

THESIS

BIOGEOCHEMICAL IMPLICATIONS OF BEAVER-MEDIATED FLUVIAL COMPLEXITY
IN RIVER-FLOODPLAIN MEADOWS

Submitted by

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ABSTRACT

BIOGEOCHEMICAL IMPLICATIONS OF BEAVER-MEDIATED FLUVIAL COMPLEXITY IN RIVER-FLOODPLAIN MEADOWS

Mountain river networks alternate between narrow, transport dominated segments and low gradient wide valley segments that can be important locations for the retention and processing of carbon and nutrients. In North America, beaver (*Castor canadensis*) engage in dam building that enables the establishment of complex river-floodplain meadows (hereafter “meadows”), characterized by wide riparian corridors, multi-thread channels, and high levels of river-floodplain connectivity. However, in many river-floodplain systems, human land-use and the removal of beaver has led to fluvial simplification characterized by reductions in riparian vegetation and channel incision. We examined differences in hydrology and biogeochemistry among four meadows of varying beaver activity and associated fluvial complexity within Rocky Mountain National Park, USA. We quantified water and dissolved organic carbon (DOC) flux, measured fluorescent dissolved organic matter (DOM) character, and monitored ecosystem metabolism. At complex meadow segments, we observed increased stability across space and through time in patterns of water flux and DOC concentration, export, and character. While DOC dynamics were stable at complex meadow segments, in simplified meadow segments we observed increases in DOC concentration and export, and shifts toward more terrestrially sourced, aromatic, and humic DOM. These results suggest that complex river-floodplain systems facilitate stability in stream flows and maintain water quality with respect to DOC concentration, flux, and form. Conversely, the loss of fluvial complexity in simplified meadow segments can lead to lost hydrologic and

biogeochemical stability and make the valley segments more sensitive to future perturbations. Because wide-complex meadow segments can act as key locations of hydrologic retention in mountain stream networks, understanding how fluvial simplification alters water and DOC dynamics may be important for developing targeted restoration strategies for altered mountain headwater systems.

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DEDICATION

To my grandmother, Meiling Alps, whose reverence and love for the natural world helped to sow my passion for the environment long ago. Your thoughtful insights and observations during our bountiful walks through Quadra's woods have helped to cultivate my own understanding of our environment. You have inspired me to work towards protecting this world's beauty for future generations to see, touch, and love.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iv
DEDICATION.....	vii
1. INTRODUCTION.....	1
2. MATERIALS AND METHODS	4
2.1. Study Sites.....	4
2.2. Hydrology and Stream Temperature	6
2.3. Dissolved Organic Matter	7
2.4. Fluorescence and Ultraviolet Absorbance Analysis.....	8
2.5. Stream Metabolism	9
2.6. Data Management, Quality Assurance and Analysis.....	11
3. RESULTS.....	12
3.1. Hydrology and Stream Temperature	12
3.2. Dissolved Organic Carbon Dynamics	13
3.3. Dissolved Organic Matter Character and Stream Metabolism.....	14
4. DISCUSSION.....	17
4.1. Fluvial Complexity Impacts on Flow, Temperature and Carbon Flux	17
4.2. Ecosystem Functioning: DOM Quality and Metabolism.....	20
5. CONCLUSIONS	24
6. FIGURES.....	26
7. TABLES	43
REFERENCES	45
APPENDIX.....	55

1. INTRODUCTION

Human land and water management has led to widespread river-floodplain disconnection and fluvial ecosystem simplification [Tockner and Stanford, 2002]. As a result, billions of dollars are spent each year in the United States alone to restore rivers with the intent of reconnecting river-floodplain systems (reversing channel incision) and increasing fluvial habitat complexity [Bernhardt *et al.*, 2005]. In North America, beaver (*Castor canadensis*) naturally engage in dam building that facilitates the formation of complex habitats and can promote prolonged overbank flooding that increases lateral hydrologic exchange [Westbrook *et al.*, 2006]. However, historical and contemporary land-use practices have resulted in the widespread extirpation of beaver from many habitats, particularly low-gradient alluvial floodplains [Naiman *et al.*, 1988; Burchsted *et al.*, 2010]. In North American headwaters, the reintroduction of beaver has recently become a common and cost-effective approach to meeting restoration goals of increasing river-floodplain hydrologic connectivity and restoring fluvial complexity to otherwise simplified systems [Bird *et al.*, 2011]. While the local impacts of beaver impoundments and resulting habitat have been examined, few studies (e.g. Bellmore & Baxter, 2014; Pam Wegener, Covino, & Wohl, 2017) have observed the influences of beaver on river-floodplain systems at valley segment scales of hundreds to thousands of square meters [Frissell *et al.*, 1986; Montgomery and Buffington, 1997].

Deepening our understanding of segment-scale river ecosystem processes is particularly important in mountain stream networks, where natural breaks in slope along the riverscape create cut and fill alluviation that occur in an alternating fashion along the stream continuum. This enables the formation of low-gradient alluvial floodplains between transport dominated narrow valley segments in a pattern resembling beads upon a string [Leopold *et al.*, 1964; Stanford *et al.*, 1996;

Weekes et al., 2012]. In the Rocky Mountains, wide valley stream segments comprise less than 25% of total stream length, yet store more than 75% of floodplain organic carbon [*Wohl et al.*, 2012; *Wohl*, 2013]. The potential storage of low-gradient wide valley segments compared to narrow segments makes them disproportionately important as retentive zones in mountain river corridors [*Wohl et al.*, 2012; *Wohl*, 2013]. Active colonization of beaver in these wide alluvial valley segments often results in the formation of wet valley bottoms referred to as “beaver-meadow complexes” [*Morgan*, 1868; *Ruedemann and Schoonmaker*, 1938; *Ives*, 1942]. These meadow complexes (hereafter “meadows”) are characterized by wide, multi-thread riparian wetlands with high lateral hydrologic connectivity between the river and floodplain [*Ives*, 1942; *Westbrook et al.*, 2006; *Wegener et al.*, 2017]. These physical characteristics make these segments important for regional biodiversity and the processing and storage of organic matter and nutrients [*Tockner et al.*, 2000; *Ward et al.*, 2002; *Polvi and Wohl*, 2013; *Hauer et al.*, 2016]. However, in beaver abandoned meadow segments, stream channels often incise, riparian vegetation decreases, and overall fluvial geomorphic complexity is diminished [*Marston*, 1994; *Burchsted et al.*, 2010].

Because most studies to date have focused on beaver impacts at the reach scale (10-100m²; *Burchsted et al.*, 2010) and little research has been conducted on how fluvial ecosystems change as a result of lost beaver activity, restoration and watershed managers have incomplete information on the ecological impacts of beaver reintroduction and long-term beaver abandonment. To address this knowledge gap, we conducted a comparison of wide alluvial valley segments of varying beaver activity (n=4), and adjacent upstream narrow (n=4) segments, located in Rocky Mountain National Park (RMNP), USA. Due to the high fluvial transport capacity [*Montgomery and Buffington*, 1997] and prevalence of narrow stream segments in mountain river networks [*Winter*, 2001], we used adjacent upstream narrow valley segments as references of simple stream segments

that are characterized by transport dominated fluvial processes and have no beaver impact. With this framework, we assessed how changes in beaver activity, planform complexity, and lateral river-floodplain hydrologic connectivity influence water flux, dissolved organic carbon (DOC) export, dissolved organic matter (DOM) fluorescent character and stream ecosystem metabolism. We used this approach to address two hypotheses: (1) simplified meadows, with low fluvial complexity, reduced riparian vegetation, and increased longitudinal continuity will behave similar to simple, transport dominated narrow valley segments in the context of hydrologic attenuation, DOC export, and DOM character, and (2) complex active meadows, with high bilateral hydrologic exchange and heterogeneous floodplain habitats will attenuate streamflow and DOC export, and have higher fluvial DOM complexity. By assessing the impact of segment-scale beaver activity and abandonment on ecosystem processes, it is our objective to provide insight to the ecological outcomes that managers can expect from beaver reintroduction and to provide a framework to explore the long-term implications of beaver abandonment in mountain alluvial floodplains.

2. MATERIALS AND METHODS

2.1. Study Sites

We conducted our research within four longitudinally adjacent narrow and wide meadow valley segments, of four nearby catchments, located on the eastern slope of Rocky Mountain National Park (RMNP; Figure 1) from May to October 2017. In this study design, narrow segments are located upstream of each meadow segment and reflect transport dominated fluvial processes with narrow riparian corridors, limited hydrologic retention, and no direct impacts of beaver activity (i.e. no beaver dams). Alternatively, all wide meadow segments historically sustained long-term beaver colonies and now vary in the presence and activity of beaver (highly active to long-abandoned) and associated fluvial habitat complexity including the width of riparian corridor, presence of anastomosing channels, and beaver dams. Each adjacent narrow-wide segment pair is comprised of three hydrologic and biogeochemical monitoring stations located at: (1) the inflow of the narrow segment ('Ref') that serves as a reference of baseline stream characteristics upstream of meadow influence, (2) the meadow inflow ('Inflow') and (3) the meadow outflow ('Outflow') (Figure 1). These three monitoring stations bracket the two segments described above with the upstream 'narrow' valley segment located between the Ref-Inflow stations and the wide meadow segment between the Inflow-Outflow stations for a total of 12 stations bracketing 8 valley segments in four catchments.

We categorize each meadow based on degree of beaver activity and associated fluvial habitat complexity by the following names: 'complex-large', 'complex-small', 'transitional' and 'simplified' (Table 1). The (1) 'complex-large' is a large active beaver meadow complex located on the North St. Vrain river with an extensive riparian corridor, multiple channels and beaver dams

that span the valley floor (Lat 40.2183889, Long -105.5352111); (2) ‘complex-small’ is a small, but similarly active meadow complex located along Mill Creek with a well-developed riparian corridor and active beaver (Lat 40.341401, Long -105.602453); (3) ‘transitional’ is a recently abandoned (<10 years) meadow along Hidden Valley creek with remnant beaver structures but no current beaver activity, multiple channels, and a transitional vegetative community (Lat 40.399166, Long -105.639485); and (4) ‘simplified’ is a long-abandoned (>60 years) meadow located along Beaver Brook that has undergone a shift to an alternative stable state known as an elk grassland prairie, characterized by high levels of channel entrenchment and bank erosion, a single-thread channel and minimal riparian vegetation (Lat 40.363733, Long -105.583248).

Contributing catchments to our study sites contain remnant landscape features from numerous glacial advances during the Pleistocene that extended to ~2300-2400m elevation [Weekes *et al.*, 2012]. All wide valley segments in this study fall between a 2500m-2800m elevation band (Table 1). Upland vegetative communities range from alpine tundra above ~3350m to subalpine forest stands dominated by spruce-fir forests that are comprised of limber pine (*Pinus flexilis*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and quaking aspen (*Populus tremuloides*) at elevations of 2700-3500m [Rocky Mountain National Park, 2006]. Wet valley bottom riparian zones are dominated by willow (*Salix sp.*) interspersed with stands of aspen (*Populus tremuloides*) and mountain alder (*Alnus incana subsp. tenuifolia*) and understory wetland graminoids and forbs. Aspen (*Populus tremuloides*) and various grassland communities dominate the transition zone between valley meadow riparian and woodland/forest zones. All sites have a snowmelt streamflow pulse that typically initiates in June and recedes until October, with baseflow conditions until the following years spring snowmelt.

2.2. Hydrology and Stream Temperature

We measured stream stage at each stream sampling location with capacitance rods (TruTrack Inc., Christchurch, New Zealand) that recorded water level and temperature at 15-minute intervals with ± 1 mm precision for water level and $\pm 0.1^\circ\text{C}$ precision for temperature. Stage-discharge rating curves were developed at each site from weekly stage and discharge measurements made from high to low flows for each site using the velocity-area [Herschy, 1993] or dilution gauging approach [Østrem, 1964; Sappa *et al.*, 2015] depending on the efficacy of the technique at that time. During dilution gauging we instantaneously injected sodium chloride (NaCl) a mixing length ($>20\text{-}50\text{m}$) upstream of the gauge site. We measured stream water specific conductance (SC) and temperature at 2-second intervals using a CS547A conductivity/temperature probe connected to a CR300 data logger (Campbell Scientific Inc., C S547A, Logan, UT). We equilibrated the probe to stream temperature and left it to record SC before, during and after breakthrough curve (BTC) arrival until the stream returned to background SC. We converted background corrected SC to NaCl concentrations using empirical calibration and calculated stream discharge as the mass of tracer injected divided by the integral of the tracer BTC:

$$Discharge = \frac{NaCl_{MA}}{\int_0^t NaCl_C(\tau) d\tau}$$

[Eq. 1]

where $NaCl_{MA}$ is the mass (grams) of NaCl added, and $NaCl_C$ is the background corrected NaCl concentration (grams/liter) across the BTC. We measured manual discharge by velocity-area method using Marsh-McBirney or Hach FH 950 portable flow meters (Hach Company, Loveland, CO). We then used our developed rating curves to convert continuous (15-min) stage measurements to discharge (Q). To better visualize seasonal streamflow dynamics between and within meadows, we binned real-time discharge to daily averages and computed cumulative

distributions and recession curves beginning at the 60th quantile of each gauge hydrograph until the end of the monitoring period.

2.3. Dissolved Organic Matter

We sampled each monitoring location for water samples at weekly intervals from May to October 2017. We collected water samples in acid washed 1 L high-density polyethylene bottles, triple-rinsed with deionized water and stream-rinsed before sampling mid-depth of the thalweg. Samples were immediately placed on ice for transport and lab filtered into acid-washed and sample-rinsed 125 mL HDPE bottles through pre-combusted 0.7 µm glass fiber filters (GF/F Whatman International, Ltd., Maidstone, UK) for DOC, total dissolved nitrogen (TDN) and fluorescence analysis, or through 0.45 µm polyvinyl filters (Durapore Membrane PVDF, Merck Millipore, Ltd, Cork, Ireland) for major ion analysis.

All DOC/TDN and geochemistry samples were analyzed at the Rocky Mountain Research Station in Fort Collins, CO [Feghel *et al.*, 2018] and stored in a dark refrigerator (~4 °C) until analysis (<7 days). We perform DOC/TDN analysis on a Shimadzu TOC-V series analyzer via the 680°C combustion catalytic oxidation method. We measured nitrate (NO₃) and nitrite (NO₂) concentrations (data not shown) on a Dionex ICS-3000 Ion Chromatograph and ammonium (NH₄) (data not shown) on a Waters 580 Ion Chromatograph. We calculated dissolved organic nitrogen (DON) concentrations as the difference between TDN and NO₃-N, NO₂-N, and NH₄-N nitrogen species. We quantified the net fluxes of dissolved constituents at each sampling station as:

$$Mass\ Flux = \frac{(C \times Q)}{Area}$$

[Eq. 2]

where C is the stream water concentration (mg L^{-1}), Q is the mean daily discharge (L sec^{-1}), and area is the contributing area for the measurement site. We then calculated mass flux balances for each river segment as the difference between segment outflow and inflow. Net change of fluvial and material flux is normalized on a per 100 meter of valley length basis between segment inflows and outflows (narrow and wide) on a weekly basis (Figure 6).

2.4. Fluorescence and Ultraviolet Absorbance Analysis

We evaluated seasonal optical dissolved organic matter (DOM) characteristics for each sampling location using measurements of ultraviolet absorbance and fluorescence excitation-emission matrices (EEM). Fluorescence samples were immediately frozen (-20°C) upon filtration and thawed in the dark to room temperature before analysis ($\sim 20^{\circ}\text{C}$). To avoid excessive inner-filter effects from the influences of high DOC concentrations, we checked each sample concentration to be less than 10 mg C L^{-1} prior to analysis. We analyzed samples on an Aqualog Spectrofluorometer equipped with a 150-watt continuous output xenon excitation source (Horiba-Jobin Yvone Scientific Edison, NJ) at EcoCore Analytical Services, Fort Collins. We measured ultraviolet absorbance and fluorescence EEMs simultaneously, with excitation and emission slits set to a 3nm band-pass and scans of 3nm wavelengths taken incrementally from 240-600 nm at 3-second integrations (wavelength accuracy $\pm 1\text{nm}$). Before scanning, we collected reference spectra from an ultra-purified sealed water blank and subtracted from subsequent sample scans. Following data acquisition, we corrected spectra for inner-filter effects, masked for 1st and 2nd order Raleigh Effects, and normalized to Ramen units.

For all samples we calculated metrics of fluorescent DOM fraction analysis including: (1) the fluorescence index (FI), which is the ratio between emission (em) wavelengths at 470nm and

520nm obtained at an excitation (ex) wavelength of 370 nm, with lower values (~1.2) representing DOM of terrestrial origin and higher values (~1.8) representing DOM of a microbial or algal origin [McKnight *et al.*, 2001]; (2) the humification index (HIX) calculated as the area of the emission spectra collected at ex 254nm under 435-480nm divided by the area under the peak of em 300-345nm (unitless), used as a means to track changes in humification and water-extractable soil organic matter; (3) the biological index (BIX) is a unitless ratio derived by the intensity at em 380nm divided by the peak intensity of em 420nm and em 435nm all at ex 310nm that is correlated to agricultural use and wetland loss [Wilson and Xenopoulos, 2009]; and (4) specific ultraviolet absorbance at 254nm (SUVA₂₅₄), which is derived from the absorption of ultraviolet light at 254nm normalized to sample DOC concentrations (L mg-C⁻¹ m⁻¹), with higher values typically indicating greater aromatic content [Weishaar *et al.*, 2003].

2.5. Stream Metabolism

As a measure of ecosystem function, we calculated daily rates of gross primary production (GPP, g O₂ m⁻² d⁻¹) and ecosystem respiration (ER, g O₂ m⁻² d⁻¹) at each meadow outflow. We determined whole-stream metabolism by monitoring open-channel diel changes in dissolved oxygen (DO) and applying an empirical structural model referred to as the single-station open diel oxygen method [Odum, 1956] given by the equation:

$$\frac{dC}{dt} = P - R - K_{O_2}D$$

[Eq. 3]

Where, C is the DO concentration (mg O₂ m⁻² d⁻¹); P is the rate of ecosystem photosynthesis (mg O₂ m⁻² d⁻¹); R is the rate of ecosystem respiration (mg O₂ m⁻² d⁻¹); K_{O₂} is the reaeration coefficient (d⁻¹) of oxygen exchange; and D provides the degree of O₂ saturation balance (deficit or surplus,

mg O₂ L⁻¹). This method integrates the cumulative product of pelagic, benthic and hyporheic production and respiration into relative daylight and night-time (dark) productivity and respiration, given that photosynthetic production during darkness should be zero.

We measured continuous (15-minute) DO concentrations at each meadow outflow using Ponsel (Fondriest Environmental Inc., Ponsel Digisens, Fairborn OH) or miniDOT (Precision Measurement Engineering Inc. MiniDOT, Vista CA) optical DO sensors. We atmospherically corrected and aggregated 15-minute DO measurements to calculate (Eq. 3) hourly rates of change in DO concentrations. Using hourly rates of change, we determined hourly saturation deficits and surpluses. We modeled temperature-calibrated reaeration coefficients using the surface renewal model given by the equation [Owens, 1974]:

$$f_{(20^{\circ}\text{C})} = 50.8 \times V^{0.67} \times H^{-0.85}$$

[Eq. 4]

Here, the term $f_{(20^{\circ}\text{C})}$ equates to the mass transfer coefficient in cm h⁻¹; V refers to velocity in cm sec⁻¹; and H is the mean depth (cm) of the stream. We collected these terms using depth measurements made at 15-min intervals using Tru-Track capacitance rods, stream velocity derived from depth-velocity relationships, and MiniDOT temperature measurements. We aggregated reaeration-corrected DO change rates to dark-period averages (sunset to sunrise) and extrapolated this value across the 24-hour period to derive daily ER rates. To calculate GPP, we calculated the difference between average hourly rates of DO change and the hourly night-time rates of DO change applied over the photoperiod; with the assumption that ER does not change between dark and light periods. Lastly, we derived estimates of net ecosystem productivity (NEP, g O₂ m⁻² d⁻¹) as the difference of the absolute values of GPP and ER [Bott, 1983].

2.6. Data Management, Quality Assurance and Analysis

We transformed continuous stage to continuous discharge using independently developed rating-curves at each site. Prior to transformation, we cleaned continuous stage data (erroneous measurements removed and intervals checked for consistency) and corrected sensor data to weekly manual measurements of stream depth. Discharge-stage relationships were fitted using R Statistical Software [*R Core Team*, 2016]. We aggregated continuous (15-min) hydrologic flux to daily mean values of discharge, and calculated segment balances as the daily difference in water flux between each segments inflow and outflow. To standardize discharge values for comparison between catchments, we first calculated daily average discharge for each site and normalized volumetric daily flow (L day^{-1}) to contributing area (mm day^{-1}).

Biogeochemical data were quality assured at Rocky Mountain Research Station (RMRS). RMRS regularly checked sample concentrations against USGS standard reference samples for calibration and maintained cross-lab sample fidelity by actively participating in Canada's National Water Research Institute proficiency testing program. Field duplicates and deionized water blanks were collected approximately monthly throughout the study period and in-lab validation of analytical results for major ions were confirmed by ionic balance of each sample [*Fegel et al.*, 2018].

3. RESULTS

3.1. Hydrology and Stream Temperature

During the 2016-2017 hydrologic year, RMNP received 1101mm of precipitation, which was above the long-term mean annual precipitation of 912mm (1979-2017, UI MetData/GridMET 1/24th degree resolution). Measured stream temperatures varied seasonally with discharge, with lowest measured temperatures occurring during peak snowmelt and highest temperatures during the baseflow period at all sites. We observed that outflow minus inflow temperature (ΔC°) for the complex-large and simplified wide segments (Table 1) were seasonally opposite to each other, with early-season increases and late-season dampening in outflow temperatures at the complex-large meadow and vice versa at the simplified meadow (Figure 2). The complex-small meadow showed seasonally stable temperatures between the inflow and outflow, with less pronounced early season increases and late-season dampening than observed at the complex-large meadow. The transitional meadow showed elevated ΔC° that were seasonally stable, with outflows remaining near 1 C[°] warmer than the inflow until snowfall in early October.

We report discharge values from May 24th to October 1st with peak flows during snowmelt typically occurring around June 15th (± 1 week) for each gauging location (Table 1, Figure 3). The timing of peak flows occurred earlier on May 28th for gauges located at the simplified meadow (Figure 3A). At the segment scale, we observed the greatest differences in hydrologic dynamics between the complex-large and simplified segments (Figure 3A). Cumulative distribution functions of each inflow and outflow gauge show notable differences in water flux dynamics between catchments, with more subtle differences between meadow inflow and outflow gauges (Figure 3B). Inflow-outflow relationships differ most strongly at the complex-large and simplified

meadows (Table 1), with the complex-large outflow accumulating water flux more slowly and the simplified outflow accumulating water most quickly among all gauges (Figure 3B). Hydrograph recession dynamics for each site reveal that both abandoned beaver meadows exhibit steeper recessions at their meadow outflows relative to inflows (Figure 3C). There was little difference between inflow and outflow hydrology at the complex-small meadow segment, with a slight trend of steeper recession at the inflow, relative to outflow, during the baseflow period (~Aug 21st onward; Figure 3). We observed an opposite trend in the complex-large meadow segment relative to the transitional and simplified sites, with a notably steeper recession limb at the inflow relative to the outflow of the complex-large meadow segment (Figure 3C). We saw pronounced increases in baseflow at the complex-large outflow compared to inflow from Aug 15th onward (Figure 3).

3.2. Dissolved Organic Carbon Dynamics

Mean DOC concentrations varied between each meadow, with the highest concentrations measured during early season flushing (May-June) and lowest concentrations occurring during late-season baseflows at all sites. Over the study period, DOC concentrations across all sites remained within the range of ~2-9 mg L⁻¹. The highest measured DOC concentration over the sampling period was at the outflow of the complex-small meadow on June 6th at 8.83 mg L⁻¹ and the lowest measured value was at the inflow of the transitional meadow on September 10th at 1.13 mg L⁻¹. We observed stable DOC concentrations from inflow to outflow across the two complex (large and small) meadows (Figure 4). To visualize trends in mean DOC concentrations, we made comparisons of the relative change in DOC concentration (Δ DOC) between segment outflows and inflows (Figure 5). Narrow segments above all meadows show mean Δ DOC centered on zero (Figure 5). The two complex-active beaver meadows demonstrate little change in Δ DOC from

inflow to outflow over the sampling period, while both the transitional and simplified meadows exhibit net mean increases in ΔDOC of 1 mg/L and 2 mg/L respectively (Figure 5). In addition to significant increases in DOC concentrations of 38.8% at the simplified meadow ($p < 0.01$, paired Wilcoxon rank-sum test) and 32.8% at the transitional ($p < 0.001$) meadow, we also observed increased variance in outflow relative to inflow concentrations at these sites (simplified: $r^2 = 0.5$, $\text{RSE} = 0.95$; transitional: $r^2 = 0.58$, $\text{RSE} = 0.52$; Figures 4 and 5).

To assess how relative changes in segment DOC flux related to water flux, we regressed the net flux balance of discharge ($\%\Delta Q$) against net DOC flux balance change of DOC ($\%\Delta\text{DOC}$) for narrow and wide valley segments (Figure 6). At all narrow segments $\%\Delta\text{DOC}$ and $\%\Delta Q$ closely followed the 1:1 line across all flow-states, indicating that as water flux of the segment increased there was a proportional increase in DOC flux balance (Figure 6A). At the complex-large and complex-small meadows segments $\%\Delta\text{DOC}$ to $\%\Delta Q$ regressions followed a 1:1 relationship across flow states, similar to the observed DOC-Q flux patterns observed along the narrow segments (Figure 6). Conversely, patterns across the transitional and simplified wide meadow segments exhibited disproportionate increases in $\%\Delta\text{DOC}$ relative to $\%\Delta Q$ (Figure 6B). The increase in $\%\Delta\text{DOC}$ relative $\%\Delta Q$ was greatest across the transitional wide meadow segment ($\sim 2:1$ relationship), and was less pronounced yet consistently positive across the simplified wide meadow segment ($\sim 1.5:1$).

3.3. Dissolved Organic Matter Character and Stream Metabolism

We evaluated differences in DOC and DON concentration, along with DOM indices including the humification index (HIX), biological index (BIX) and fluorescence index (FI) across wide meadow segments (Figure 7). We observed strong inflow-outflow differences in all metrics

across the transitional and simplified meadows, but not across the complex-active meadows (Figure 7). At the transitional and simplified meadows, measurements of HIX revealed significant increases in fluorescent humic DOM proportions, indicating an increase in DOM aromaticity (Figure 7). While only the transitional meadow demonstrated a significant shift towards more terrestrial sources (-25%, $p < 0.01$), mean FI values at the simplified meadow decreased by 13% (shift toward terrestrial) and variance (standard deviation) increased by 43% (Figure 7). We saw that BIX, a measure that is linked to DOM freshness and microbial activity [Wilson and Xenopoulos, 2009], showed significant decreases at both the transitional ($p < 0.001$) and simplified wide valley segments ($p < 0.01$) (Figures 7 and 8). Conversely, we saw significant increases in DON concentrations of 53% at the transitional ($p < 0.01$) and of 116% at the simplified ($p < 0.01$) wide meadow segments (Figures 7 and 8).

Specific ultraviolet absorbance at 254nm ($SUVA_{254}$) normalized to sample DOC concentration is a commonly applied metric used as a semi-quantitative measure of DOC aromaticity and molecular weight [Weishaar et al., 2003]. Excluding outliers, $SUVA_{254}$ values for all meadows ranged from about 2 to 5 L mg-C⁻¹ m⁻¹, equating to approximate aromatic contents of 20-35% as determined using ¹³C-NMR (sensu Weishaar et al., 2003). At the complex meadow inflows and outflows, we observed higher (~3.5-4.5 L mg-C⁻¹ m⁻¹) and less variable $SUVA_{254}$ values compared to the transitional and simplified meadows (Figure 7). While inflows and outflows of the transitional and simplified meadows had overall lower mean $SUVA_{254}$ values, the relative increases between inflow and outflow were significant. There was an increase of 19% ($p < 0.05$) and 31% ($p < 0.001$) at the transitional and simplified meadows respectively (Figure 7). Alternatively, both complex-active beaver meadows showed no significant trend in $SUVA_{254}$ values between inflows and outflows over the study period.

From mid-June to mid-July, we observed low levels of instream metabolism (near zero) at the simplified meadow, with higher values (GPP, 3-5 g O₂ m² day⁻¹; ER, -5-7 g O₂ m² day⁻¹) typically occurring during early season peak flows or late-season baseflows. The complex-large meadow exhibited seasonally stable levels of productivity, with a slight increasing trend of higher GPP and ER across the growing season (GPP, 2-3 g O₂ m² day⁻¹; ER, -4-6 g O₂ m² day⁻¹). The complex-small meadow had high and sustained rates of GPP, ER and NEP for much of the season compared to the other meadows, with a slightly decreasing trend in GPP and ER across the growing season (May 15th - Sept 15th). Mean respiration rates across the study period were the highest (in negative flux) at the complex-small meadow followed by the complex-large meadow (Figure 9). Regressions of ER and outflow DOC concentrations showed that higher ER rates tended to correspond with higher DOC concentrations for all sites, particularly at the complex-small meadow. However, we also observed elevated rates of ER during moderate or low DOC concentration periods at each site during periods of high flow (low residence time, high mass flux), cold temperatures, and across a wide range of DOM index values (FI, BIX, SUVA₂₅₄; Figure 10).

4. DISCUSSION

4.1. Fluvial Complexity Impacts on Flow, Temperature and Carbon Flux

We measured increased variability and magnitudes in the concentration and export of DOC coupled with flashier hydrology in both the transitional and simplified meadows. Similar to the findings of Wohl and Beckman (2014), who highlighted the connection between fluvial disconnectivity and ‘leaky’ rivers, these data suggest that instability and increased export of water and DOC at simplified meadows is a product of lost fluvial complexity (Figure 11 and 12B). Conversely, we saw stability of flow, temperature, DOC concentration and flux, DOM character, and metabolism at the complex active beaver meadows. Specifically, the complex-large meadow showed the strongest seasonal patterns in streamflow attenuation, mirrored to a lesser extent by the complex-small meadow. Both complex meadows showed stability in carbon flux and concentration across all flow periods, while the complex-large meadow exhibited temperature attenuation (warmer outflow temperatures during colder periods and vice versa). This enhanced retention and stability observed at complex meadows may be an emergent product of heterogeneous flow paths, diverse habitats, and increased system integrity that is facilitated by the long-term presence of beaver (Figure 12A and 13; Burchsted et al., 2010).

Because diversity in landscapes and hydrologic flow paths have been shown to confer catchment scale stability [Moore *et al.*, 2015], the lack of fluvial complexity and associated instability at the transitional and simplified meadows may decrease system resilience to environmental and climate variability. Similar to stability patterns observed at catchment scales, our results demonstrate that planform complexity and lateral river-floodplain connectivity result in hydrologic and biogeochemical stability at the valley segment scale. This observed stability is

linked to beaver activity and the fluvial complexity that beaver activity creates in the wide valley segments of mountain catchments (Polvi & Wohl, 2012; Wegener et al., 2017; Westbrook et al., 2006). Because mountain river networks are generally dominated by narrow, steep valley segments [Wohl, 2010], the loss of fluvial complexity and retention capacity in the limited wide valley segments is likely to have strong impacts on catchment water and DOC export and ecosystem function. Additionally, given the projected changes in climate [Tockner and Stanford, 2002] and population growth of Rocky Mountain states [Golubiewski, 2006], conservation and restoration of fluvially complex wide valley segments is important to mediate potential impacts of future change on aquatic ecosystems and the quantity and quality of water delivered downstream.

Stream flow, temperature, and DOC are key biophysical variables that represent the cumulative signals of stream-terrestrial linkages [Minshall et al., 1985], and as such they are subject to changes in habitat and fluvial complexity that regulate and drive stream ecosystem processes across scales (Figure 14 and 15). It has been shown that beaver fundamentally alter the geomorphic setting of streams, increasing fluvial complexity and altering the local hydrologic regime (Wegener et al., 2017; Westbrook et al., 2006). Because we observed flow and temperature attenuation at both complex active meadows, we posit that observed segment-scale patterns of flow and temperature attenuation are a product of bilateral exchange with floodplain habitats (Figure 14) that enhance overbank storage, heighten water tables, and increase residence times. Recent research supports this hypothesis, indicating that beaver ponds contribute to warming and temperature buffering of connected streams [Majerova et al., 2015], and have shown that the presence of beaver dams can increase surface water storage capacity at reach scales [Puttock et al., 2017].

Because DOC is a biologically reactive substance in dissolved form, the temperature, residence time and storage of water has strong impacts on the distribution and cycling of DOC [Kaplan *et al.*, 2008; Cory and Kaplan, 2012]. The Pulse-Shunt Concept (PSC; Raymond, Saiers, & Sobczak, 2016) suggests that large, low-frequency hydrologic events (e.g. snowmelt) dominate the flux of DOM by ‘shunting’ terrestrial carbon downstream that was produced (‘pulsed’) over longer, low-flow periods. The PSC is premised on the idea that low-residence times and temperatures during high flow periods create relatively ‘passive’ stream segments whereas warmer, low-flow periods create more ‘active’ river corridors (*sensu* Casas-Ruiz *et al.*, 2017). During periods of high DOC mass flux in complex meadows, DOC routed into ‘active’ floodplain habitats likely enters flow paths and timescales favorable to microbial metabolism [Battin *et al.*, 2009; Hall *et al.*, 2012], potentially enhancing overall floodplain productivity for time periods far beyond peak flows. Alternatively, terrigenous DOC routed through simplified abandoned meadows during high flows would be shunted further down the network [Raymond *et al.*, 2016], providing little buffering to water or DOC. At the simplified meadow segment, little riparian vegetation, up to 3 meters of incision, and no surface floodplain connectivity (Figure 11) create conditions that would likely enhance erosion [Wohl and Beckman, 2014], making this segment not simply a ‘passive’ pipe for carbon flux but a source of carbon export [Casas-Ruiz *et al.*, 2017]. The low temperatures observed during peak flows at the simplified site (counter to complex meadows) may further decrease the reactive capacity of DOC at this time [Perkins *et al.*, 2012], shunting even more carbon downstream. Additionally, counter to complex meadows, we observed increased export and higher concentrations of DOC during low-flow periods in simplified segments. This indicates that DOC supply exceeds the retentive and reactive capacity of the simplified valley segments, even during low-flow periods of high productivity and reactivity. In

already retention limited mountain stream networks, the transition of retentive zones (complex meadows; Figure 13) to passive, export dominated zones (simplified meadows; Figures 11 and 16) has implications for decreased fluvial network carbon storage, downstream changes to water quality, and shifts in ecosystem functioning beyond the segment scale [Wohl and Beckman, 2014; Harvey and Gooseff, 2015; Proia et al., 2016; Casas-Ruiz et al., 2017].

4.2. Ecosystem Functioning: DOM Quality and Metabolism

We observed altered fluorescent qualities of DOM at the transitional and simplified abandoned meadows that indicate exported DOM is more terrigenous, aromatic, and soil-sourced than DOM flowing into these meadows. As a primary form of energy flux in river networks [Karlsson et al., 2005; Jaffé et al., 2008], DOM dynamics strongly affect ecosystem function based on its role in energy and nutrient cycling [Wetzel and Steward, 1981; Wetzel, 1992], trace metal transport [Lawlor and Tipping, 2003], and photochemistry [Zafariou et al., 1984]. Furthermore, reactivity is highly variable among DOC forms [Kaplan et al., 2008; Cory and Kaplan, 2012], and our observed changes in source could alter DOC cycling and processing both within meadow segments and downstream.

The export of older, terrestrially-based aromatic DOM from simplified systems, particularly during high flow periods appears to align with the principles of the PSC. The enhanced export of more aromatic (i.e. ‘recalcitrant’) DOM, has implications for downstream energetics that could influence microbial processing beyond the meadow-scale or cumulatively at the network scale. In the case of the two abandoned-simplified meadow segments, reductions in residence times coupled with potentially large contributions of terrigenous material (e.g. bank erosion), may cause these systems to behave more like ‘passive’ pipes as opposed to reactive ‘active pipes’ [Casas-Ruiz et al., 2017]. However, in the simplified segments we not only observed increased DOC

export during colder high flow periods, but also increased export during warmer low-flow periods when the PSC would predict that the system's ability to process and store organic carbon would be high.

Because stream ecosystem respiration is supported by DOM [Mulholland *et al.*, 2001; Cole *et al.*, 2007], the combination of higher concentrations and altered carbon reactivity could fundamentally alter the downstream processing of carbon and thus change the timing, magnitude and distribution of stream microbial metabolism [Battin *et al.*, 2009; Guillemette and del Giorgio, 2011; Wollheim *et al.*, 2015]. Because this basal productivity provides resources to higher trophic levels (e.g. macroinvertebrates) and supports stream ecosystem productivity, particularly in low-order streams, this could have ramifications for ecosystem structure downstream [Lowe and Likens, 2005; Kaplan *et al.*, 2008]. Though we cannot attribute causality, our measurements of lower seasonal ecosystem respiration at the transitional and simplified meadows may in part be a product of altered carbon reactivity. Our observations of increased DOC concentrations mirror those of widespread increases observed across Northern Europe and North America in recent decades [Evans *et al.*, 2005] that have been generally attributed to increased agricultural land-use and the alteration of wetlands on both continents [Evans *et al.*, 2005; Wilson and Xenopoulos, 2009]. Furthermore, Lou *et al.* (2014) observed significant increases in both DOC export and concentration, as well as increased aromatic content DOM following experimentally controlled rapid water-table draw down in a large Chinese peatland. Similar to both continental scale monitoring and experimental findings, our observations of increased DOC concentration are likely associated with the mobilization of DOM from different sources [Butman *et al.*, 2012] that are acquired within the meadow. This differs from our initial hypothesis that simplified meadows behave as passive conduits of DOC and water flux similar to their adjacent upstream narrow

segments. Instead, the combination of altered DOM sources and increased DOC concentration and fluxes suggest that simplified meadow segments become sources of previously stored floodplain DOC as they lose fluvial complexity and water retention capacity.

Because river-floodplain systems are extensively impacted by humans [*Tockner and Stanford*, 2002], particularly in the Rocky Mountains [*Hauer et al.*, 2016], our findings of increased DOC concentration and export, altered carbon composition, and lower ecosystem productivity in simplified systems are not likely isolated to the sites included in this study. Rather, considering the historical abundance of fluvially complex meadows in the Rocky Mountains [*Dahl*, 1990; *Wohl et al.*, 2012], it is probable that the widespread simplification of these systems has had network scale impacts on water quality and system productivity (Figure 17; *Freeman, Pringle, & Jackson*, 2007). Contrary to the simplified-abandoned meadows, we observed stable fluorescent DOM qualities at the complex meadows with no significant trends between inflows and outflows across flow states. This stability in DOM character is counter to our hypothesis that as bilateral exchange of DOM varies across complex floodplain habitats as a function of flow state, we would see a strong shift in DOM character toward floodplain habitat sources. Instead, our finding is similar to that of *Thomaz et al.*, (2007) who reported that flood pulses within tropical river-floodplains increased homogeneity in temperature, depth, and chemical characteristics (pH, Conductivity, Chlorophyll- α) between aquatic habitats. However, in the headwater snowmelt dominated systems of the complex meadows, a singular large snowmelt pulse coupled with prolonged overbank flooding due to beaver activity [*Westbrook et al.*, 2006] may enhance habitat homogeneity and stability of DOM longer than seen by *Thomaz et al.* (2007) in tropical rainfall dominated systems.

The stability observed across complex segments is likely a function of ecosystem heterogeneity that induces system resilience to perturbation [Polvi and Wohl, 2012; Moore *et al.*, 2015], allowing complex segments to operate in a steady-state relative to catchment inputs. These results illustrate the importance of beaver and associated fluvial complexity in contributing toward ecosystem stability. Conversely, the lack of heterogeneity in simplified meadow segments leads to alteration of hydrologic and biogeochemical signals from inflows to outflows. Because simplified meadow segments frequently exist in an alternative stable state [Wolf *et al.*, 2007], reconnecting these rivers with their floodplains and returning complexity is often difficult to accomplish [Suding *et al.*, 2004]. Additionally, as a consequence of the lack of heterogeneity and associated stability, simplified meadow segments are likely to be more sensitive to extreme events (e.g. flooding, fire, etc.); further highlighting the importance of fluvial habitat conservation for ecosystem resilience and maintenance of ecosystem services. In lieu of conservation, beaver remediation in simplified meadows may be an effective tool in managing water and DOC export, and returning ecological resilience toward historical levels [Naiman *et al.*, 1988; Burchsted *et al.*, 2010].

5. CONCLUSIONS

Numerous studies [*Correll et al.*, 2000; *Hood and Bayley*, 2008; *Majerova et al.*, 2015; *Koschorreck et al.*, 2016] have evaluated beaver dam-pond pairs and reach-scale (10s-100s meters) impacts on hydrology, water temperature, and aquatic biogeochemistry (DOC and nutrients); but few have expanded these analyses to the valley segment scale or quantified these processes across a gradient of beaver activity. While our study was limited to 4 narrow segments and 4 wide meadow segments of varying beaver activity, our findings suggest that physical complexity attributed to beaver activity may confer hydrologic and ecosystem stability at valley segment scales. Furthermore, abandoned meadows with diminished fluvial complexity and limited lateral hydrologic connectivity may shunt water and DOC downstream, while complex meadows have greater capacity to retain water and DOC. The enhanced retention of water and DOC in complex meadows has the potential to interrupt the DOC pulse-shunt sequence, and alter network energetics. Many historically complex river-floodplain systems, are now much simpler [*Tockner and Stanford*, 2002; *Dodds and Oakes*, 2008], suggesting that the historical capacity to retain water and DOC in complex meadows along mountain river networks was once considerably larger. The historical retention of water and DOC in wide, complex mountain valley segments has consequences for the longitudinal transport and processing of carbon. Specifically, multiple complex meadows in series interrupt longitudinal hydrologic connectivity, and enhance the capacity for local DOC processing, as opposed to the distal DOC processing hypothesized in the pulse-shunt concept. To expand on the results presented here, future research should continue to quantify the impacts of lost fluvial complexity and bilateral river-floodplain hydrologic connectivity in the context of beaver abandonment and ecological function across diverse

landscapes and climates. With this objective, we propose that future research focus on the impacts of beaver with respect to hydrologic and ecosystem function at scales relevant to both restoration and natural resource managers. Specifically, we suggest the following questions: (1) in what quantifiable ways have water, carbon, and ecosystem productivity regimes changed in simplified meadows, and (2) how far down the stream network do changes associated with fluvial complexity or simplification persist? With these two questions it is our hope that a clearer understanding of the impacts of beaver reintroduction across scales (e.g. reach, segment and network) can help guide managers in the effective implementation of beaver restoration with targeted ecosystem services in mind. Quantifying the impacts of extensive river-floodplain disconnection on stream temperature, hydrology, and carbon cycling is a crucial first step in understanding network-scale implications of floodplain connectivity in the context of restoration and in approximating lost historical ecosystem services.

6. FIGURES

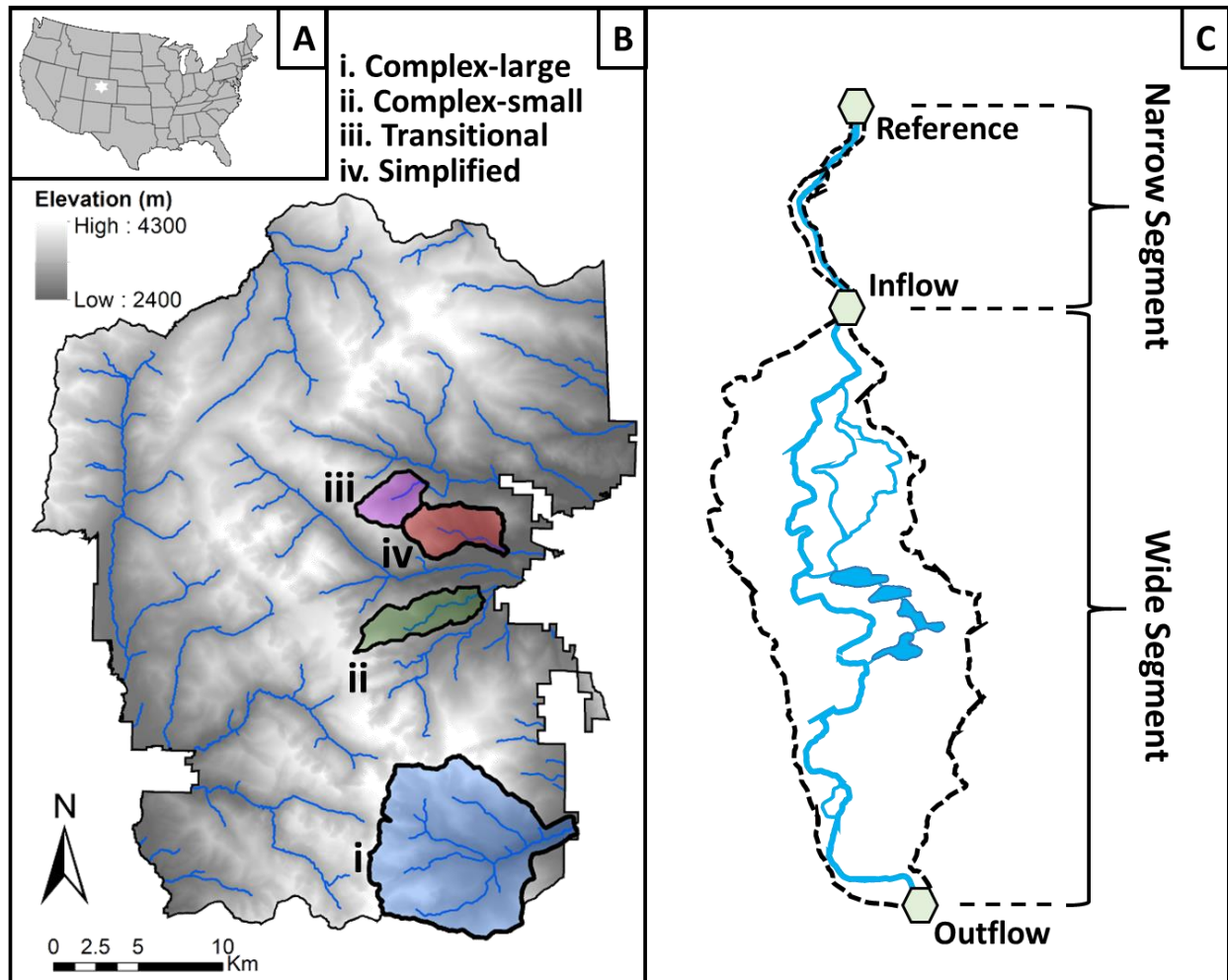


Figure 1 | Panel A: Location of Rocky Mountain National Park (RMNP) within the state of Colorado, USA. Panel B: Digital elevation model and boundaries of RMNP with contributing catchments of each meadow. Catchment outflows coincide with meadow outflow gauges. Panel C: Depiction of sampling layout of narrow and wide valley segments. Dashed boundaries indicate valley margins. Hydrologic and biogeochemical sampling locations are denoted by hexagons labeled by their respective gauge names.

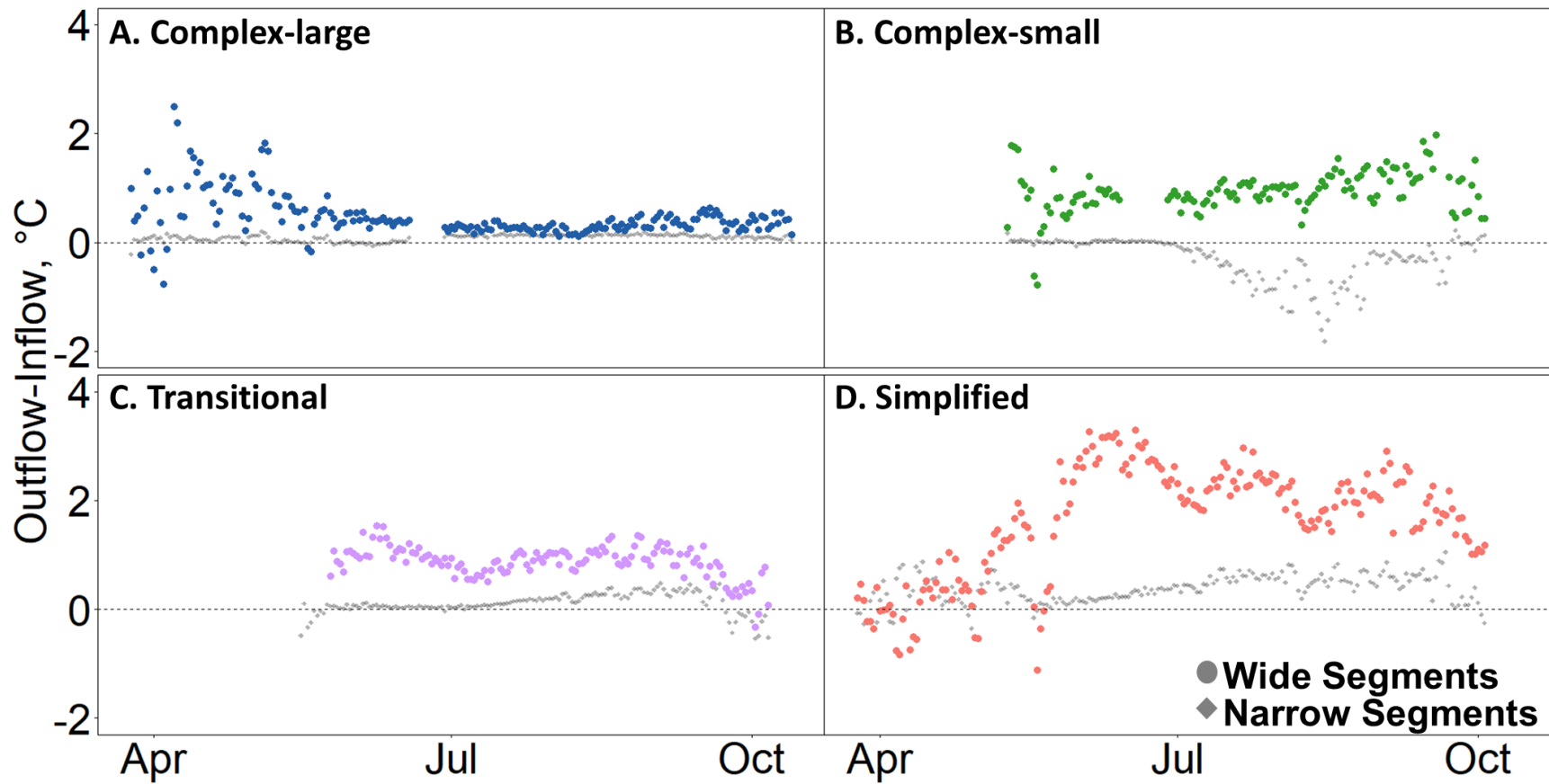


Figure 2 | Change (delta) in stream temperature across for narrow (gray diamonds) and wide valley segments. Positive values indicate an increase in outflow temperatures relative to inflow, negative values a decrease. Data are shown for: A. Complex-large; B. Complex-small; C. Transitional; and, D. Simplified valley segments.

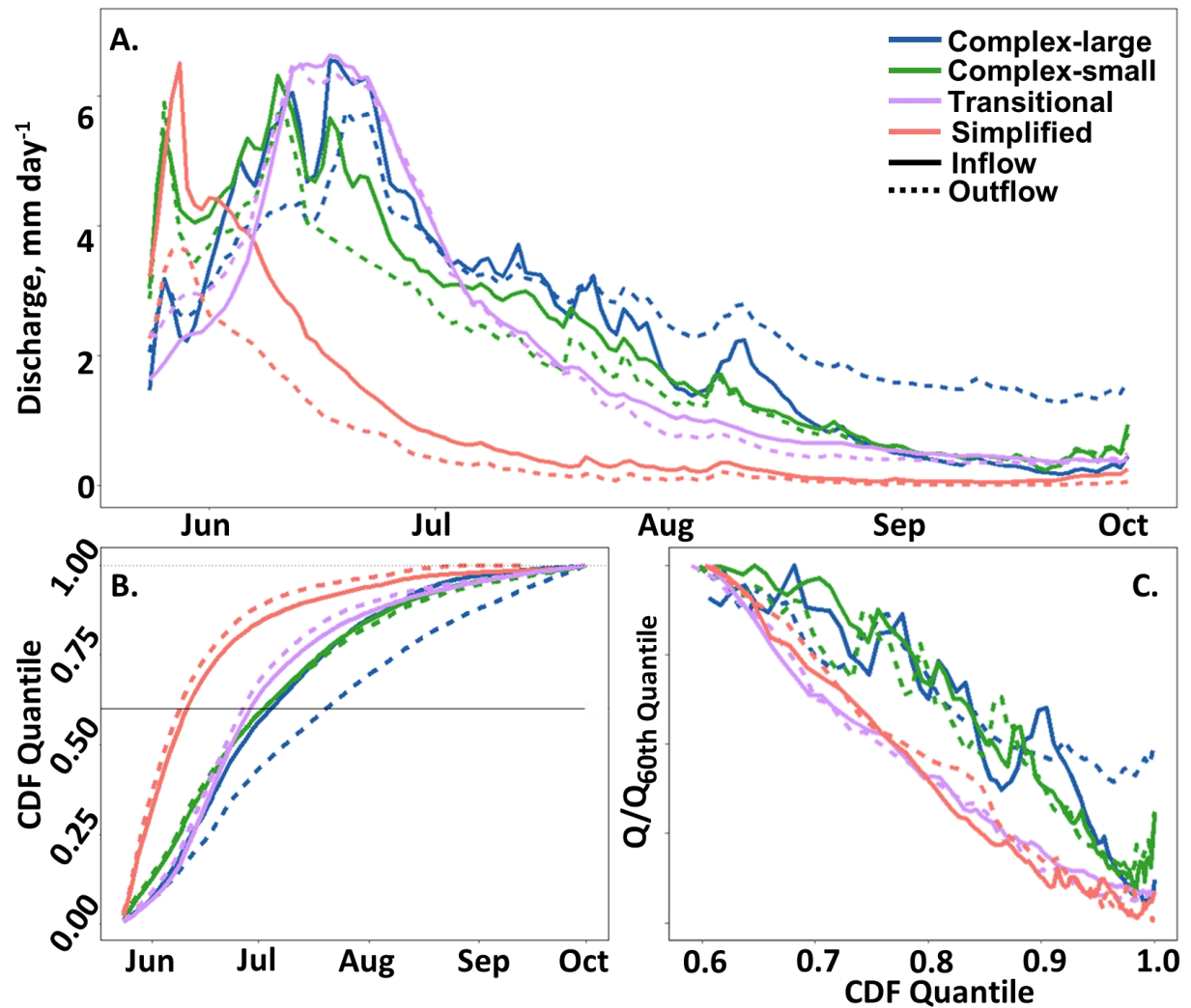


Figure 3 | Panel A: hydrographs of each meadow inflow (solid) and outflow (dashed) across the study period, May 24th to October 1st. Panel B: Cumulative water flux (presented as a cumulative distribution function) for all meadow gauges across the same period, horizontal black line indicates 60th quantile of each flow distribution. Panel C: Recession (Q/Q_0) plot beginning with the 60th quantile (0.6) of each gauge's cumulative flux.

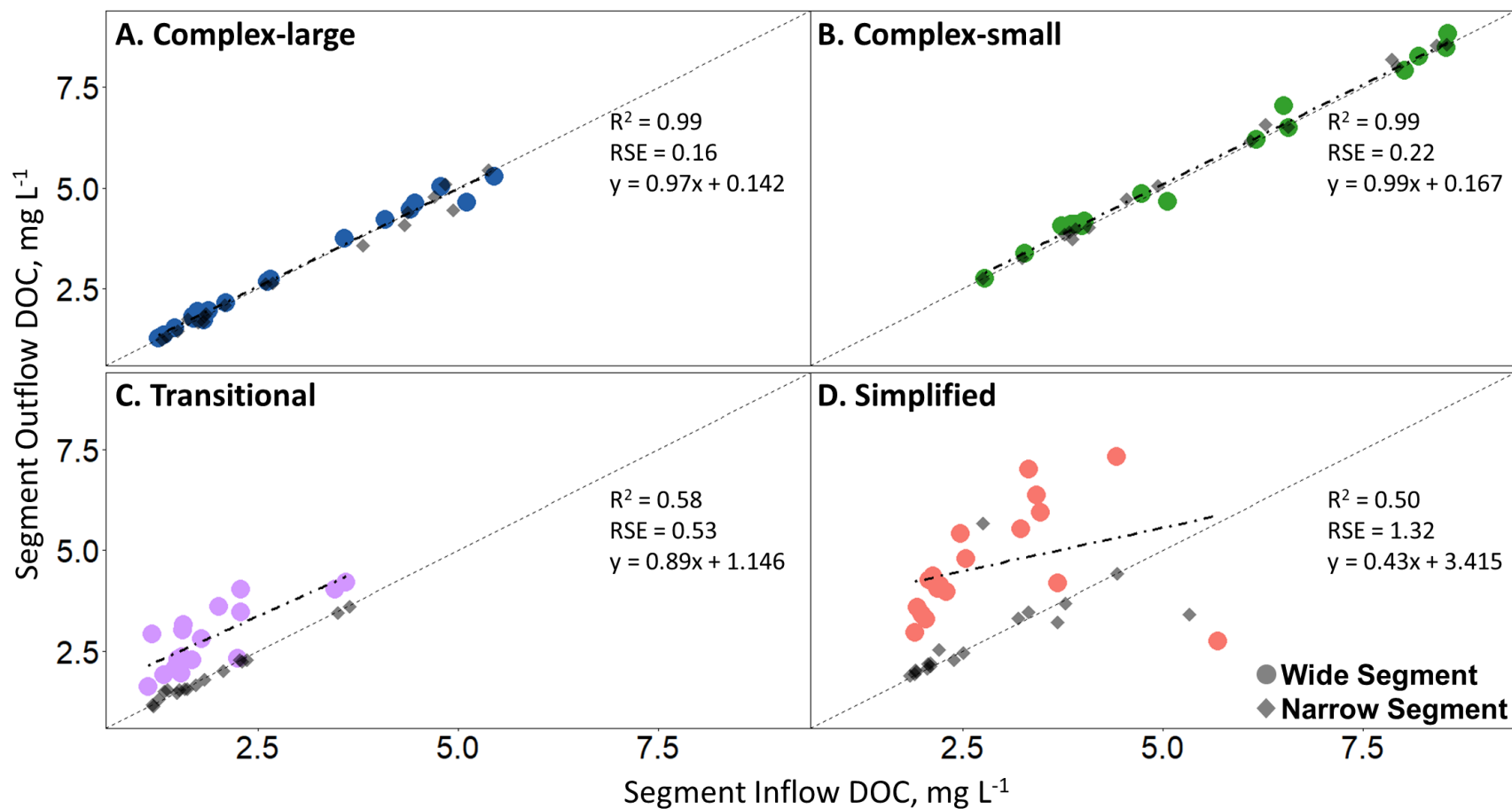


Figure 4 | Regressions of segment outflow vs the reference gauge DOC concentrations. Colored values show segment outflow minus segment inflow gauge relationship and grey diamonds represent the meadow inflow minus the reference gauge (narrow segment). Finely dashed lines show the 1:1 line and thick dashed lines indicates the line of best fit (least square method) for the meadow segment regression. Goodness of fit (r^2), residual standard error (RSE), and linear equations are given for the wide meadow segment only.

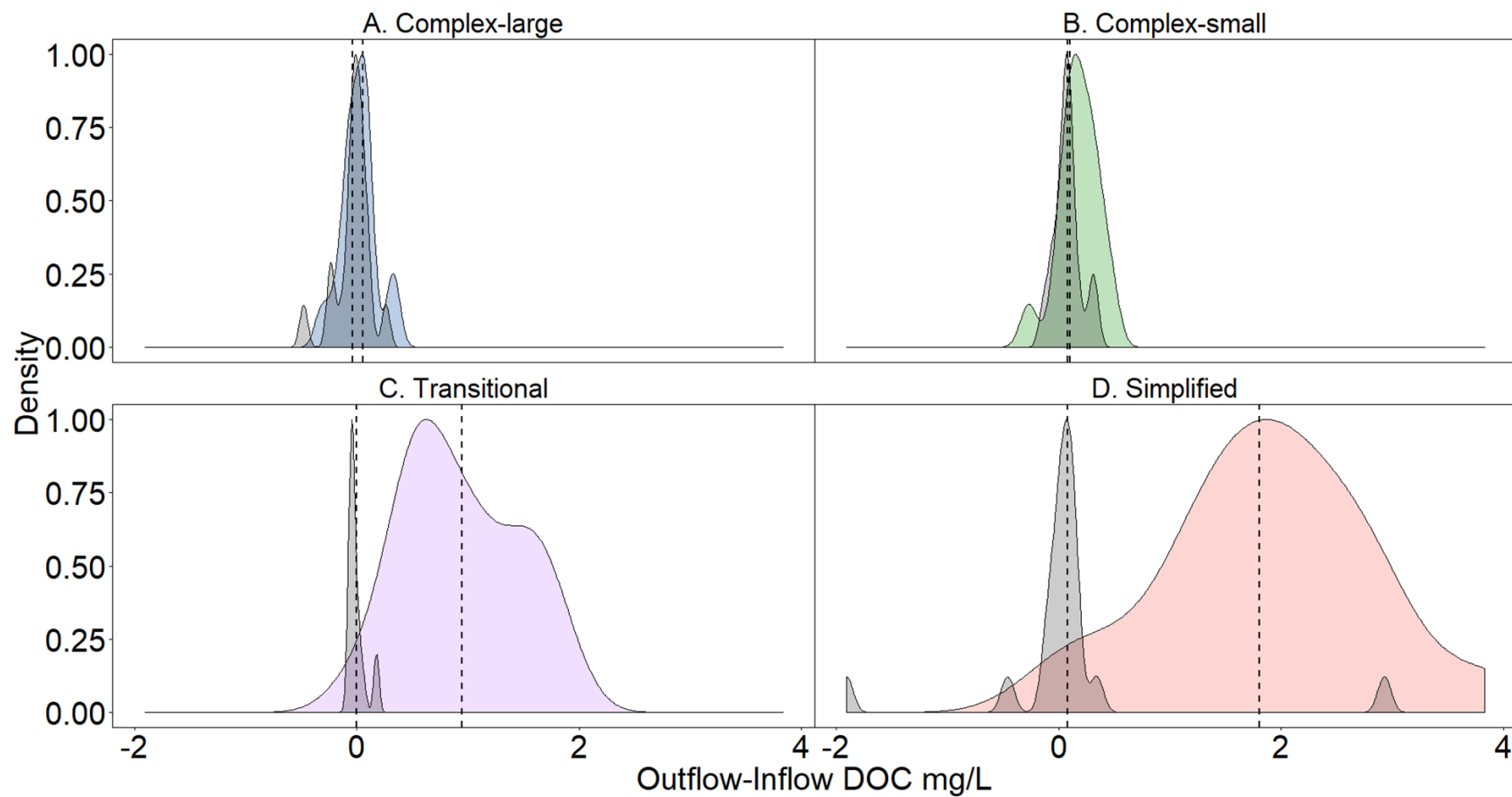


Figure 5 | Scaled density plots of change in dissolved organic carbon (ΔDOC) calculated as segment outflow minus inflow in milligrams per liter. Grey density curves show the distribution of the narrow valley segment and colored curves represent wide meadow segments. Distributions centered near zero indicate relatively little change between segment inflows and outflows. Positive means indicate seasonal increases in DOC concentrations at the segment outflows. Dashed lines show the distribution mean.

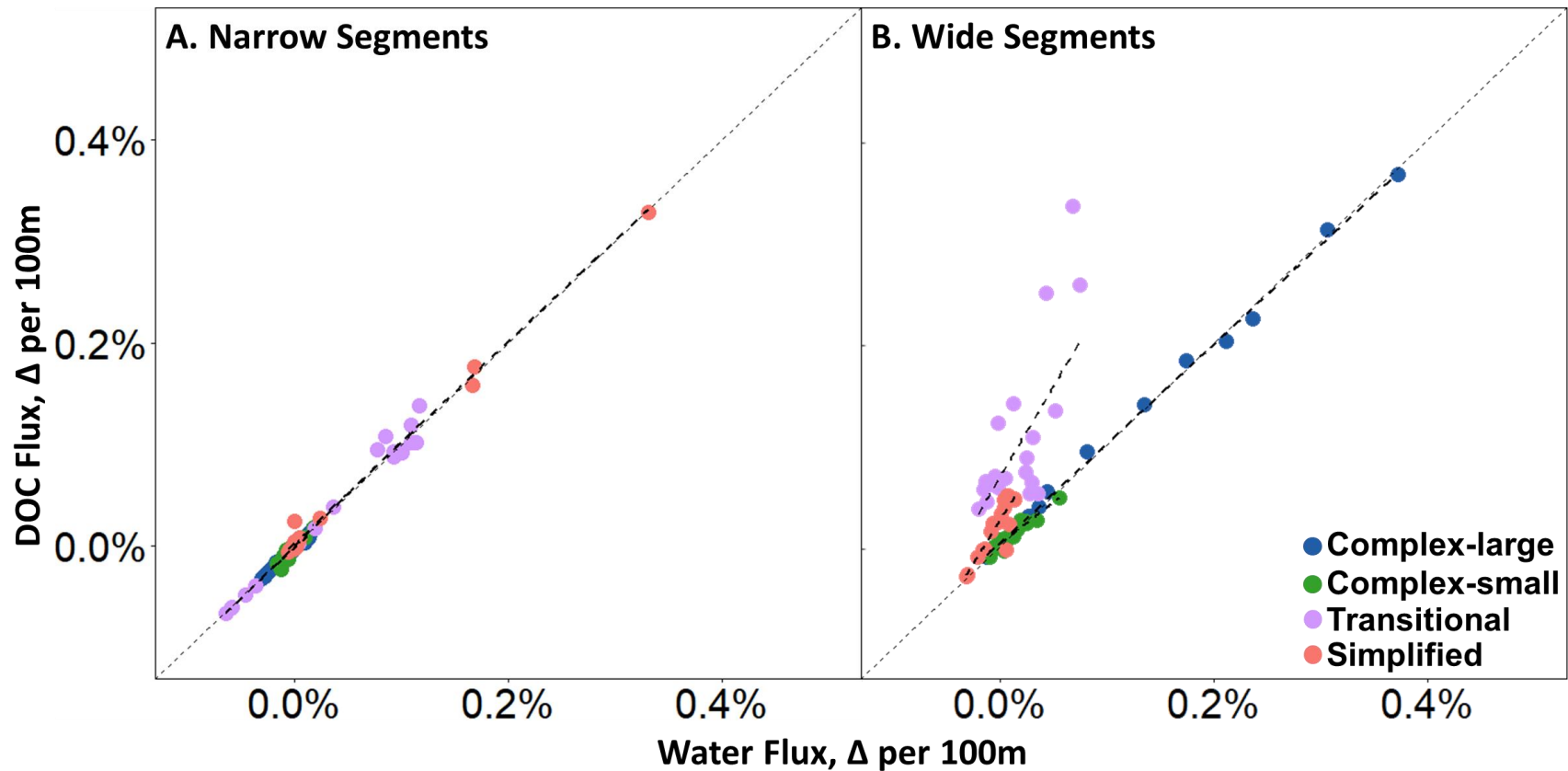


Figure 6 | Percent change per 100 meters of stream length of narrow segment water flux versus percent change per 100 meters of DOC flux balance (Panel A). Panel B shows the regression of the wide meadow segment percent change water flux versus percent change DOC flux balance. We define segment flux balances as the difference between outflow and inflow, divided by the inflow, multiplied by 100 to give values in percent. *Note: Simplified narrow segment high point not shown on panel A falls along the 1:1 at 0.012 % Δ per 100m.

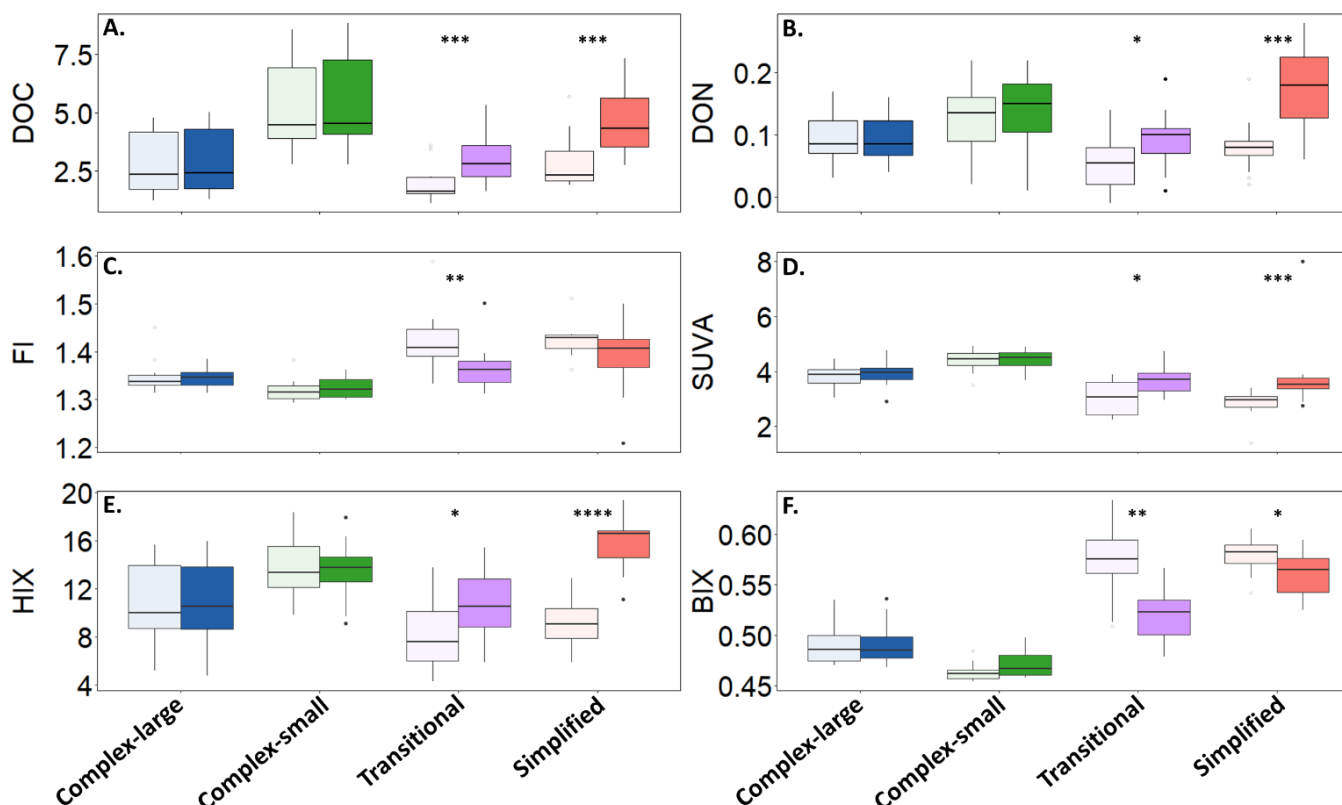


Figure 7 | Boxplots of dissolved organic carbon (DOC), dissolved organic nitrogen (DON), specific ultra violet absorbance at 254nm (SUVA), fluorescence indices (FI, fluorescence index; HIX, humification index; BIX, biological index). Light shaded boxes represent wide meadow segment inflow values and darker colored boxes indicate wide meadow segment outflows. FI values (Panel C) closer to 1.2 represent more terrestrially derived organic matter and values closer to 1.8 represent more microbial or autochthonous sources. SUVA₂₅₄ values in Panel D relate to dissolved organic matter aromaticity and molecular weight, with higher values indicating more aromatic and heavier molecular weight. Higher HIX values (Panel E) are indicative of higher proportions of humic substances. Higher values of BIX (Panel F) correlate to more recently produced microbial by-products. Centerline shows distribution median, boxes extend to the 25th and 75th quartiles, and whiskers extend to 1.5 times the upper and lower interquartile range. Circles denote outliers, if present. * = $p < 0.05$, ** = $p < 0.001$, *** = $p < 0.0001$, **** = $p < 0.00001$ (Paired Wilcoxon Rank-Sum Test). Relationships without asterisks show no significance ($\alpha=0.05$).

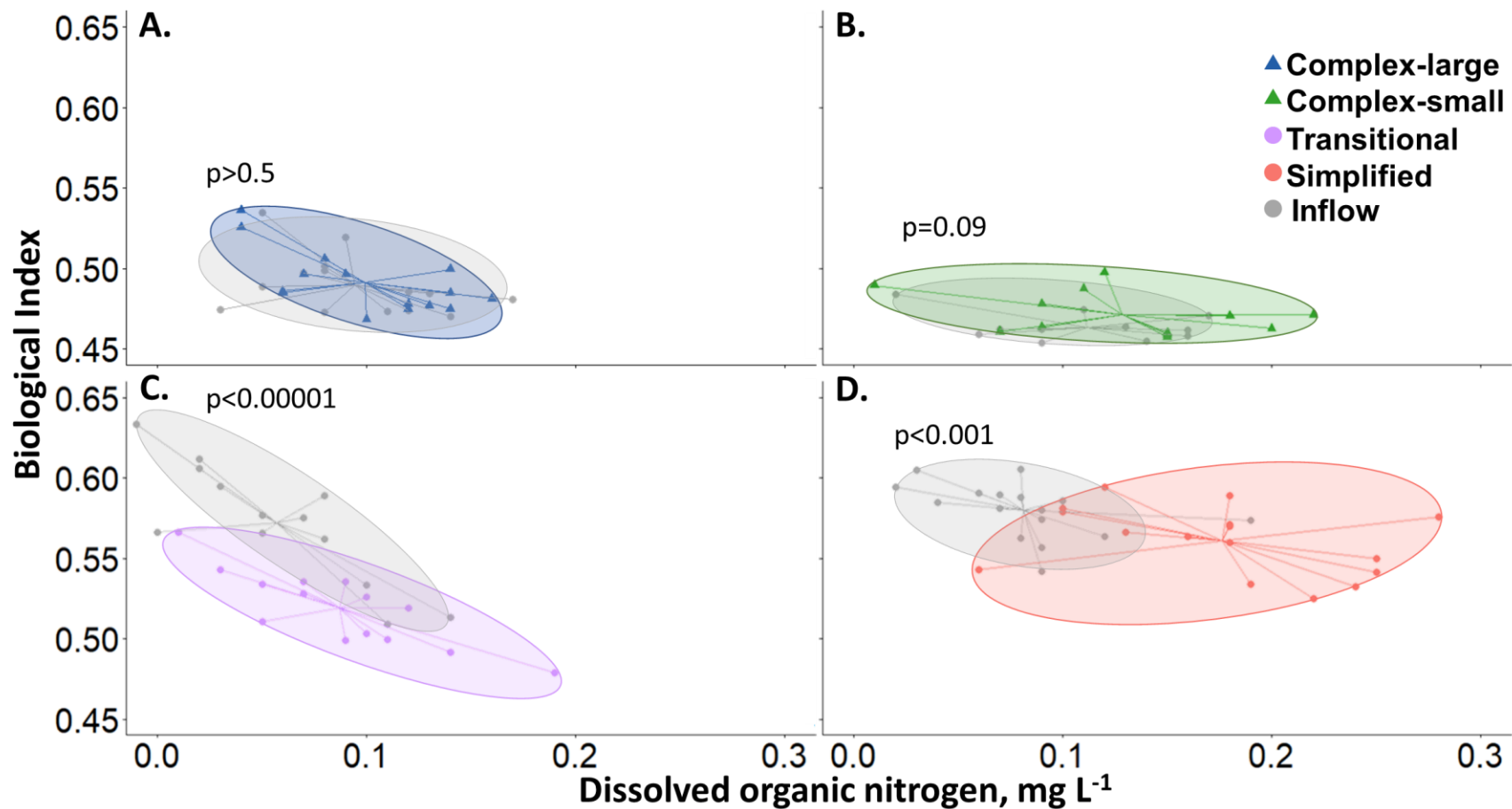


Figure 8 | Star plots of dissolved organic nitrogen (DON) and the fluorometric index referred to as the Biological Index (BIX). DON is a component of dissolved organic matter that is often correlated to increased reactivity. BIX is often correlated with increases in recently produced microbial products and DON. Note that both the transitional and simplified wide meadows segments exhibit decreases in mean BIX values while DON values increase relative to their upstream-narrow segments. Conversely, DON-BIX patterns are more stable between narrow and wide segments in complex-large and small sites. Center points of stars indicate the group mean of values for that group (each point is a single grab sample). Panel C and D demonstrate significant shifts between inflow and outflow. Reported p-values were calculated using multiple analysis of variance (MANOVA).

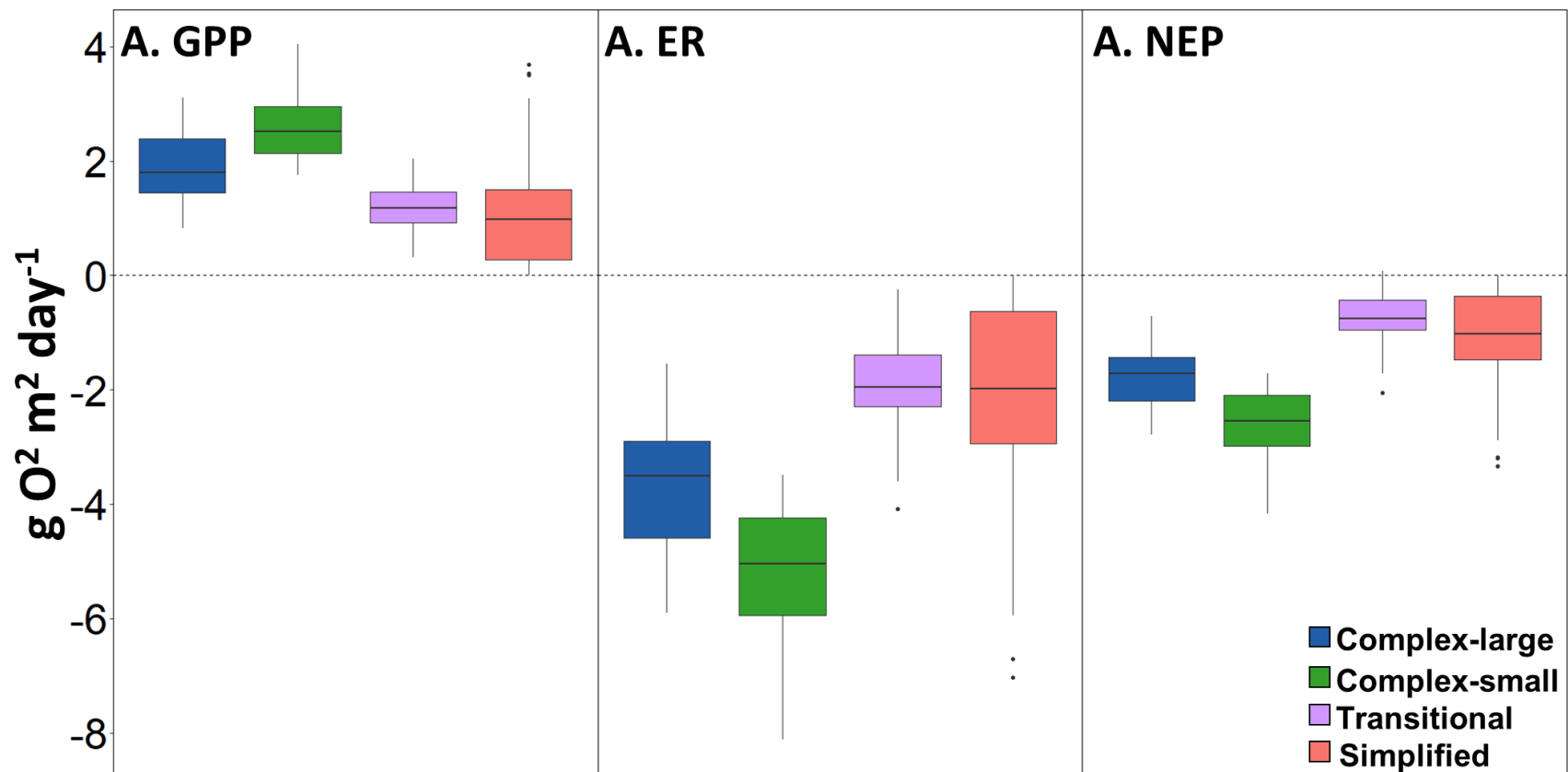


Figure 9 | Daily instream metabolism calculations of the complex-large (blue), complex-small (green), and simplified (red) meadows. The upper panel displays both gross primary production (GPP) and ecosystem respiration (ER) as positive and negative values respectively. The lower panel displays net ecosystem productivity, the difference between daily GPP and ER. Missing data within timeseries represent incomplete data, or periods of model uncertainty when reliable reaeration calculations were impossible due to prolonged supersaturation of dissolved oxygen.

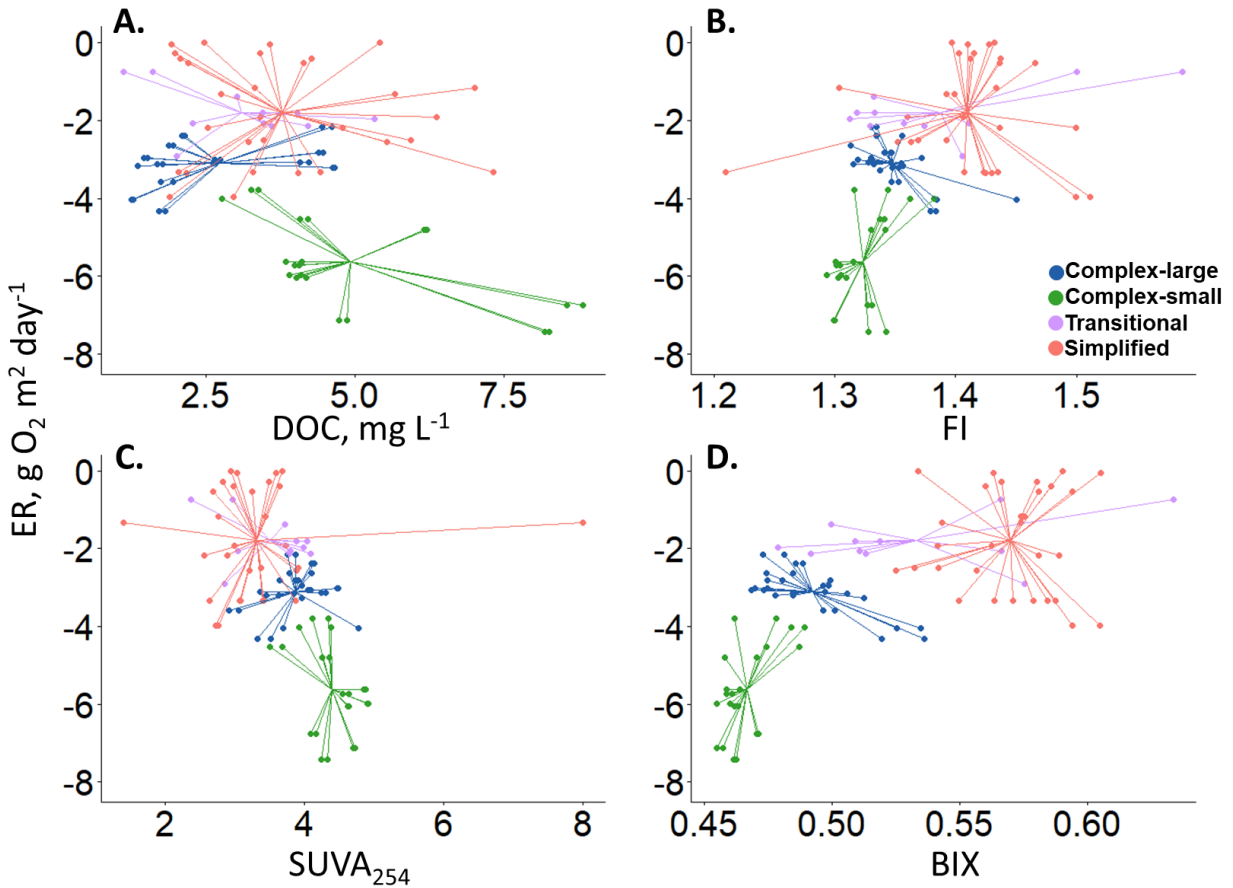


Figure 10 | Dissolved organic carbon concentration (DOC; Panel A) and measurements of dissolved organic matter (DOM) optical properties (Panels B-D) against Ecosystem Respiration (ER). Panel A shows variability in respiration with respect to DOC concentrations. Note that the highest rates of respiration tend to coincide with high concentrations of DOC, but this is not always the case. High residence times and temperatures can facilitate higher ER rates despite low concentrations. ER may also be high during moments of high carbon mass flux, despite low temperatures and concentrations. Panels B and D show qualitative fluorescent metrics that correlate to carbon source and freshness. Panel B shows fluorescence index (FI) as an indicator of source, where values indicate DOM of more autochthonous origin and lower values terrestrial sources. Panel C shows higher values of specific ultraviolet absorbance at 254nm ($SUVA_{254}$), indicating higher aromaticity, at the complex meadows. Higher biological index values (BIX) in panel D indicate a larger proportion of fresher microbial by-products within DOM. Note that higher values in both indices correspond with lower respiration values at the simplified meadows. They may be representative of a mismatched catchment-scale DOM signals with meadow-scale respiration signals or may represent elevated allochthonous inputs from riparian sources within the complex meadows. Star center points indicate group means.

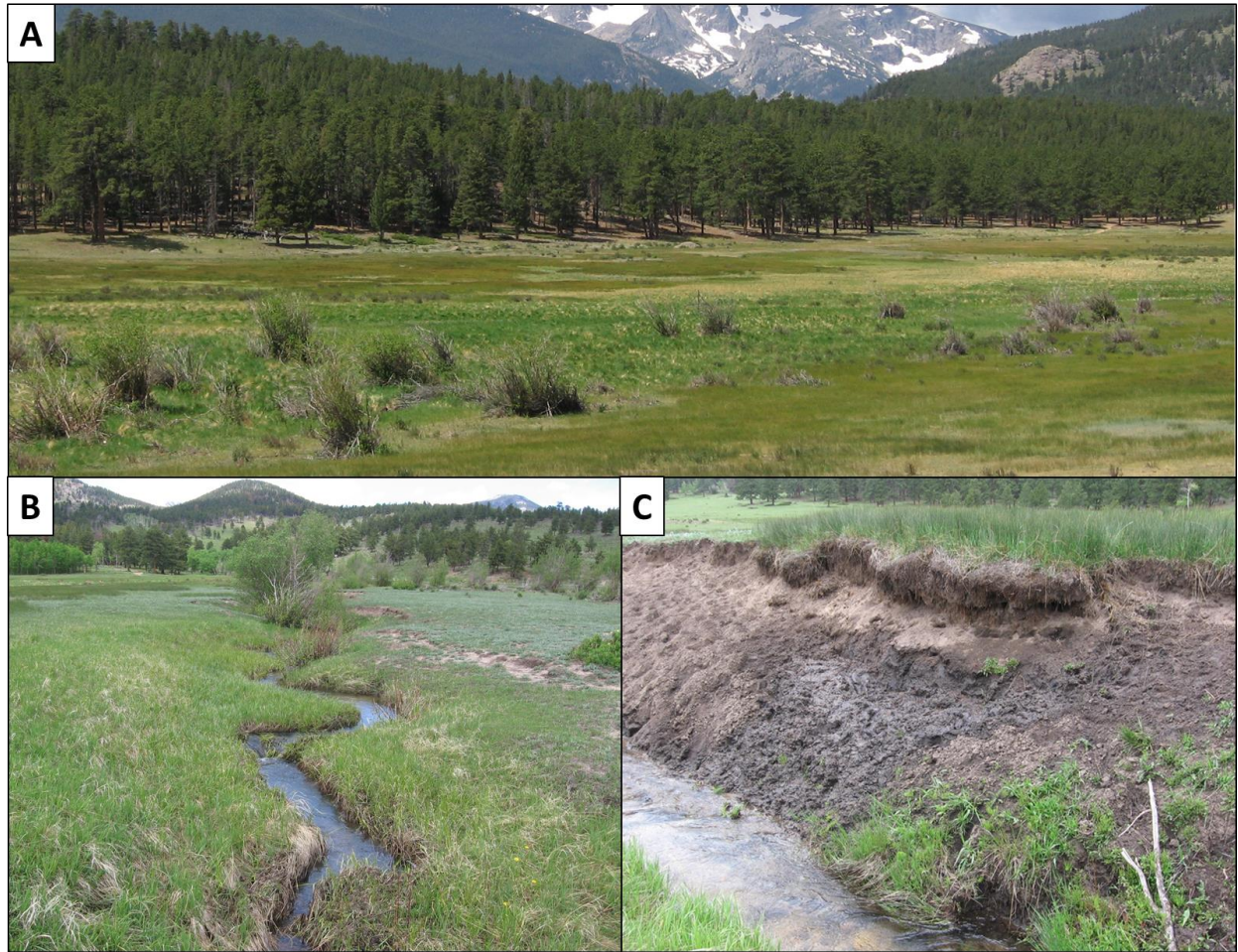


Figure 11 | Image series of the simplified meadow, showing the lack of riparian vegetation (Panels A and B), single-thread channel, and high level of channel incision. Channel incision causes river-floodplain hydrologic disconnection. The fluvial simplification of wide valley segments leads to loss of hydrologic retention and alters biogeochemical, and ecological function. Accordingly, as wide valley segments transition from fluvially complex to simplified as a result of beaver abandonment, or other perturbation, they lose river-floodplain connectivity, hydrologic retention, and riparian vegetation. Panel B and C photo credit: Ellen Wohl.

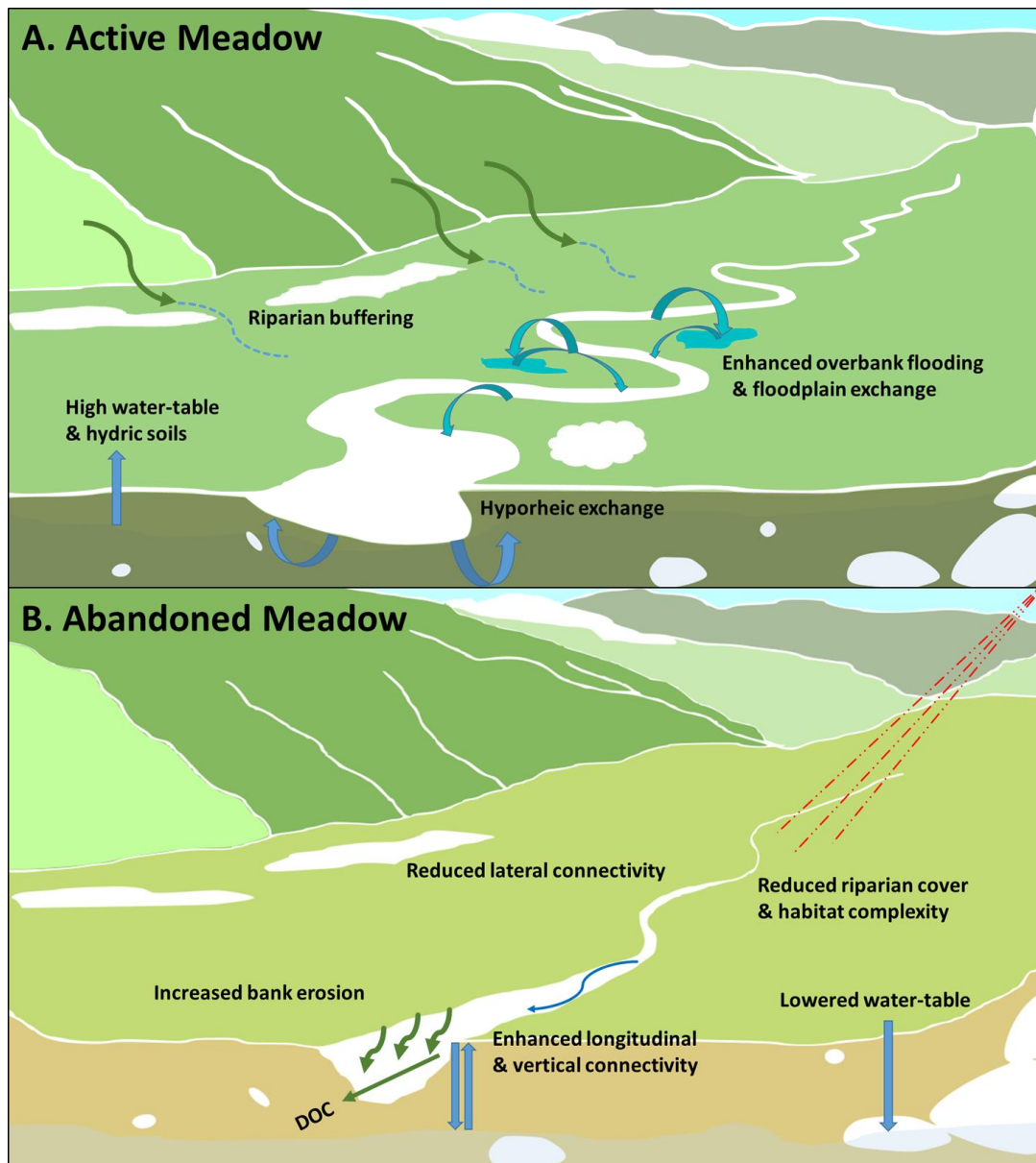


Figure 12 | Conceptual representation of spatial heterogeneity and hydrologic dynamics in an active (Panel A) and abandoned meadow (Panel B). In the complex meadow scenario (Panel A), beaver-mediated prolonged overbank flooding and habitat complexity lead to a diversity of flow paths that enhance the lateral exchange of water and fluvial materials. Dam features that reduce stream power enhance hyporheic exchange and facilitate heightened water tables, leading to riparian vegetative communities that improve hillslope buffering. Cumulatively, we believe that these dynamics play a strong part in facilitating segment-scale stability. In Panel B, the loss of retentive features increases stream power and longitudinal connectivity while simultaneously reducing lateral exchange, lower the water table and increasing vertical connectivity (hydrologic turnover). These characteristics lead to a lowered-water-table and vegetative regime that further reduces bank stability, and alters DOC export, radiation input to stream ecosystems, and ecosystem productivity.

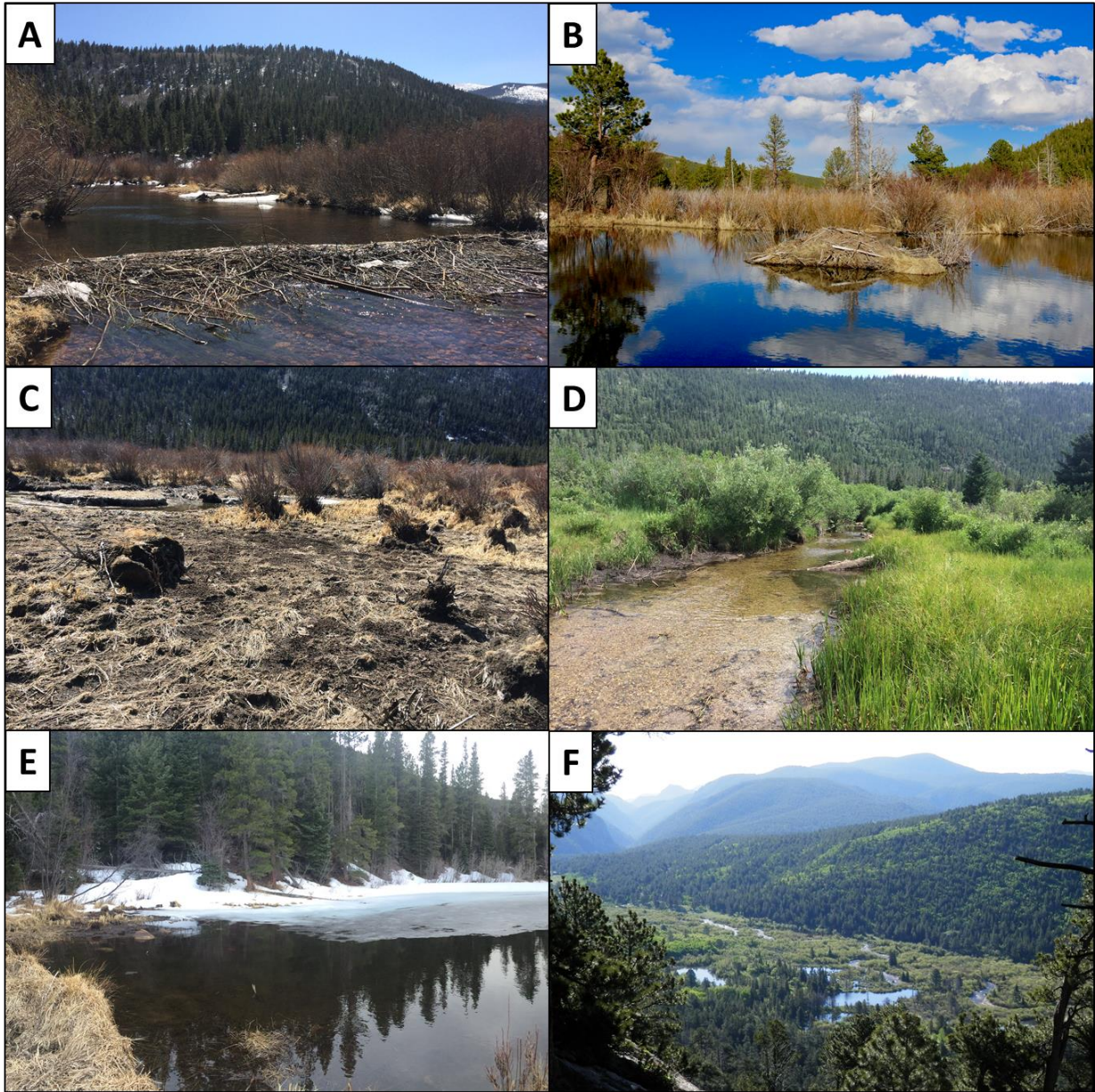


Figure 13 | Series demonstrating the wide range of habitat types within the complex-large meadow. Panel A shows a main-channel spanning beaver dam during winter low flows. This seasonally breached dam was rebuilt in the same location during low flows for two consecutive years. Panels B and C show beaver pond habitat, one actively maintained (B) and one recently drained following a dam breach (C). These images depict the dynamic nature of complex meadows and show that while we observe stability in flow and chemistry, disturbance is a frequent occurrence in these systems. Panel D shows a main-channel connected side-channel that varies in connectivity depending on stream stage, while Panel E shows a hillslope connected beaver pond with no direct channel connectivity. Panel F is an overview of the complex-large meadow during peak-flows (photo credit: Ellen Wohl). Lateral connectivity during peak flow is extremely high, with observed flowing water hundreds of meters from the main-channel during this time.

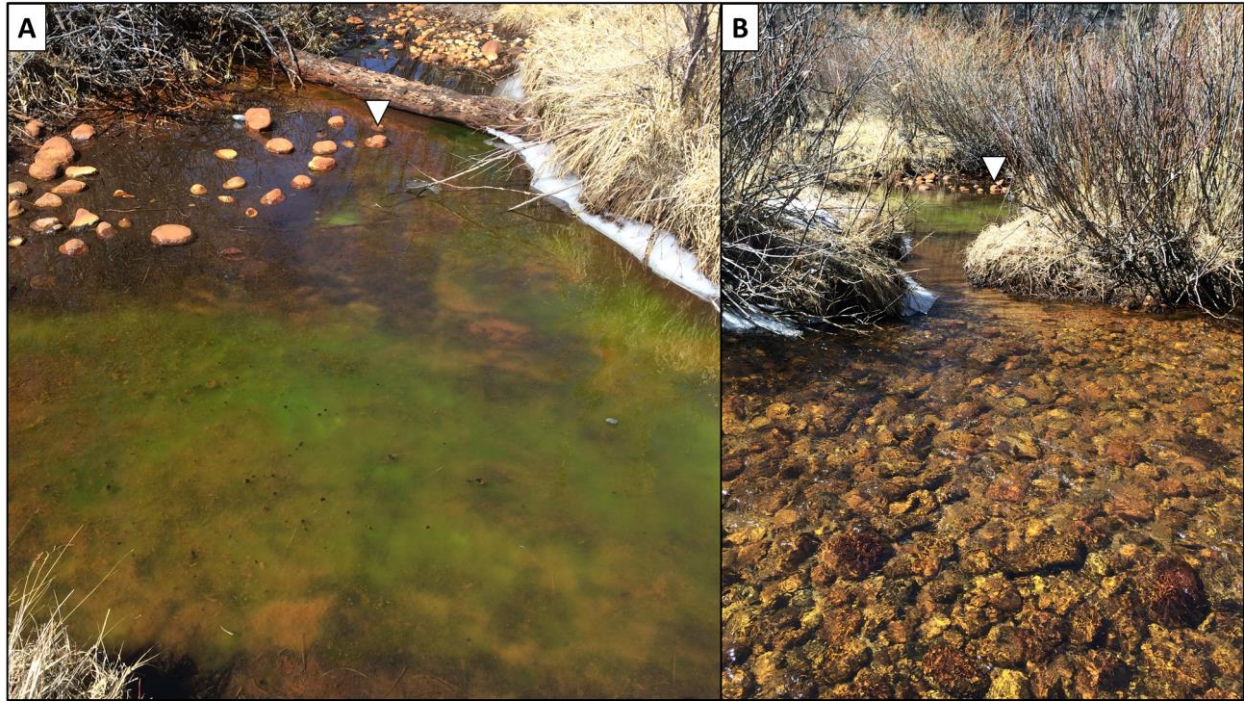


Figure 14 | Autochthonous production in river-connected off-channel habitat of the complex-large meadow (Panel A). The vantage of Panel B, taken from the middle of the main-channel shows the off-channel habitat and associated algal production. White triangles denote the same point between panels A and B for reference.

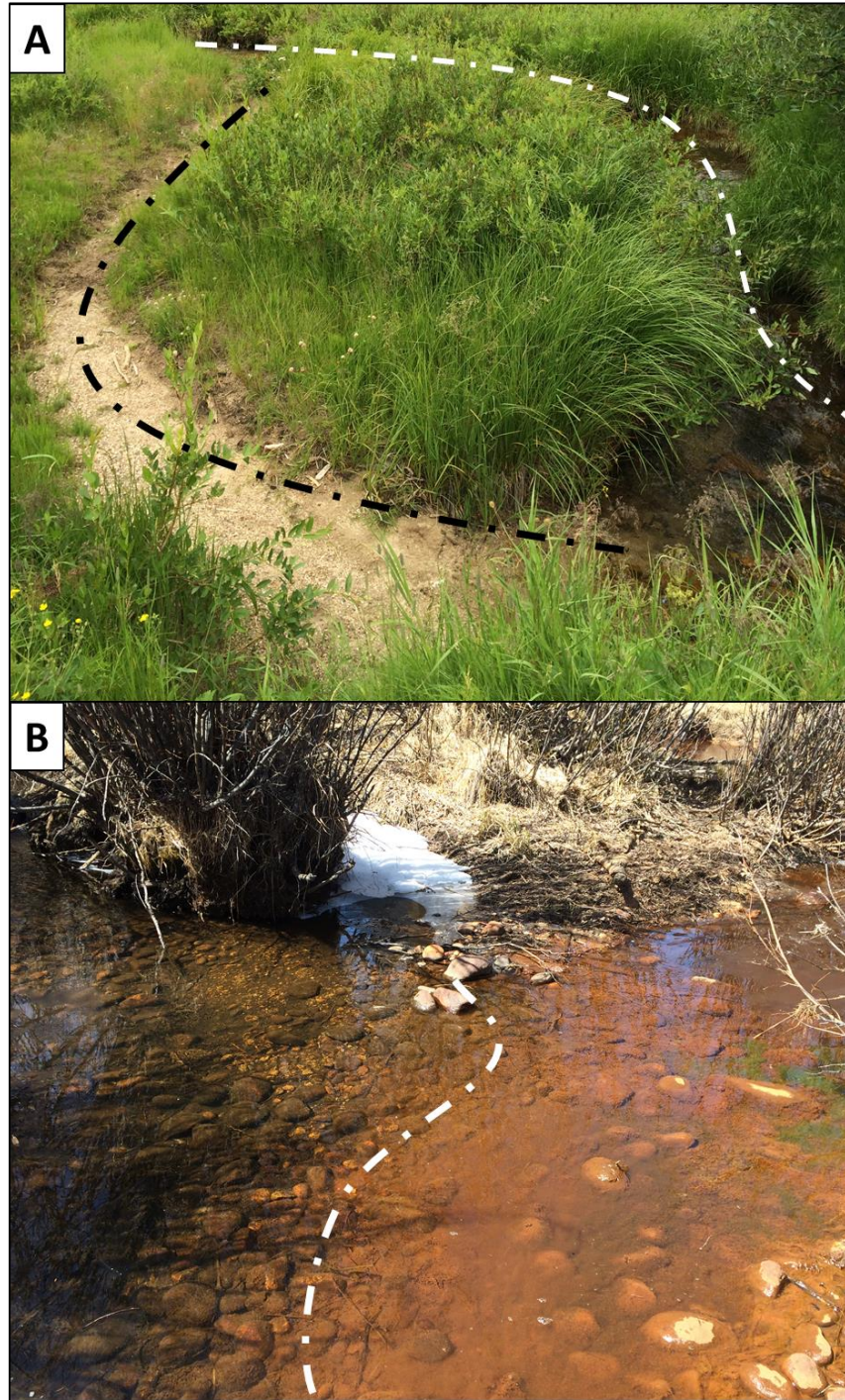


Figure 15 | Fluvially connected complex meadows, while demonstrating chemical stability at the meadow outflow, show remarkable temporal and spatial variability. Panel A shows a dry channel (black line) that becomes seasonally connected to an adjacent flowing channel (white line) depending on stream stage. Panel B shows the convergence of two flowing side channels, one with warmer water, high levels of light and high productivity (image-right) and the other with cold,

clear shaded water. The white line marks the convergence zone and between these two strongly contrasting off-channel habitats that are spatially near.

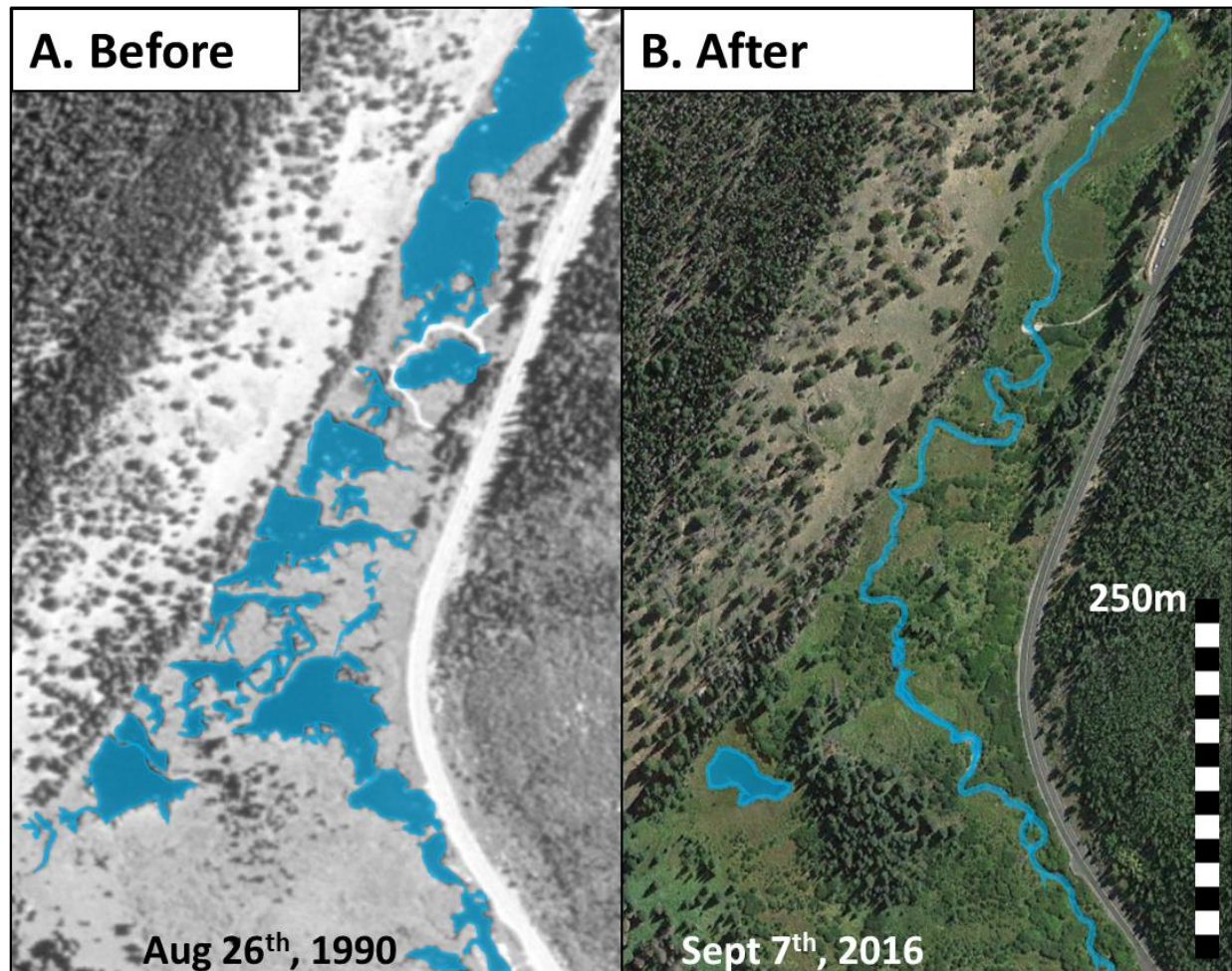


Figure 16 | Historical imagery of the transitional meadow (Hidden Valley Creek), taken before beaver abandonment (Panel A) and after (Panel B). Red dashed lines (Panel A) highlight areas of beaver induced inundation, while analog white dashed lines (Panel B) highlight areas of reduced fluvial complexity following beaver abandonment. Images were both acquired during late-season low-flow periods. *Image Sources: U.S. Geological Survey*

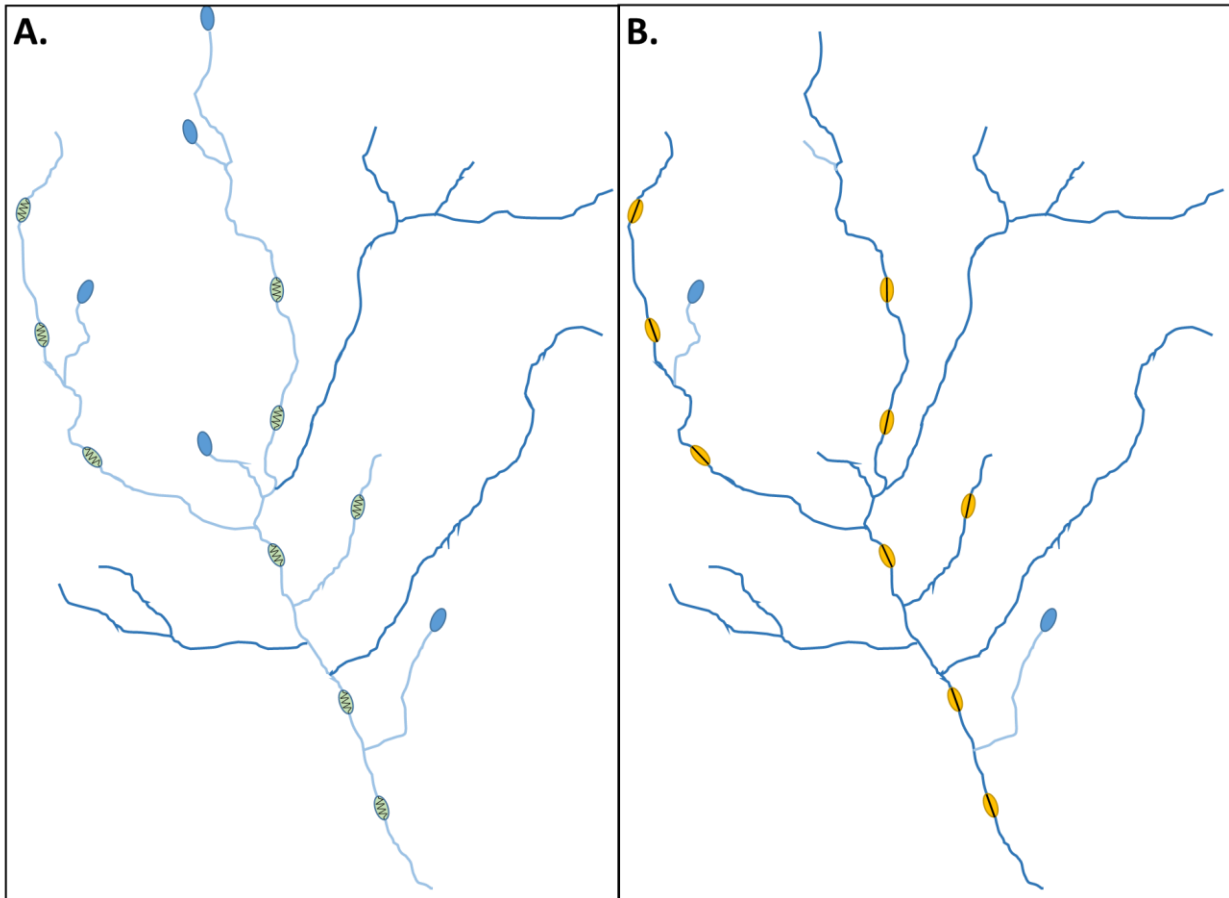


Figure 17 | Conceptual depiction of one stream network under two scenarios of varying watershed resilience and retention. Panel A depicts a resilient network with two forms of retentive buffers: lakes and wet alluvial valley bottoms maintained by the presence of beaver. Darker streams represent channel corridors with no major retentive features along their continuum, light blue represents channels with one or more retentive features. Panel B represents a channel network where land and water resources management have led to the reduction of lakes and the drying of wet valley bottoms. Individually, wet valley bottoms appear to confer stability at the segment scale, while dry, simplified valley bottoms export more carbon and elevate downstream carbon concentrations. Cumulatively, diversity of habitat and retentive features lead to increased lateral hydrologic connectivity that can lead to improved system resilience as observed by Moore et al. (2017) at the catchment scale. Given this, alterations to retentive features such as beaver meadows may decrease system resilience and lead to reduced network water quality.

7. TABLES

Table 1 | Summary table of meadow and catchment characteristics. Activity refers to level of long-term beaver activity. We define recently abandoned by beaver presence less than 10 years prior to the study, and long abandoned as greater than 60 years since last beaver activity. Column ‘Lat. Conn.’ refers to the qualitative level of lateral connectivity between each stream and its floodplain.

<i>Site</i>	<i>Beaver Activity</i>	<i>Type</i>	<i>Veg.</i>	<i>Lat. Conn.</i>	<i>*BA km²</i>	<i>*MA km²</i>	<i>BA:MA %</i>	<i>Elev. m</i>	<i>Slope %</i>	<i>Valley Length m</i>	<i>Channel Length m</i>	<i>Wetland %</i>	<i>Forest %</i>	<i>Precip. mm</i>
<i>Complex-Large</i>	Active	Meadow Complex	Riparian Shrubs	High	84.24	0.38	0.45%	2529	1.46	1548	2094	0.6	48.1	976
<i>Complex-Small</i>	Active	Meadow Complex	Riparian Shrubs	High	13.56	0.20	1.46%	2541	2.15	935	1397	1.2	79.7	862
<i>Transitional</i>	Recently Abandoned	Altered Complex	Riparian Shrubs	Medium	8.72	0.10	1.13%	2787	1.71	727	994	0.9	63.5	887
<i>Simplified</i>	Long Abandoned	Prairie	Grassland	Low	13.19	0.38	2.89%	2483	2.39	2856	3989	0.4	70.7	677

*BA refers to the contributing basin area (measured from meadow outflow) and MA equates to meadow area. BA:MA is the percent of the basin covered by the meadow. Elevation references the minimum meadow elevation. We derived wetland and forest % catchment coverage from the 2011 National land Cover Dataset (classes 90 and 95, and 41-43 respectively) obtained through U.S. Geological Survey Stream Stats. Precipitation is the mean annual precipitation for that catchment.

Table 2 | Geomorphic and morphological summary of each site's narrow-wide segment pair.

<i>Site</i>	Valley Setting	Valley Margin Confinement	Morphology	Planform	Valley Setting	Valley Margin Confinement	Morphology	Planform
	<i>Narrow Valley Segment</i>				<i>Wide Valley Segment</i>			
<i>Complex-Large</i>	Confined (terrace)	$C_V \geq 90\%$	Pool-riffle	Single-thread	Unconfined	$C_{VB} \leq 10\%$	Pool-riffle	Multi-thread
<i>Complex-Small</i>	Confined (bedrock)	$C_V \geq 90\%$	Pool-riffle	Single-thread	Unconfined	$C_{VB} \leq 10\%$	Pool-riffle	Multi-thread
<i>Transitional</i>	Confined (bedrock)	$C_V \geq 90\%$	Step-pool	Single-thread	Unconfined	$C_{VB} \leq 10\%$	Pool-riffle	Single-thread (sinuous)
<i>Simplified</i>	Confined (terrace)	$C_V \geq 90\%$	Pool-riffle	Single-thread	Entrenched	$C_{VB} \leq 10\%$	Pool-riffle	Single-thread (sinuous)

*Terms ' C_V ' and ' C_{VB} ' refer to 'valley confinement' and 'valley bottom confinement' respectively. Definitions of valley margin confinement are from Fryirs et al., (2016).

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APPENDIX

Supplemental Table 1 | Summary statistics (Mean $\pm$ SD) of dissolved constituents (mg L⁻¹) and fluorometric indices from each meadow's gauging location.

	<i>Complex-Large</i>			<i>Complex-small</i>			<i>Transitional</i>			<i>Simplified</i>		
	<i>Reference</i>	<i>Inflow</i>	<i>Outflow</i>	<i>Reference</i>	<i>Inflow</i>	<i>Outflow</i>	<i>Reference</i>	<i>Inflow</i>	<i>Outflow</i>	<i>Reference</i>	<i>Inflow</i>	<i>Outflow</i>
DOC	3.045 $\pm$ 1.504	3.128 $\pm$ 1.472	3.18 $\pm$ 1.437	5.415 $\pm$ 1.969	5.622 $\pm$ 2.117	5.686 $\pm$ 2.095	1.896 $\pm$ 0.736	1.885 $\pm$ 0.690	3.031 $\pm$ 0.993	2.748 $\pm$ 1.004	2.831 $\pm$ 1.025	4.634 $\pm$ 1.355
NH₄-N	0.018 $\pm$ 0.009	0.018 $\pm$ 0.008	0.017 $\pm$ 0.007	0.023 $\pm$ 0.011	0.027 $\pm$ 0.009	0.032 $\pm$ 0.014	0.030 $\pm$ 0.010	0.029 $\pm$ 0.008	0.030 $\pm$ 0.006	0.042 $\pm$ 0.014	0.039 $\pm$ 0.008	0.045 $\pm$ 0.007
NO₃-N	0.085 $\pm$ 0.039	0.074 $\pm$ 0.027	0.069 $\pm$ 0.018	0.008 $\pm$ 0.007	0.006 $\pm$ 0.008	0.002 $\pm$ 0.005	0.105 $\pm$ 0.051	0.093 $\pm$ 0.046	0.063 $\pm$ 0.030	0.004 $\pm$ 0.006	0.001 $\pm$ 0.003	0.000 $\pm$ 0.002
DON	0.092 $\pm$ 0.045	0.105 $\pm$ 0.043	0.103 $\pm$ 0.038	0.121 $\pm$ 0.045	0.132 $\pm$ 0.053	0.141 $\pm$ 0.053	0.051 $\pm$ 0.034	0.053 $\pm$ 0.038	0.095 $\pm$ 0.042	0.077 $\pm$ 0.045	0.082 $\pm$ 0.038	0.176 $\pm$ 0.059
SUVA₂₅₄	NA	3.824 $\pm$ 0.387	3.941 $\pm$ 0.440	NA	4.395 $\pm$ 0.406	4.439 $\pm$ 0.367	NA	3.085 $\pm$ 0.601	3.678 $\pm$ 0.478	NA	2.852 $\pm$ 0.460	3.752 $\pm$ 1.181
HIX	NA	10.495 $\pm$ 3.450	10.705 $\pm$ 3.487	NA	13.794 $\pm$ 2.564	13.541 $\pm$ 2.549	NA	8.281 $\pm$ 3.020	10.823 $\pm$ 3.069	NA	9.231 $\pm$ 1.950	15.843 $\pm$ 2.099
FI	NA	1.347 $\pm$ 0.033	1.346 $\pm$ 0.021	NA	1.320 $\pm$ 0.023	1.324 $\pm$ 0.021	NA	1.420 $\pm$ 0.046	1.366 $\pm$ 0.061	NA	1.424 $\pm$ 0.031	1.396 $\pm$ 0.071
BIX	NA	0.491 $\pm$ 0.019	0.491 $\pm$ 0.019	NA	0.463 $\pm$ 0.008	0.471 $\pm$ 0.013	NA	0.572 $\pm$ 0.036	0.519 $\pm$ 0.023	NA	0.579 $\pm$ 0.017	0.560 $\pm$ 0.021

*Dissolved Organic Carbon = DOC; Dissolved Organic Nitrogen = DON; Ammonium-nitrogen = NH₄-N; Nitrate-nitrogen = NO₃-N; Specific Ultraviolet Absorbance @ 254nm = SUVA₂₅₄; Humification Index = HIX; Fluorescence Index = FI; Biological Index = BIX