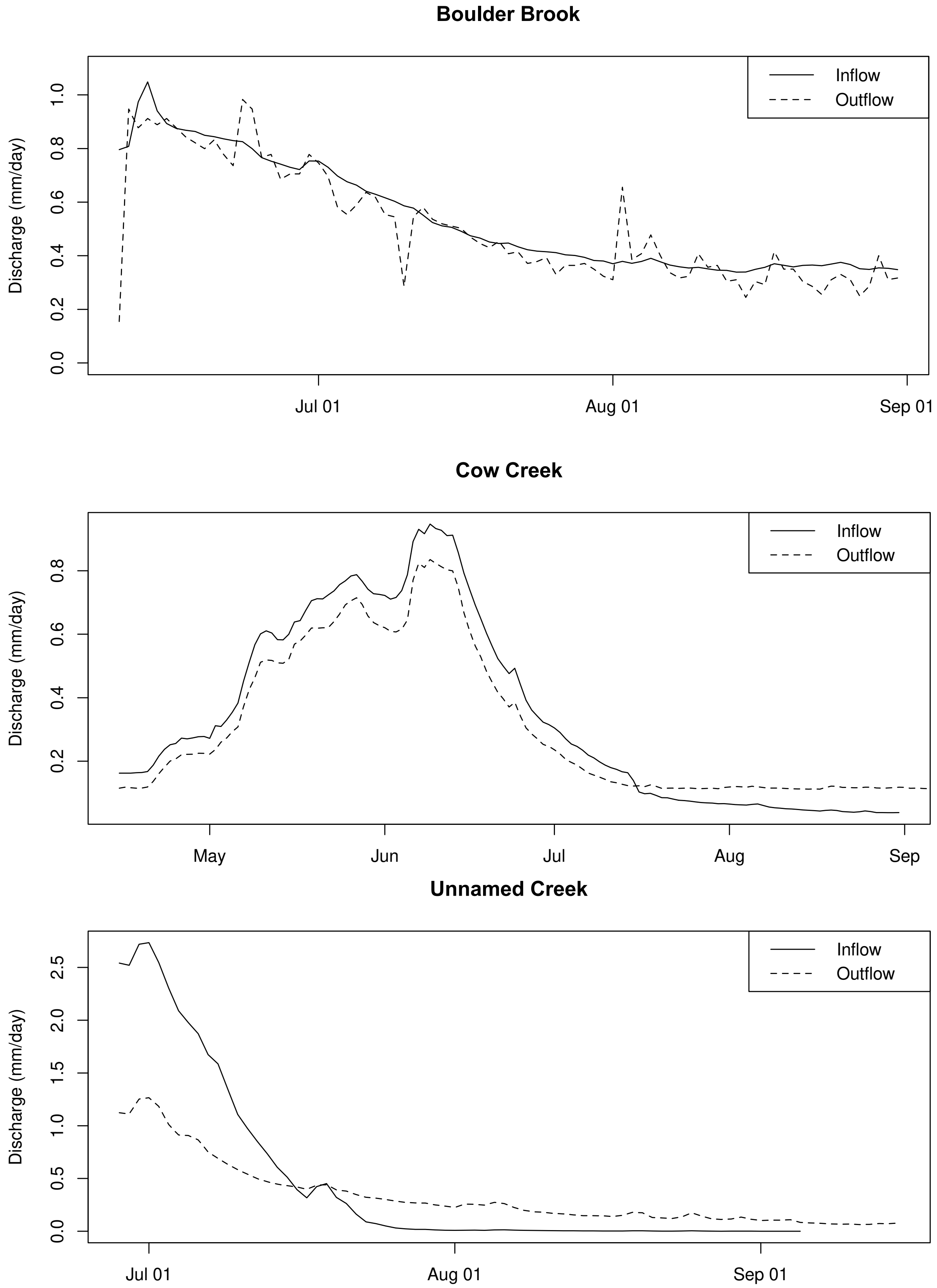


Figure S3.1b. Stream hydrographs for the remaining recently abandoned meadows.

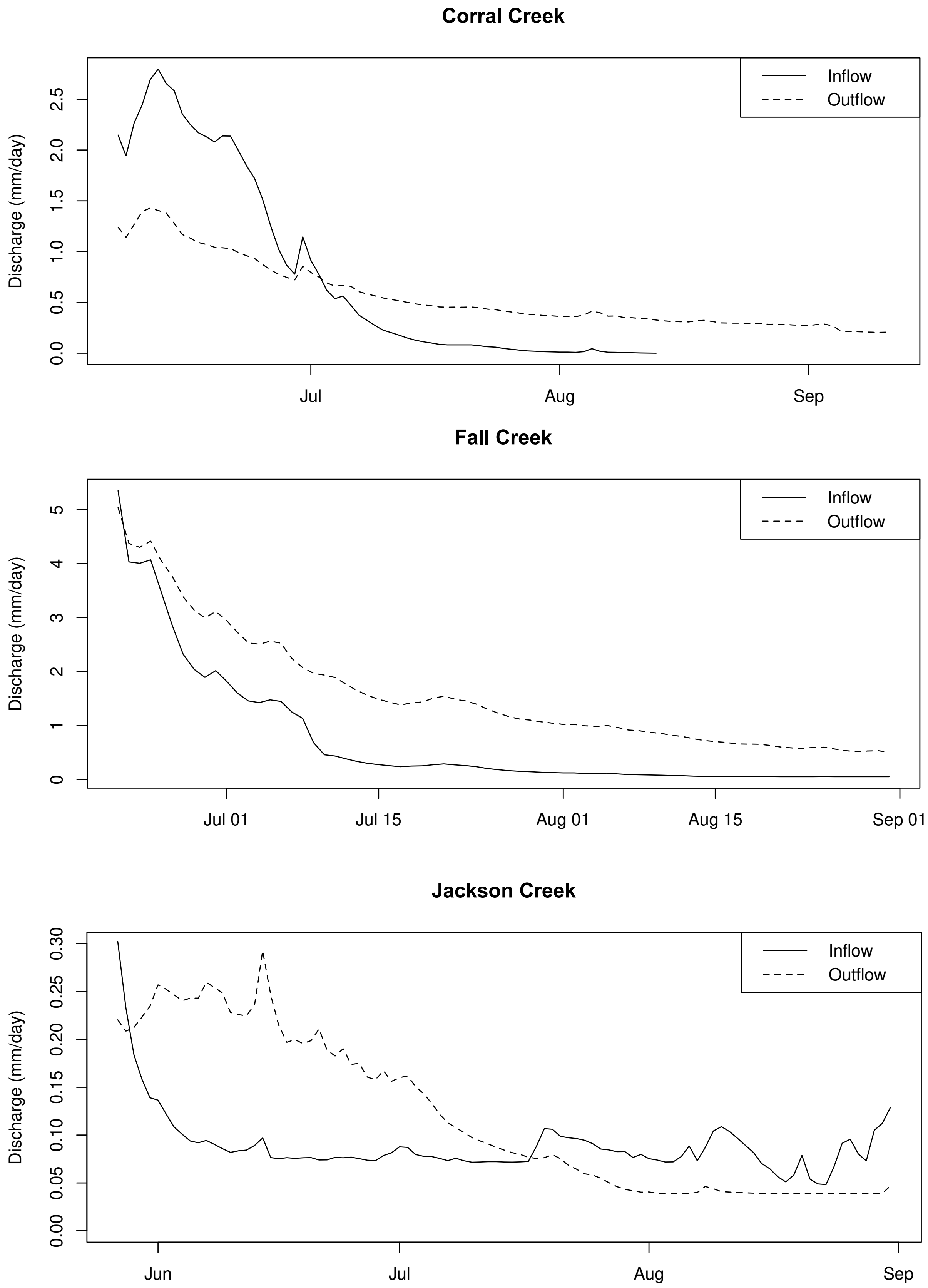
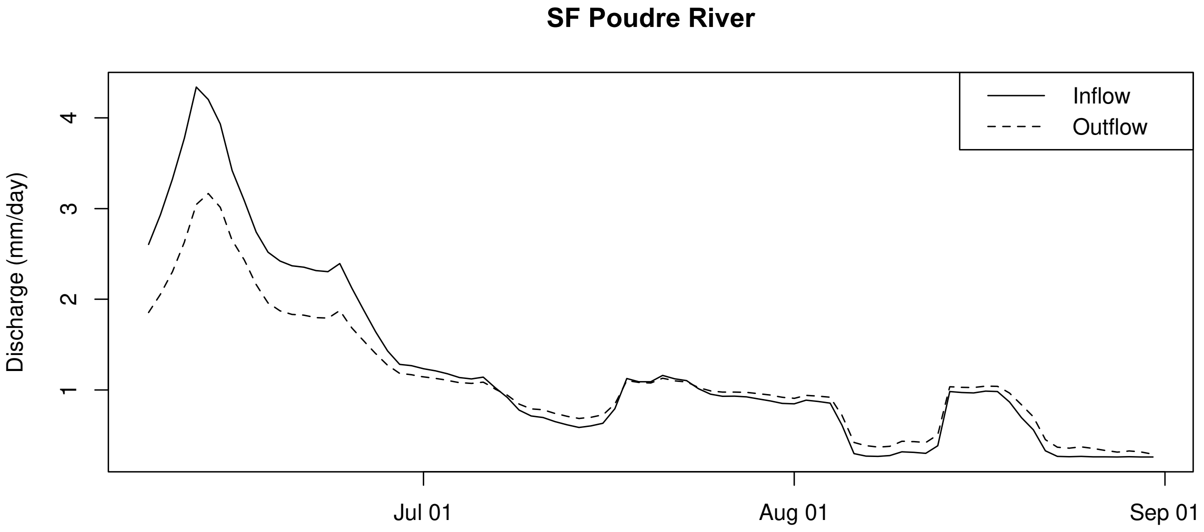


Figure S3.1c. Stream hydrographs for the remaining long abandoned meadows.



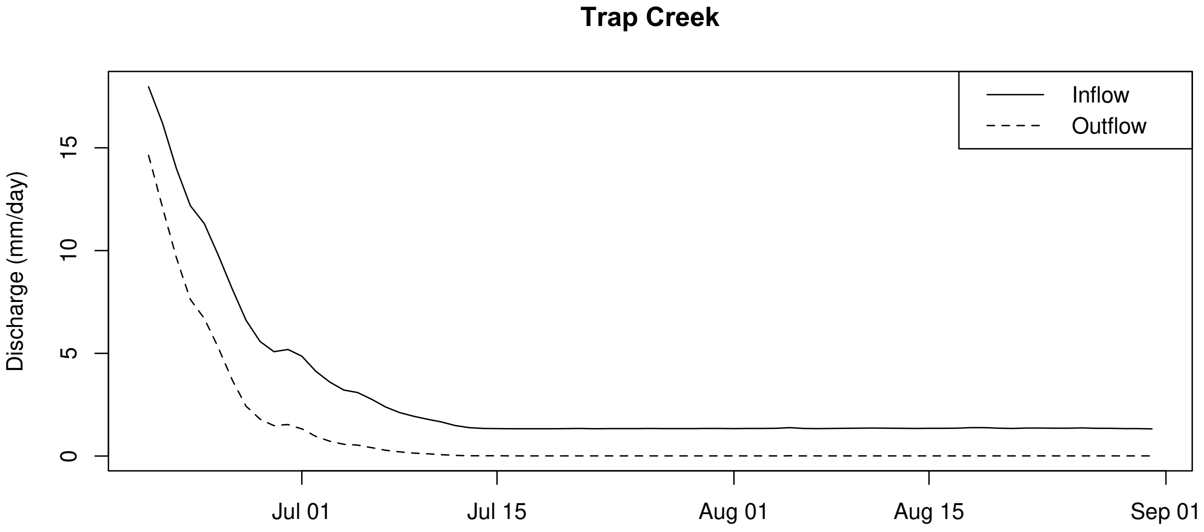


Figure S3.1c continued. Stream hydrographs for the remaining long abandoned meadows.

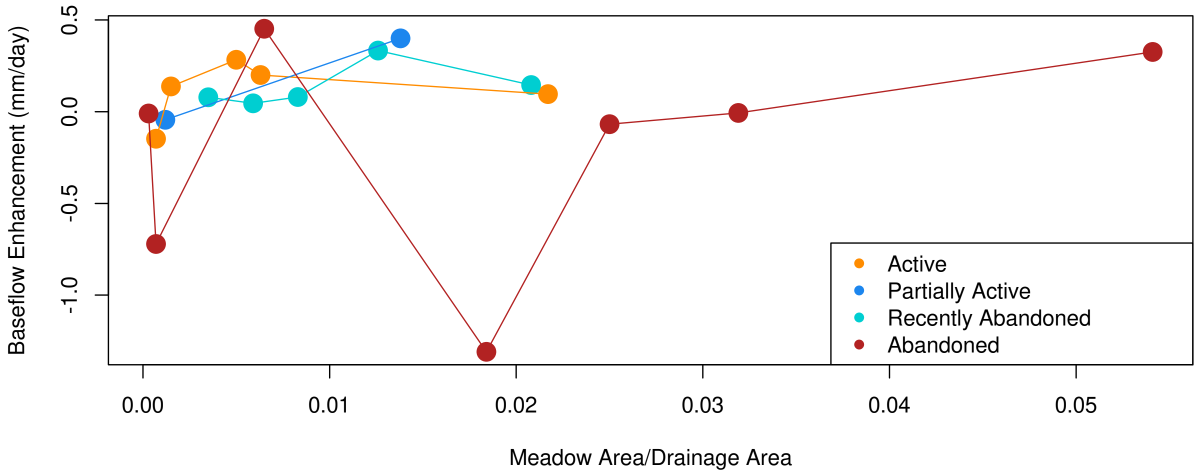


Figure S3.2. Baseflow augmentation plotted against the ratio of meadow area to drainage area in the style of the conceptual diagram. The measured data is not as straightforward as the conceptual diagram.

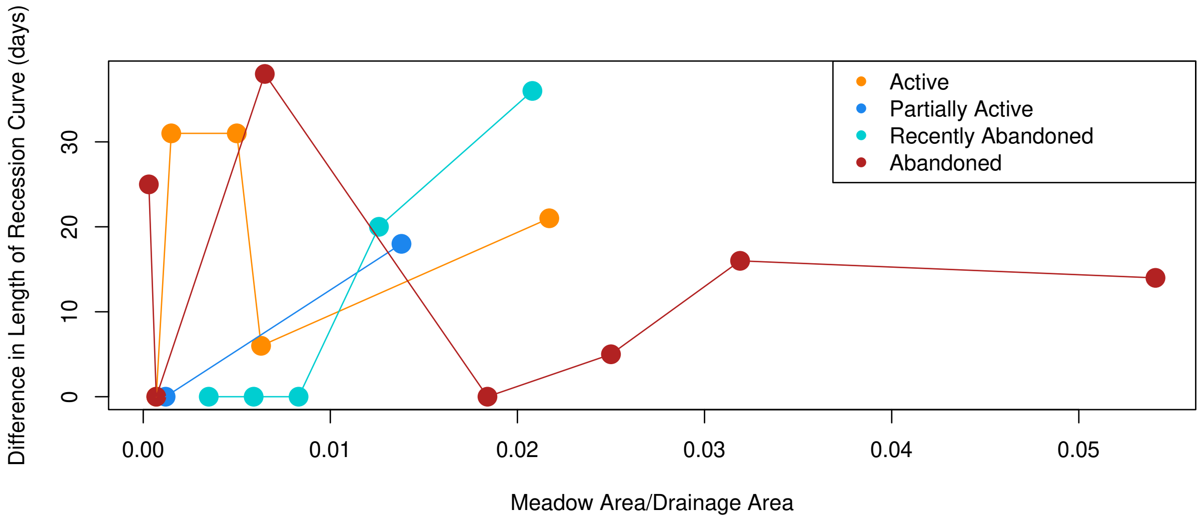


Figure S3.3. Recession curve lag plotted against the ratio of meadow area to drainage area in the style of the conceptual diagram. The measured data is not as straightforward as the conceptual diagram.