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Beaver dam analogs (BDAs) alter carbon pools, fluxes, and concentrations of intermountain headwater streams

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BEAVER DAM ANALOGS ALTER CARBON POOLS, FLUXES, AND CONCENTRATIONS OF INTERMOUNTAIN HEADWATER STREAMS

By

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Beaver dam analogs alter carbon, pools, fluxes, and concentrations of intermountain headwater streams

Chairperson: Benjamin Colman

Beaver dam analogs (BDAs) have emerged as a climate adaptation and restoration strategy for water resource management in the drought-prone Western U.S., yet, the focus has been on their influence on water quantity, overlooking effects on broader ecological components. By increasing water residence time and facilitating sediment retention, BDAs have the potential to influence carbon pools, fluxes, and concentrations. To examine the influence of BDAs on instream and riparian organic C and trace gases, we studied three intermountain headwater streams restored with BDAs two years after restoration during the summer of 2021. We found that there were small differences in instream dissolved organic C concentrations and trace gas fluxes of carbon dioxide (CO_2) and methane (CH_4) from riparian soils between sections of stream treated with and without BDAs. For concentrations of suspended particulate organic C and dissolved CO_2 and CH_4, differences were site-specific. The most notable differences occurred in benthic organic C pools, which were on average 3-fold higher in the BDA-complexes across sites, suggesting that BDAs show a promising avenue for C storage in restored stream ecosystems.

Introduction

Resource managers use beaver dam analogs (BDAs) to improve ecosystem functioning and mitigate the effects of climate change on water availability in the Western United States. Streams in semi-arid, drought-prone areas of this region often become degraded as their channels become incised, disconnect from their floodplains, and water tables drop due to land-use change and the historical extirpation of beaver (Fairfax and Small, 2018; Naiman et al., 1988; Pilliod et al., 2018). Rising temperatures associated with climate change are compounding stream vulnerability and are projected to increase the frequency and intensity of droughts (Gutzler and Robbins, 2011; Cook et al., 2004, 2015) and alter the timing and form of precipitation. Shifts in the timing of snowmelt runoff to earlier in the calendar year (Regonda et al., 2005; Hidalgo et al., 2009; Marshall et al., 2019) and increases in the fraction of precipitation that falls as rain rather than snow will likely lower stream baseflows (Barnett et al., 2005; Stewart, 2009) and decrease water availability for agriculture, urban areas, and ecosystems, particularly during summer, when water demand is highest (Stewart, 2009; Melillo et al., 2014). To address these climate impacts on water resources, managers are implementing BDAs as an inexpensive strategy that is modeled after natural beaver dams (Pollock et al., 2014; Pilliod et al., 2018; Lautz et al., 2019). By reducing stream velocity, promoting water retention, elevation of water tables (Munir and Westbrook, 2021; Silverman et al., 2019; Wade et al., 2020), and driving sediment deposition (Niezgoda, 2019; Scamardo and Wohl, 2020), BDAs can enhance stream-floodplain connectivity (Pearce et al., 2021). In water-limited regions vulnerable to drought, especially those dominated by snowmelt hydrology, BDAs show promise as an effective climate adaptation and restoration strategy for watershed management.

Though BDAs have the potential to increase water storage, the focus of research on water quantity endpoints neglects the potential influence of BDAs on broader ecological components. Managing water quantity through BDAs will affect carbon pools,

fluxes, and concentrations in stream networks, which may have positive and negative implications for ecosystem structure and function. BDAs are likely to retain particulate organic carbon (POC) in the stream channel and in riparian soils. By restoring riparian vegetation (Orr et al., 2020) and promoting stable channel conditions (Wade et al., 2020), BDAs can reduce erosion and sediment transport, storing POC in the stream. Larger organic C pools and longer water residence times influence the availability of particulate and dissolved organic C, which can serve as energy sources for aquatic insects and heterotrophic microorganisms (Meyer et al., 1988). During peak flows, BDAs will likely restore stream connectivity, providing organic C subsidies to the floodplain and enhancing vegetation that supports terrestrial and emerging aquatic insects, which are primary food sources for salmonids, riparian songbirds, and bats (Baxter et al., 2005; Nakano and Murakami, 2001; Wesner, 2010). To the extent that they raise the water table, BDAs will increase the saturation of riparian soils and decrease soil oxygen concentrations. The resulting hypoxia and anoxia slow the decomposition rate of organic matter, potentially leading to carbon accumulation over time (Cross and Phillips, 1990; McCabe, 1985). However, wetter soils and the subsidy of carbon-rich fine sediments can increase carbon dioxide (CO_2) and methane (CH_4) fluxes. These same conditions prevalent in soils are also present in the stream channel, and coupled with the accumulation of gases in riparian soils, CO_2 and CH_4 concentrations may increase in the stream channel. Shifts in C pools, fluxes, and concentrations in BDA-influenced streams may alter carbon biogeochemistry, affecting ecosystem processes in ways that are not yet well understood.

To expand our understanding of the effects of BDAs on C biogeochemistry, we measured C pools, fluxes, and concentrations in three BDA-treated intermountain headwater streams in Summer 2021. At each site, we took measurements in stream segments treated with BDAs and compared the measurements to those taken in an upstream, unrestored stream segment. We measured benthic particulate organic C (BPOC) in the stream channel and riparian soil organic C for C pools. For concentrations, we

measured suspended particulate organic C (SPOC), dissolved organic carbon (DOC), and dissolved gases, CO_2 and CH_4, in stream water. To investigate the potential for BDAs to affect trace gas emissions from riparian soils, we measured fluxes of CO_2 and CH_4 as well as controls on soil gas fluxes like soil moisture and temperature.

Materials and Methods

Field sites

As part of a project broadly focused on assessing the influences of beaver dam analogs on aquatic ecosystems, researchers from the University of Montana, in collaboration with the US Forest Service - Lolo National Forest, the Clark Fork Coalition, and the Nature Conservancy installed BDAs on three impaired headwater streams in Montana during Fall 2019 (Figure 1). These streams exhibited geomorphological features characteristic of degraded streams, including incised stream channels, intermittent flow, lack of stream-floodplain connectivity, and headcuts. Two of the three sites, Fish Creek (46.9343, -113.3541) and Lost Prairie Creek (47.0764, -113.4572), are on Nature Conservancy land in the upper Blackfoot River basin. Collaborators installed 8 BDAs at Fish Creek to reverse stream incision and reestablish connectivity and at Lost Prairie Creek to address the ephemeral nature of the creek by promoting increased water supply into the late summer. To address channel incision and lack of connectivity and to mitigate headcut erosion, Teepee Creek in Lolo National Forest (46.78117, -114.5247) received 14 BDAs. Though our current study is focused on carbon pools, fluxes, and concentrations, this work was part of a broader study designed to expand our understanding of the ecosystem-level effects of BDAs in the Intermountain West. The broader study included examining fish passage and movement, water temperature, groundwater recharge, and changes in aquatic invertebrate communities.

Figure 1: Beaver dam analogs constructed on Fish Creek, Montana in Fall 2019 using wooden posts and interwoven conifers. Photo credit: Ben Colman.

To examine the influence of BDAs on carbon quantities in restored streams, we first divided the stream into an upstream unrestored reference segment and the downstream BDA-restored segment in each of the three headwater streams two years after restoration. These segments will hereafter be referred to as the Reference segment (upstream, unrestored) and Treatment segment (downstream, BDA-restored segment). Segment lengths for the upstream Reference and downstream Treatment segments for each site are as follows: Fish Creek, 60 m Reference and 80 m Treatment; Lost Prairie Creek, 76 m Reference and 55 m Treatment; and Teepee Creek, 120 m Reference and 121 m Treatment. To minimize the potential influences a given segment may have on the other, the two segments were separated by a distance similar to the length of the segments themselves at each site. Within the Treatment segment, the stream was subdivided into reaches by pairs of BDAs, and we sampled three of these reaches, including between the top two BDAs in the segment (Upper), between two BDAs in the middle of the segment (Middle), and between the bottom two BDAs in the segment (Lower). Given that there were no analogous regularly spaced discontinuities in the Reference segment, we delineated three reaches of similar length and position to the corresponding ones in the Treatment segment and defined them as Upper, Middle, and Lower. Thus,

our sites are structured hierarchically (Figure 2), with three sites (Fish, Lost Prairie, and Teepee Creek), each containing two segments (Reference, Treatment), and each Segment containing three sampling reaches (Upper, Middle, Lower).

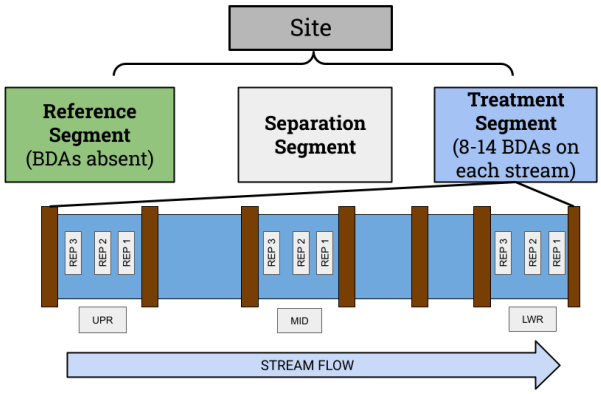

Figure 2: Schematic of the sampling locations for each of the three sites. Each site contains a Reference and Treatment segment, separated by a segment of similar distance. The Treatment was subdivided into three Reaches (Upper, Middle, Lower), and locations for replicate samples within a reach were taken just upstream of the downstream BDA, in the middle of the pool formed by the BDA pair, and downstream of the top BDA.

Field methods

Suspended particulate and dissolved organic carbon

To characterize differences in suspended particulate and dissolved organic C concentrations in the Reference and Treatment segments, we measured carbon concentrations in samples collected biweekly from late May through September 2021 in the Lower reach of each segment. We collected SPOC and DOC samples using a drill pump (Woessner, 2007), which consists of a handheld peristaltic pump head (Masterflex Standard pump head Model 7015-00; Cole-Parmer, Vernon Hills) powered by a rechargeable variable-speed drill and 6 mm LS/DS silicone tubing (GeoTech, Kirkland) fit with a 45 mm ID in-line filter holder (Advantec, Gold Beach) the pump, we filtered 1 L of water through 0.7 µm glass fiber filters (GF/F; Whatman, Maidstone, UK) that were pre-ashed at 500 °C for 4 hours. For the SPOC sample, we recorded the volume filtered and placed

the folded filter in pre-cut tinfoil. For the DOC sample, we added 40 ml of filtrate into pre-ashed 40 ml amber glass vials (500 °C for 4 hours) for DOC analysis. We transported the samples on ice to the laboratory and preserved particulate samples in the freezer and DOC samples in a 6°C refrigerator until analysis.

Benthic particulate organic carbon

To address how the pools of BPOC in the stream differed between segments, we collected triplicate samples in each reach once monthly from June through August. Beginning at the Lower reach in the Treatment, we sampled longitudinally moving upstream using the stovepipe method (Golladay et al., 1989) to collect the coarse (CPOC) and fine particulate organic C (FPOC) size fractions that constitute BPOC. For the coarse component, we split it into larger materials (> 1 mm) that were easily grasped by hand within the sampler (hereafter, CPOC(a)) and smaller materials that were resuspended and then collected by pouring a 1 L of water through a 1 mm sieve (hereafter CPOC(b)) with both splits put into separate Whirl-pak bags (Nasco, Fort Atkinson). For the fine fraction, we refiltered a portion of the 1 L filtrate through a pre-ashed 0.7 µm GF/F and recorded the filtered volume. We wrapped filters containing FPOC in tinfoil, transported all benthic samples on ice to the laboratory, and stored them in the freezer until analysis.

Flux chamber trace gases and covariates

We collected gas samples to estimate CO_2 and CH_4 fluxes from riparian soils using a modified version of the chamber-based flux method that Parkin and Venterea (2010) adopted from a common design (Hutchinson and Livingston, 2001; Livingston and Hutchinson, 1995; Rochette and Hutchinson, 2005). Our flux chambers consisted of a chamber body, vent, lid, sampling port, temperature probe, and a battery-powered fan. We constructed the chamber body using white polyethylene 5-gallon bucket (Leaktite, Phoenix), reducing its height to 30 cm. We designed the top 20 cm to serve as the

headspace and the bottom 10 cm as the soil anchor. To minimize the influence of solar radiation on the gas fluxes, we wrapped the chamber body with reflective insulation (Reflectix, Markleville). We installed an interior vent 5 cm below the bucket's top by fitting a 10 cm section of clear 6 mm ID vinyl tubing onto a 3 mm ID × 1/4-28 UNF polypropylene threaded adapter (P/N 65597; U.S. Plastic Corp., Lima), conforming to the optimum measurements outlined by Hutchinson and Mosier (1981) to avoid pressure perturbations. For the lid assembly, we used a white 19 L bucket lid (Leaktite, Phoenix) fitted with a 20 mm round rubber injection stopper (Cole-Parmer, Vernon Hills) as the sampling port, a 127 mm temperature probe (M/N: 9840N; Taylor, Oak Brook) for temperature measurements, and an 11.1 V LiPo battery (2200mAh 3S; Zippy Compact), which powered a 40 mm × 10 mm DC Axial Fan 12 V 4.7CFM (Ebmpapst, San Jose) that we attached to the underside of the lid for circulation. In late May, we installed six chambers approximately 1 m from the stream edge in both the Reference and Treatment segments at each site, where they remained for the rest of the sampling season.

From late May to early September 2021, we collected biweekly gas samples for CO_2 and CH_4 analysis. We used 60 mL syringes equipped with a 1-way stopcock (Cole-Parmer, Vernon Hills) and a 20 G hypodermic needle (McKesson, China). Before sampling, we first trimmed the vegetation within the chamber, activated the fans, and attached the lid assembly to the flux chambers. At intervals of 5, 35, and 65 minutes after lid installation, we collected 60 mL of gas through the sampling port (Parkin and Venterea, 2010). We immediately closed the stopcock to prevent leakage, removed the needle, and capped the stopcock end with a luer-lock cap (Cole-Parmer, Vernon Hills). We stored all gas samples in the shade and transported them to the lab for analysis of CO_2 and CH_4 concentrations using an isotope analyzer within 3 d.

To gather covariates of riparian soil gas fluxes, we promptly measured soil temperature and moisture in the chamber after our final gas sample collection timepoint using a handheld time domain reflectometry probe(HydraGO; Stevens Water, Portland), and

collected riparian soil samples for estimation of soil organic C (SOC) concentrations at the end of the field season. We collected 12 riparian soil samples, one adjacent to each flux chamber, using the plaster cast volume extraction method developed for use in stony soils on modest slopes (Frisbie et al., 2014). To extract the soil sample, we removed the top inch of soil and inserted a cardboard ring (1 cm high $\times$ 6 cm diameter), scraping the soil away to create a soil surface even with the upper rim of the ring, and excavated the soil from within and below the ring's depth into a paper bag using a laboratory spoon spatula. To form a cast of the excavation volume, we mixed a volume ratio of one part gypsum-based dental plaster (USG, Chicago) to three parts water, poured the plaster into the excavation, and allowed the plaster to harden before removing it from the soil. We removed excess soil particles from the plaster cast with a small paint brush and abraded any plaster protruding above the top of the ring with a rasp so that the top of the cast was level with the rim of the ring, the original soil surface. We labeled the plaster cast with the corresponding soil sample and then transported it to the lab.

Headspace equilibration for dissolved CO_2 and CH_4

From June through September 2021, we performed biweekly collections of gas and water samples to measure the concentrations of dissolved CO_2 and CH_4 using the immediate headspace equilibration method (Roberts and Shiller, 2015). We collected headspace samples from each reach within the Reference and Treatment segments from the pool between the paired BDAs in the Treatment or similar locations in the Reference. We also collected 0.5 L of water from the bottom of the Reference and Treatment for alkalinity measurements.

We collected triplicate samples of 80 mL of water approximately 10 cm below the stream's surface at the thalweg using 140 mL syringes (Monoject; Cardinal Healthcare, Dublin) with 3-way polycarbonate luer lock stopcocks (Cole-Parmer, Vernon Hills). We then recorded the air and stream temperature, pH, and conductivity using a handheld

sampling meter (YSI Professional Plus; Xylem, Yellow Springs). For the headspace equilibration, we connected 60 mL syringes (McKesson, China) prefilled with zero-air (Norco, Boise) to the 3-way stopcock of each of the 140 mL syringes. We then introduced the zero-air from the 60 mL to the 140 mL syringe, closed the stopcocks of both syringes, and detached the 60 mL syringe. To equilibrate the headspace with the water, we vigorously shook the 140 mL syringes for 3 minutes. After equilibration, we reattached the 60 mL syringe, opened both stopcocks, and transferred all the headspace air into the sample syringe without introducing any water. We then closed the 60 mL syringe stopcock and sealed it with a luer lock cap (Jensen Global, Santa Barbara), expelled the water from all three triplicate 140 mL syringes into a 250 mL graduated cylinder, and recorded the temperature of the composited water. All headspace samples were stored in the shade to maintain a relatively constant temperature and analyzed for CO_2 and CH_4 concentrations using an isotope analyzer within 3 d.

Sample analysis and calculations

Particulate, dissolved, and soil organic carbon concentrations and pool size

To measure the organic C concentration in water samples, particulate organic matter, and riparian soils, we used several methods. To measure DOC concentrations (mg C L^{-1}), we used a Total Organic Carbon Analyzer (Aurora 1030W; Xylem Analytics, Weilheim, Germany) that uses a heated persulfate wet oxidation technique. To measure the organic C concentration of particulate organic matter and riparian soils, we oven-dried samples at 60 °C for 24 hours and performed loss on ignition. Prior to oven drying samples, we processed particulate and soil samples using two separate methods. For BPOC, we removed macroalgae, macrophytes, and moss from the coarse BPOC samples (CPOC(a & b)) such that these materials comprised < 10 percent of the total sample and placed the material in pre-weighed aluminum tins. For air-dried soil samples, we recorded the total sample weight and used a 2 mm sieve to remove the coarse fragments, weighed both the coarse and fine fractions, and placed subsamples

of the fine fraction in pre-weighed aluminum tins. We oven-dried suspended, fine, and coarse benthic particulate organic C samples at 70 °C and SOC samples at 105 °C for 24 hours and recorded the total dry weight. To prepare samples for loss on ignition, we homogenized and subsampled larger CPOC samples (> 3 g) using a coffee grinder, and used a mortar and pestle to break up aggregates in soil subsamples. We performed loss on ignition on all organic C samples at 450 °C for 4 hours (Pribyl, 2010) and recorded the ash-free dry mass (AFDM).

To calculate organic C pools and concentrations, we converted the AFDM of each sample type into organic C, assuming a 52 % C content (Pribyl, 2010), and back-calculated the organic C concentrations of subsamples to the original samples by volume, weight, and area sampled. For riparian soil organic C, we calculated pools (g C m^{-2}) from soil bulk density and loss on ignition-derived C. We measured soil bulk density using equation 1 (Blake and Hartge, 1986) where W_{ods} is the oven-dry weight of soil (g), W_{gvl} is the weight of gravel (g), V_{pcw} is the volume of the plaster cast (cm^{-3}) measured by water displacement, and V_{gvl} is the volume of gravel (cm^{-3}) calculated as the gravel weight divided by its density of 2.65 g cm^{-3}. To calculate C pools per unit area (g C m^{-2}), we multiplied the loss on ignition-derived C concentration (g C $g_{soil}{}^{-1}$) by the bulk density (g cm^{-3}) to obtain the C content by soil volume (g C cm^{-3}). Then, we extrapolated the C content by soil volume and the core depth interval (10 cm) to the volume of the soil in 1 m × 1 m × 0.1 m (0.1 m^{-3}).

$$\rho_b = (W_{ods} - W_{gvl}) \,/\, (V_{pcw} - V_{gvl}) \tag{1}$$

For SPOC concentration (g L^{-1}), we divided the C content of the collected material by the volume of water filtered. For benthic C pools, we multiplied CPOC(b) and FPOC concentrations (g L^{-1}) by the volume of water for each stovepipe sample, then divided the resulting mass by the stovepipe area to calculate CPOC(b) and FPOC (g m^{-2}) pools. Then, we took the sum of these pools (CPOC(b) & FPOC) and CPOC(a) (g m^{-2}) to calculate the total BPOC pool for each sample.

Trace gas concentration analysis

To analyze gas samples for CO_2 and CH_4 concentrations, we used a Picarro cavity ring-down spectrometer (G2201-*i*; Picarro, Santa Clara). To analyze small sample volumes, we built a manifold consisting of 6 mm ID copper and Bev-A-Line tubing (U.S. Plastic, Lima) with luer-lock and Swagelok fittings. This configuration allowed the direct attachment of gas sample syringes to the manifold, where the Picarro can then automatically draw each sample into the instrument cavity. To remove water vapor from headspace samples for dissolved gases, we attached a 10 mL polyethylene drying tube with tapered end caps (Bel-Art, South Wayne) filled with calcium chloride anhydrous (Fisher Scientific, Waltham) in the chamber and glass wool (Acros Organics, Geel, Belgium) in the end caps. Each sample reached a stable peak CO_2 and CH_4 concentration, which we then extracted from a continuous raw data file using a sequence of peak-picking functions we developed in RStudio (Team et al., 2015).

Riparian soil CO_2 and CH_4 fluxes

We calculated riparian soil CO_2 and CH_4 fluxes from the rate of change of the analyte concentration within the chamber headspace over time. We first corrected the concentration measurements for the influence of temperature fluctuations using data collected at each sampling point. We then used linear regression to calculate the slope of the relationship between headspace concentration (ppmv or µL gas L^{-1}) and time (h^{-1}). Rather than using an R-squared value to evaluate the quality of slope data, which is consistent with the linear regression approach (Parkin and Venterea, 2010), we calculated the t-statistic of each slope as the coefficient divided by its standard error. We excluded slope estimates with t-statistics < 1 for both CO_2 ($n = 15$) and CH_4 ($n = 11$) from 287 samples, as this threshold identifies samples with high variability around the estimated slope, reflecting low precision. This t-statistic cutoff retained more meaningful data by emphasizing precision over fit.

Dissolved CO_2 and CH_4 concentrations

We calculated dissolved CO_2 concentrations (mol L^{-1}) of water samples after headspace equilibration using measured alkalinity, pH, and temperature. We measured total alkalinity using an open cell titration system consisting of a syringe pump (Kloehn Co LTD, Las Vegas), pH electrode (P/N 6.0262.100; Metrohm, Riverview), and pH meter (M/N AR 25; Fisher Scientific, Waltham), using a non-modified Gran Plot titration method (Gran, 1952). First, we calculated Henry's law constant (K_H) in mol L^{-1} atm^{-1} at the sampling and equilibration temperature (K) using parameters from Weiss (1974) (Eq. 12, Table 1). We then used the respective K_H values to estimate CO_2 concentrations in the sample water (mol L^{-1}) at the time of sampling and at equilibration. Next, we solved for the first set of carbonate species (HCO_3^{-1}, CO_3^{-2}) using the measured AT, altitude corrected headspace CO_2 concentrations (ppmv), and temperature-dependent equilibrium constants, K_1 and K_2, from (Millero et al., 2006) (Eq. 12-13). We then corrected the initial DIC calculation following the method from Hall (2020), who applied the method from Koschorreck et al. (2021) for freshwater systems to estimate the original DIC of the water sample. This correction considers the difference in CO_2 concentrations before and after equilibration and the headspace and water sample volumes. We then recalculated dissolved CO_2 concentrations using the corrected DIC, alkalinity, and equilibrium constants.

To calculate dissolved methane from headspace concentrations, we used a more general form of the atmospheric equilibrium solubility equation (Eq. 7) from Wiesenburg and Guinasso (1979) (2) and mass balance equations (3 & 4). Wiesenburg and Guinasso (1979) revised the solubility equation in Weiss (1970) to calculate the atmospheric equilibrium solubility for dissolved methane under any given temperature, salinity, and atmospheric concentration condition. Using the solubility equation and constants A_1-A_4, we calculated the dissolved concentration of methane (C^*) in equilibrium with pCH_4 at temperature T (K), where pCH_4 is the altitude corrected concentration (ppmv) of methane in the equilibrated headspace. Given that salinity (S) concentrations (ppt)

were nearly zero, we omitted the later section of the equation.

$$C^* = exp\Bigg[\left(ln\left(\left(pCH_4 \times 10^{-6}\right)\right) + A_1 + A_2\left(\frac{100}{T}\right) + A_3 ln\left(\frac{T}{100}\right) + A_4\left(\frac{T}{100}\right) + S^{\frac{00}{100}}\left\{B_1 + B_2\left(\frac{T}{100}\right) + B_3\left(\frac{T}{100}\right)^2\right\}\Bigg] \tag{2}$$

$$n_{CH_4} = n_{CH_4 w} + n_{CH_4 HS} = (C^* V_w) + \left(\frac{\left(pCH_4 \times 10^{-6}\right) V_{HS}}{R(273.15 + T)}\right) \tag{3}$$

$$[CH_4] = \frac{n_{CH_4}}{V_w} \tag{4}$$

We then used the following series of equations to calculate dissolved methane concentrations. The molar quantity of methane gas, n_{CH_4} (mol), in the equilibrated syringe is the sum of the amount of methane dissolved in the water, $n_{CH_4 W}$ (mol), and the amount of methane in the headspace $n_{CH_4 HS}$ (mol). Where V_w and V_{HS} are the volumes of sample water and headspace, respectively. The concentration of methane [CH_4] (mol L^{-1}) in water at the time of sampling is then represented in Eq.3.

Statistical analyses

To quantify the effects of BDAs on C quantities in headwater streams, we estimated the relationship between C pools, fluxes, and concentrations in the Reference and Treatment segments. We performed all statistical analyses with the R Statistical Computing platform R version 4.1.3 (2022-03-10) (R Core Team et al., 2022) using Rstudio (Team et al., 2015). We developed generalized linear mixed models (GLMM) using different distribution families and link functions in combination with nested interactions and the main effect of Date in the R package **lme4** (Bates et al., 2015). We tested models by comparing their sample size corrected Akaike Information Criterion (AICc) using the **car** package (Fox and Weisberg, 2018), and selected the most parsimonious model with

the best fit. To obtain the estimated marginal means (least-squares means) and generate pairwise comparisons, we used the `emmeans` function in the **emmeans** package while using the built in p-value adjustment, Tukey HSD, to control for the familywise error rate (Lenth et al., 2018). To accurately represent the underlying patterns and relationships in the data, we removed outliers due to likely contamination from DOC (n = 1) and SPOC (n = 2) data sets. We used the `glmer` function with Gamma distribution and log link for all models with the exception of riparian soil methane fluxes, which allowed us to account for the positive skewness typically observed when measuring C stocks and fluxes. For riparian soil methane fluxes, we used a Gaussian distribution to support the negative values that were associated with this variable due to methane consumption.

Our models included full pooled effects (date, site, and segment) and partially pooled effects (replicate and reach). Specifically, models of all variables contained replicate as a pooled effect, with the addition of reach for benthic particulate organic C and both dissolved gases. We treated the pooled effects as nested variables, reflecting the hierarchical structure of our sampling design: we sampled two segments (Treatment and Reference) within each site (Fish, Lost Prairie, Teepee), and we sampled each site on multiple dates. The nested structure allowed us to account for potential interactions between segments that might vary depending on the site or the date. The partially pooled effects allowed us to account for unobserved heterogeneity associated with these variables.

To move away from typical null-hypothesis significance testing that uses an arbitrary P-value cutoff, we adopted the language of evidence to write the results section as described in Muff et al. (2022). The authors argue against the use of $P = 0.05$ as an arbitrarily sharp cutoff to make binary decisions (e.g., significant versus nonsignificant, there is an effect versus there is not an effect), and suggest a language of evidence as a more nuanced approach to communicate scientific findings. The suggested ranges to approximately translate the P-value into the language of evidence are based on the

ranges described in Bland (1986).

Results

Dissolved organic carbon concentrations

There was no clear effect of BDAs on dissolved organic C (DOC) concentration, despite evidence for small differences in DOC at a single time point mid-late season. Though there were similar trends in DOC concentrations between segments, concentrations were, on average, 7% higher in the BDA-treated segments than in the Reference (Treatment, 3.06 [2.43 to 3.84]; Reference, 2.86 [2.26 to 3.61] mg $L^{-}1$) (Figure 3). Pairwise comparisons of segments by site and date revealed strong to moderate evidence of differences in DOC concentration between segments mid-late season at each site (Tukey HSD; $P = 0.003$, 0.046, and 0.002 for FH, LP, and TP, respectively), and weak (Tukey HSD; $0.05 \geq P \leq 0.1$) to little or no evidence (Tukey HSD; $P > 0.1$) during the majority of the season. During mid-late season, concentrations were 4% and 6% higher in the Reference at Fish and Lost Prairie creeks (FH: 2.95 [2.35 to 3.70], 1.84 [1.47 to 2.31]; LP: 2.36 [1.88 to 2.96], 1.71 [1.37 to 2.15] mg $L^{-}1$ Reference and Treatment segments, respectively), and 8% higher in the Treatment at Teepee creek (4.22 [3.36 to 5.29] 2.31 [1.84 to 2.90] mg $L^{-}1$ Reference and Treatment segments, respectively).

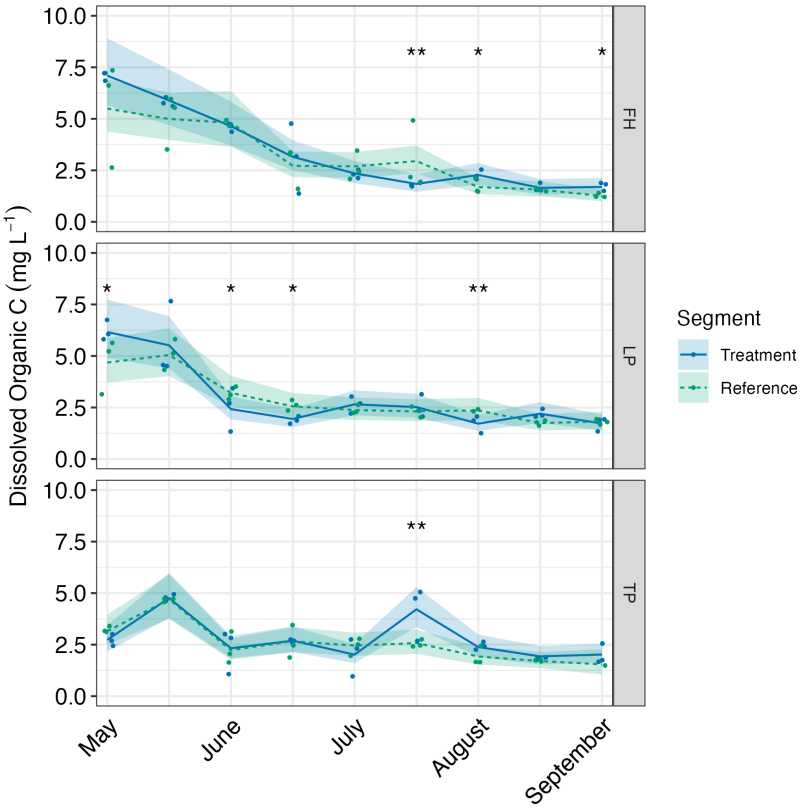

Figure 3: Dissolved organic C concentrations (mg L^{-1}) measured at the bottom of the Reference and Treatment segments throughout Summer 2021. The solid and dashed lines represent the means of pairwise comparisons of Segment by Site and Date, and the shaded areas represent the 95% confidence intervals. No asterisks indicate little to no evidence ($P > 0.1$), a single asterisk indicates weak evidence ($0.05 \geq P \leq 0.1$), and a pair of asterisks indicate moderate to very strong evidence ($P \leq 0.05$) for differences between Segments.

Suspended particulate organic carbon concentrations

Despite evidence for differences across the season, there was no clear effect of BDAs on suspended particulate organic C (SPOC) concentration. The average SPOC concentrations were 30% higher in the Treatment segments than in the Reference (Treatment, 0.62 [0.47 to 0.82]; Reference, 0.48 [0.37 to 0.63] mg L^{-}1) (Figure 4). The magnitude of this difference in SPOC concentrations varied among sites, with the Treatment higher than the Reference by 43, 25, and 14% at Lost Prairie, Fish, and Teepee, respectively. There was moderate to very strong evidence of higher SPOC concentrations in Treatment segments (Tukey HSD; $P \leq 0.05$), but the differences were distributed throughout

the field season at Lost Prairie and Fish creeks, with late-season differences at Teepee Creek. At Lost Prairie, Reference SPOC concentrations were higher at the beginning and end of the season, as supported by very strong (Tukey HSD; June: $P < 0.001$) and weak evidence (Tukey HSD; September: $P = 0.06$).

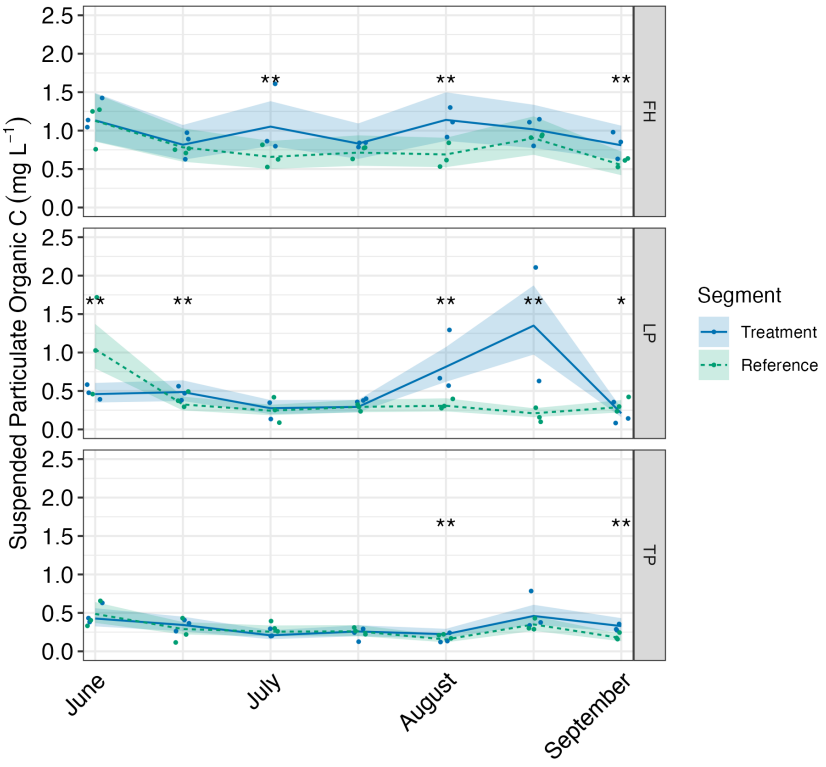

Figure 4: Suspended particulate organic C concentrations (mg $L^{-}1$) at the bottom of the Reference and Treatment segments throughout Summer 2021. The solid and dashed lines represent the means of pairwise comparisons of Segment by Site and Date, and the shaded areas represent the 95% confidence intervals. No asterisks indicate little to no evidence ($P > 0.1$), a single asterisk indicates weak evidence ($0.05 \geq P \leq 0.1$), and a pair of asterisks indicate moderate to very strong evidence ($P \leq 0.05$) for differences between Segments.

Benthic particulate organic carbon pools

In all three sites, there was very strong evidence that Treatment segments stored more benthic particulate organic C (BPOC) than the Reference segments across the entire season. Average pools of BPOC in BDA-treated segments were nearly 3-fold

higher across the season (Treatment, 3.95 [3.23 to 4.84]; Reference, 1.47 [1.14 to 1.89] g m^-2) (Figure 5). At Lost Prairie there was one timepoint where there was weak evidence of the Treatment being higher than the Reference segment (Tukey HSD; $P = 0.07$), and another time point in July where there was strong evidence (Tukey HSD; $P < 0.001$) that pools were higher in the Reference than in the Treatment in (Treatment, 1.42 [1.13 to 1.80]; Reference, 2.29 [1.75 to 2.99] g m^-2). Treatment BPOC averaged across the season were 16-fold higher than the Reference at Fish and 2-fold higher at Teepee, with Lost Prairie exhibiting much smaller differences that were only 34% higher.

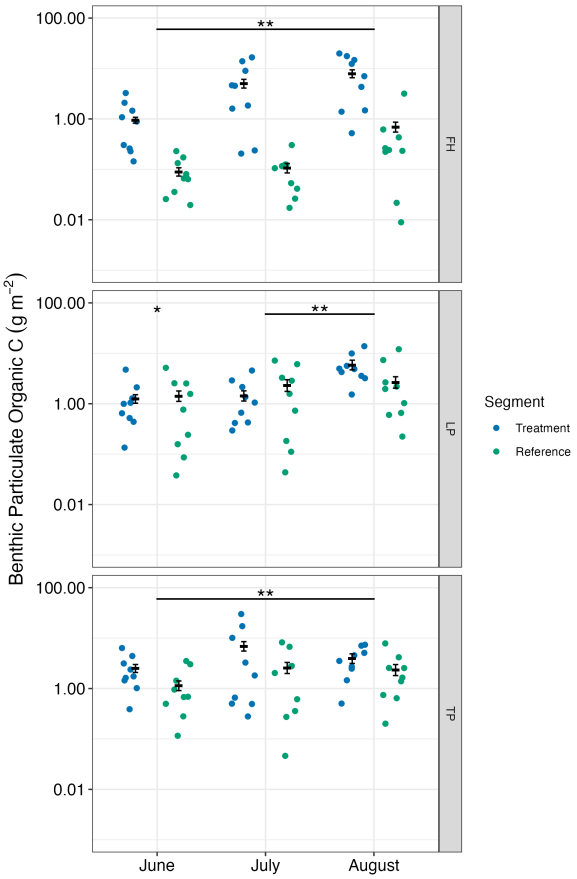

Figure 5: Benthic particulate organic C pools (g m^{-2}) pooled across Reaches in Treatment and Reference segments at the three field sites in Summer 2021. The mean-error bar represents the 95% confidence intervals with the means of pairwise comparisons of Segment by Site and Date. A single asterisk indicates weak evidence ($0.05 \geq P \leq 0.1$), and a pair of asterisks indicate moderate to very strong evidence for differences between Segments at $P \leq 0.05$.

Riparian soil CO_2 and CH_4 fluxes

For most of the season at all sites, there was no evidence of differences in riparian soil carbon dioxide (CO_2) and methane (CH_4) fluxes between segments. There were two exceptions to this overarching pattern, namely in the late-season for CO_2 at Fish and a single timepoint for CH_4 at Lost Prairie when there was very strong evidence (Tukey HSD; $P < 0.001$) and strong evidence (Tukey HSD; $P = 0.01$), respectively, that fluxes were higher in the Reference than in the Treatment. Across the season and our study sites, CO_2 and CH_4 fluxes were slightly higher in the Reference segment than the Treatment by 22%, and 83%, respectively (CO_2, 58.0 [37.9 to 88.8]; 71.0 [46.5 to 108] mg C m^{-2} h^{-1}; CH_4, 24.7 [-53.2 to 103]; 45.1 [-31.7 to 122] µg C m^{-2} h^{-1}, in the Treatment and Reference, respectively) (Figure 6). Thus there is no evidence of a consistent influence of BDAs on CO_2 fluxes and CH_4 from riparian soils.

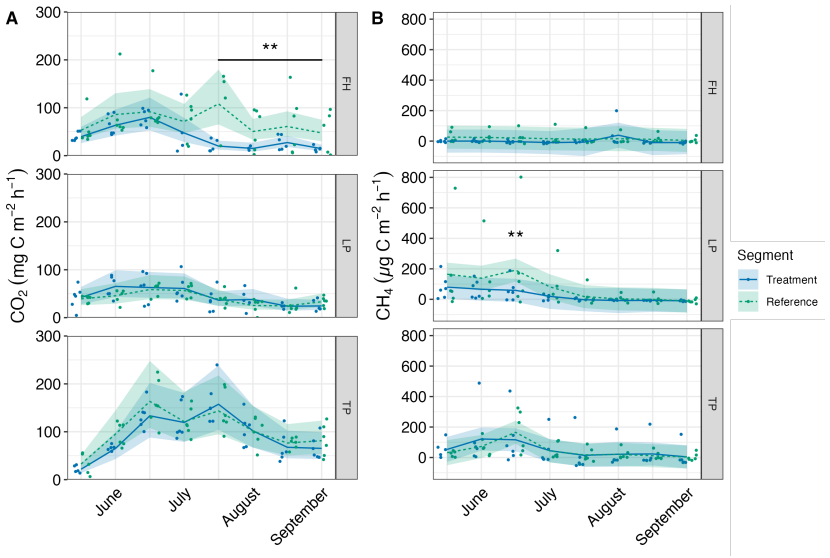

Figure 6: Riparian soil CO_2 (A) and CH_4 (B) fluxes (mg CO_2-C/µg CH_4-C m^{-2} h^{-1}) in Treatment and Reference segments at the three field sites during Summer 2021. The solid and dashed lines represent the means of pairwise comparisons of Segment by Site and Date, and the shaded areas represent the 95% confidence intervals. No asterisks indicate little to no evidence ($P > 0.1$), a single asterisk indicates weak evidence ($0.05 \geq P \leq 0.1$), and a pair of asterisks indicate moderate to very strong evidence ($P \leq 0.05$) for differences between Segments.

Dissolved CO_2 and CH_4 concentrations

Though there was moderate to very strong evidence of differences in dissolved CO_2 and CH_4 between segments at most sites at most times, those differences were not consistent in direction between Treatment and Reference segments (Figure 7). Differences in CH_4 concentrations occurred at each site across the season, but differences in dissolved CO_2 only occurred at Lost Prairie and Teepee, with no evidence of differences at any timepoint at Fish. The average dissolved CH_4 concentrations were >10-fold higher in the Treatment than in the Reference at both Fish and Lost Prairie, but the pattern was reversed at Teepee, with the Reference being 9-fold higher than the Treatment. There was evidence of differences in dissolved CO_2 for both Lost Prairie and Teepee, but the segment with higher dissolved CO_2 differed for the two sites with the Reference 50% higher at Lost Prairie, and the Treatment 27% at Teepee. Much like soil gas fluxes, there was no evidence of consistent influences of BDAs on dissolved gases in stream water across sites.

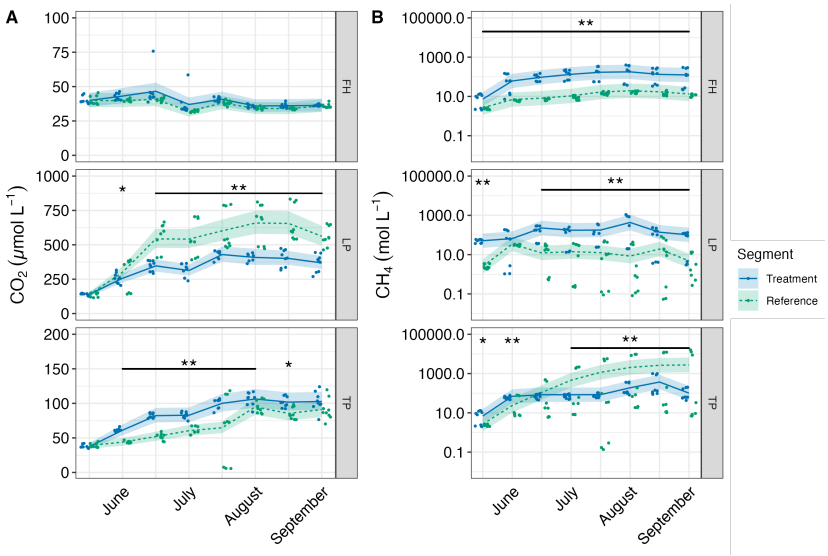

Figure 7: Dissolved CO_2 (A) and CH_4 (B) concentrations (CO_2 µg CH_4 nmol L^{-1}) in Treatment and Reference segments at the three field sites during Summer 2021. The solid and dashed lines represent the means of pairwise comparisons of Segment by Site and Date, and the shaded areas represent the 95% confidence intervals. No asterisks indicate little to no evidence ($P > 0.1$), a single asterisk indicates weak evidence ($0.05 \geq P \leq 0.1$), and a pair of asterisks indicate moderate to very strong evidence ($P \leq 0.05$) for differences between Segments.

Discussion

Our investigation of the effects of beaver dam analogs (BDAs) on carbon pools, fluxes, and concentrations in three headwater streams revealed that for most variables, there were not clear effects of BDAs in these three streams. Though there were timepoints where DOC, riparian soil gas fluxes, and dissolved gas concentrations differed between Reference and Treatment segments, they were not consistently higher in either segment across sites, and there were few timepoints when there were any differences. However, there were notable differences in both BPOC and SPOC. Given that this study was conducted on three similar streams, all with relatively short restored reaches and all restored with the same general approach, that may have limited the strength of the signal we saw for several of the variables.

Though we anticipated that BDAs would reduce DOC concentrations due to their potential to slow stream velocity, increase residence time (Munir and Westbrook, 2021; Silverman et al., 2019; Wade et al., 2020), and potentially allow for additional decomposition of the DOC, the lack of evidence of differences was unexpected (3). Factors such as discharge and water travel time are recognized as the main drivers of DOC concentrations in headwater streams (Jantze et al., 2015). However, the intricate interplay of catchment-specific characteristics, including local geology, topography, and organic matter input to soils, could also contribute to the observed variation (Aitkenhead et al., 1999; Yamashita et al., 2011), potentially explaining the absence of distinct concentration differences attributed directly to BDAs. Even within natural beaver dam complexes, the changes in DOC concentrations appear to be context-dependent, increasing or decreasing downstream of dams based on the specific site location and characteristics of the beaver dam complexes (Gatti et al., 2018; Larsen et al., 2021; Puttock et al., 2017). The complexity of interactions between DOC concentrations, BDAs, and various environmental factors emphasizes the need to measure more specific controls on DOC. Additionally, investigating the composition of DOC could offer

additional insights into more subtle changes in DOC due to BDAs that may influence downstream ecosystem carbon cycling.

Although we expected that BDAs might decrease suspended particulate organic C concentrations, there was evidence that BDAs drove increases in concentrations across our sites. Though BDAs can increase sediment and POC deposition (Lautz et al., 2019; Scamardo and Wohl, 2020), as BDAs reconnect the stream to its floodplain (Pearce et al., 2021), they may also allow allochthonous POC to enter the stream as particles entrained from banks and side channels and mobilized from terrestrial POC pools deposited near stream edges (Hedges et al., 1986; Mulholland and Hill, 1997). Increased SPOC concentrations may also stem from greater allochthonous inputs from heightened primary productivity within the stream, as algal sloughing can contribute to SPOC (Dolph et al., 2017). Though we found higher SPOC concentrations in BDA complexes (4), beaver dam complexes can have higher or lower SPOC exports downstream of dams (Larsen et al., 2021) depending on the amount and age of dams present (Kroes and Bason, 2015), factors that have been largely unexplored in BDA-treated streams and did not vary in our study.

As we expected, benthic particulate organic C pools were consistently higher in the BDA-treated segments of the stream (5). Like beaver-driven modifications that enhance C storage by expanding lentic open water areas and anaerobic conditions (Johnston, 2014; Naiman and Melillo, 1984; Wohl, 2013), BDAs also have the potential to alter environmental conditions conducive to C storage. Naiman et al. (1986) found that beaver engineering induced anaerobic conditions, which reduced decomposition rates of labile and non-labile woody biomass inputs by 81% and 61%, respectively. Given that much of the woody biomass inputs to beaver complexes are used in construction, which is relatively refractory compared to other carbon sources (Hodkinson, 1975), a similar scenario could be applicable to BDA-treated streams due to the inclusion of woody biomass in dam construction materials. Anaerobic conditions promoting slower decomposition, combined with the abundance of refractory woody carbon, create an

environment conducive to increased long-term C storage in beaver complexes (Mann and Wetzel, 2000; Wohl et al., 2012; Wohl, 2013), and to the extent that BDAs alter these environmental conditions, we would expect similar results. Though no studies have investigated the long-term impacts of BDAs on benthic particulate organic C storage, this study shows that BDAs may increase short-term carbon storage. Longer-term impacts may depend on the degree to which structures persist and are maintained by humans or through colonization by beavers.

Contrary to our expectations of observing higher riparian soil CO_2 and CH_4 fluxes in the BDA-treated stream segments, the differences were small, except for the notably elevated CO_2 fluxes at a single site, Teepee, during the late-season (6). Though soil moisture, soil temperature (Bowden et al., 1998; Silverthorn and Richardson, 2021), and soil organic C (Janzen, 2004; Mosier et al., 1998; Smith, 2004) influence greenhouse gas emissions from riparian soils along headwater streams, these properties did not covary with gas fluxes, suggesting that the higher rate of soil respiration in this one site was not a direct consequence of these variables. The deposition of nutrients transported from upstream locations in floodwaters could drive elevated CO_2 fluxes as floodwaters dissipate and soils become aerated (Jacinthe, 2015). This mechanism aligns with Samaritani et al. (2011), who observed delayed surges in soil respiration following flooding. Alternatively, this same study also noted higher CO_2 fluxes in riparian buffers along flood-affected stream sections compared to areas near channelized sections. At the site exhibiting heightened CO_2 fluxes, the Treatment segment was noticeably channelized while the Reference segment was above the headcut that motivated the BDA installation and thus was much less incised. Though the two segments did not differ in soil moisture in the top 10 cm, it may be that deeper soils were wetter in the reference, which may have led to the observed elevated CO_2 fluxes. In contrast, the stream banks at the other two sites exhibited relatively similar degrees of incision, and thus, their similar CO_2 fluxes may be due to a lack of differences in soil moisture in deeper soils.

Concentrations of dissolved CO_2 and CH_4 differed by segment for most sites, but

not in a way that consistently matched our expectations. We expected higher dissolved CH_4 concentrations in Treatment reaches due to increased anaerobic conditions in soils and sediments and did see this pattern in two of the three streams (Lost Prairie and Fish) (7). Interestingly, the third stream (Teepee) is the same stream that had higher CO_2 fluxes in the late season in the Reference segment, and it may be that the lower degree of incision in the Reference segment led to more extensive anaerobic conditions in the surrounding soils, which may have led to higher dissolved CH_4 concentrations. The presence or direction of differences was less consistent for the CO_2 data, showing no evidence of differences in concentrations between segments at Fish, higher concentrations in the Reference segment at Lost Prairie, and higher concentrations in the Treatment segment at Teepee. The differences between segments and sites for these dissolved gases may be rooted in a range of factors that have a larger influence than the presence or absence of BDAs, including seasonal changes in discharge and turbulence Hope et al. (2001, 2004), alterations in hydrologic flowpaths that transport groundwater and soil water with distinct chemistries (Crawford et al., 2013), as well as variations in stream slope (DelVecchia et al., 2023). Though the exact influence of these drivers on dissolved gas concentrations remains an area of ongoing investigation, the observations from our study potentially capture the consequences of these mechanisms.

In the broader scientific context, headwater streams are often sources of CO_2 and consistently exhibit dissolved CH_4 supersaturation across diverse environments, including Alaska (Crawford et al., 2013), New Hampshire (Schade et al., 2016), peatland catchments (Hope et al., 2001), and high-alpine settings (Flury and Ulseth, 2019). Moreover, beaver ponds are substantial net sources of CO_2 relative to the surrounding river networks (Roulet et al., 1997; Yavitt and Fahey, 1994), and CH_4 fluxes from such ponds are notably elevated (Ford and Naiman, 1988; Lazar et al., 2015). This pattern highlights the considerable impact of small water bodies on natural CO_2 and CH_4 evasion (Holgerson and Raymond, 2016), thereby warranting attention to the potential contribution of the expanding areal coverage of small water bodies created by BDAs to

the global carbon balance.

This study expands the existing body of research on BDAs, building on historical work that largely focused on hydrogeomorphological changes (Pearce et al., 2021; Lautz et al., 2019; Scamardo and Wohl, 2020) by adding insights into the potential influences of BDAs on carbon pools, fluxes, and concentrations. Though the effects of BDAs on dissolved organic C concentrations were small, and their effects on suspended POC were variable, potential increases in organic C concentrations may lead to changes in water quality, composition of microbial assemblages, and food web dynamics. Our findings reveal that BDAs may notably enhance benthic particulate organic C pools, suggesting a potential avenue for C storage in restored stream ecosystems. The minimal differences in CO_2 and CH_4 fluxes between segments suggest that BDA-induced changes in hydrogeomorphology in these three streams may not alter decomposition rates in riparian soils to the extent that they enhance gas fluxes. Despite the lack of apparent influence of BDAs on riparian soil gas fluxes, BDAs affect dissolved CO_2 and CH_4 concentrations; however, differences between segments are variable among sites. The complex and site-specific nature of the effects of BDAs on carbon pools, fluxes, and concentrations underlines the importance of avoiding broad generalizations about the impacts of this restoration tool on carbon.

Our investigation focused on three streams within 100 km of one another and sharing a variety of characteristics, including stream size, gradient, number of BDAs installed, construction materials, and time since restoration. It may be that the magnitude and direction of impacts we observed on carbon biogeochemistry may differ from other projects that use a diverse array of construction materials and vary extensively in their scale and the ecosystems in which they are constructed. Other BDA restoration projects have complexes that differ in the numbers of structures per length of the stream channel, and the streams into which they are installed differ greatly in size, gradient, hydrology, and sediment supply. These and other attributes collectively are likely to influence the extent of ponds, wetlands, and meadows that constitute the footprint directly in-

fluenced by the BDA complex. To gain deeper insights into the impacts of BDAs on carbon biogeochemistry, it would be valuable to conduct broader investigations across a diverse range of BDA-treated streams throughout the Intermountain West, encompassing varying complex characteristics. Moreover, we conducted research just two years post-restoration, and as the time since restoration increases, we might expect larger differences to emerge. Long-term monitoring could provide insights into how the effects of BDAs on carbon biogeochemistry develop over time, helping to clarify whether the patterns observed in our study become more pronounced with time. By addressing these existing gaps in knowledge, we can potentially generalize the effects of BDAs on ecosystem processes, thereby providing scientific insights that better inform water resource management and restoration practitioners.

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