

THESIS

ECOLOGICAL CHARACTERISTICS OF STREAM REACHES WITH AND WITHOUT
LOW-TECH PROCESS-BASED RESTORATION IN A WILDFIRE-AFFECTED
WATERSHED

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ABSTRACT

ECOLOGICAL CHARACTERISTICS OF STREAM REACHES WITH AND WITHOUT LOW-TECH PROCESS-BASED RESTORATION IN A WILDFIRE-AFFECTED WATERSHED

Wildfires can alter community structure and ecosystem function of montane streams, leading to management challenges. Low-tech process-based restoration (LTPBR) may be a useful tool in post-wildfire catchments, but relatively few studies have examined how LTPBR may influence ecological responses following wildfire. This study compared abiotic and biotic characteristics of a stream reach that received LTPBR, untreated reaches without LTPBR, and a reach with relict beaver activity that had relatively intact berms. All sites had unconfined floodplains and were affected by wildfire four years prior to the surveys. The treatment reach received post-assist log structures two years prior to field surveys. Our objective was to characterize differences in sediment size, water temperature, benthic algae, fine and particulate organic matter, large wood, riparian vegetation, macroinvertebrate communities, and brook trout density and size structure. The relict beaver site had more shallow, lentic habitat, finer substrate, increased particulate organic matter, and greater temperature variability. The untreated reach had a deep, simpler channel, larger substrate, lower particulate organic matter, and more uniform temperatures. The treatment reach had a channel with depth and substrate sizes intermediate between the relict beaver and untreated reaches, higher chlorophyll-a, and moderate temperature variability. Benthic macroinvertebrate biomass and composition varied across habitat types; standing biomass was highest on wood and lotic hard substrates. When scaled to habitat area at

the reach scale, macroinvertebrate biomass was highest at the relict beaver reach and comparable at the treatment and untreated reaches. Insect inputs to the stream and emergence showed temporal variation, but did not differ consistently between stream reaches. The treatment reach had slightly higher brook trout density than the other reaches although the most downstream untreated reach had slightly larger fish, particularly in spring. Our results highlight potential differences in stream function and community structure between wildfire-affected streams with and without LTPBR treatments. Continued research on ecological impacts of LTPBR in addition to geomorphic effects may provide valuable insight to success of LTPBR in post-fire watersheds.

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Introduction

Wildfires have increased in frequency, size, and severity in recent decades and are a common form of disturbance to stream-riparian corridors (Higuera et al., 2021; Westerling, 2016). Severe fires remove vegetation and alter soils to a hydrophobic state, often increasing overland flow, sediment runoff, erosion, and in-stream nutrient concentrations (Ice et al., 2004; Shakesby & Doerr, 2006). Sedimentation and geomorphic changes can affect a range of ecological characteristics after wildfire, including the density, composition, and distribution of macroinvertebrate communities (Bixby et al., 2015; Preston et al., 2023). Stream fishes, especially those living in fragmented habitat, are also vulnerable to mortality from wildfire impacts (Dunham et al., 2003). Post-fire floods regularly occur after fire events, especially in high gradient, confined mountain streams, potentially extending the effects of the initial fire disturbance for many years (Shakesby & Doerr, 2006). Increasingly, land managers are interested in mitigating undesirable effects of wildfires on stream ecosystem services and aquatic-riparian habitat.

Beaver dams and their associated ecological effects may provide resistance or resilience to fire events by mediating fire impacts to stream corridors. Prior to fires, lentic areas associated with beaver dams may be less susceptible to wildfire impacts due to the elevated water table, increased channel complexity, and floodplain connectivity (Brazier et al., 2021; Burchsted & Daniels, 2014; Pollock et al., 2007). This may allow beaver meadows to serve as fire refugia, potentially facilitating species recolonization after fire (Fairfax & Whittle, 2020). Following a fire, beaver dams can also capture additional large wood and sediment resulting from post-fire flooding (Dunn et al., 2024; Puttock et al., 2021; Wohl et al., 2022) and may capture or transform nutrients (Brazier et al., 2021). Due to these possible desirable effects, there has been

growing interest in stream management practices in wildfire-impacted watersheds that replicate aspects of ecosystem functioning associated with beaver meadows and additions of in-channel large wood (Fairfax et al., 2024; Wohl et al., 2021).

Low-tech process-based restoration (LTPBR) is increasingly being implemented after wildfires, especially in the western United States (Fairfax et al., 2024). LTPBR, often consisting of large wood additions such as beaver dam analogues (BDAs) or post-assisted log structures (PALS), are manmade, permeable structures designed to promote specific fluvial and ecological processes, such as connectivity of floodplains to main river channels. Prior research has shown that LTPBR in small streams in the Rocky Mountains can reduce stream velocity and erosion, promote sediment aggradation, and widen the stream channel (Davis et al., 2021; Scamardo & Wohl, 2020). In some cases, streams that received LTPBR have experienced greater hydraulic connectivity to surrounding floodplains and increased natural beaver activity following implementation (DeVries et al., 2012). Additional studies have observed an immediate increase in groundwater table height and creation of new channels (Bouwes et al., 2016; Larsen et al., 2021; Norman, 2020). Despite its popularity, relatively few studies have evaluated effects of LTPBR on ecological characteristics of streams in the Intermountain West following wildfires.

The changes to abiotic stream characteristics caused by LTPBR are expected to have a range of direct and indirect effects on aquatic and riparian biota. For instance, large wood additions may influence community composition of macroinvertebrates by creating spatial heterogeneity in basal resources, substrate characteristics, and flow velocity. Large wood can trap organic matter that can be broken down and consumed by microbes and macroinvertebrates, potentially increasing secondary productivity (Herdrich et al., 2018; Wohl et al., 2016). Large wood can also facilitate habitat heterogeneity for fish by creating plunge pools and providing

cover from predators, potentially leading to increased fish growth, density, and biomass (Fausch & Northcote, 1992; White et al., 2011). If habitat changes enhance invertebrate production, LTPBR may also have desirable effects on prey availability for fishes (Herdrich et al., 2018; Jennings et al., 2023). More broadly, habitat heterogeneity has also been linked to greater stability in population dynamics and reduced likelihood of ecosystem shifts to alternative stable states (Oliver et al., 2010; Schröder et al., 2005). When implemented, monitoring of stream restoration projects often focuses on physical characteristics rather than biological responses; however, these changes are often tightly linked (Baxter et al. 2005, Herdrich et al. 2018). Therefore, when wildfire and LTPBR occur in areas with native stream fish of conservation concern – such as cutthroat trout in the Intermountain West – it is especially important to understand ecological changes that might be expected following LTPBR implementation.

Our objective for this study was to document ecological characteristics of stream reaches with and without LTPBR in a wildfire-affected watershed of the southern Rocky Mountains. In 2020, over 41,000 km² burned across the western United States, including the Cameron Peak Fire in northern Colorado, which was the largest recorded wildfire in state history at 845 km² (NOAA, 2021; CO Division of Fire Prevention and Control, 2024). We surveyed abiotic and biotic characteristics of four nearby stream reaches in the Cameron Peak Fire burn scar. In addition to a treatment reach that received LTPBR in 2022, we selected three additional stream reaches to serve as references for physical and biotic characteristics. Among these untreated reaches were two reaches with unconfined valley morphology and a less complex stream channel; one was scheduled for future LTPBR implementation, and the other was chosen as an untreated reach for trout populations. We also included one unrestored site with relatively intact beaver berms and high connectivity between the stream and floodplain. We predicted that the

reach that received LTPBR would show physical characteristics that were intermediate between the site with intact beaver berms and the untreated site. We anticipated higher sedimentation, organic matter, and water storage capacity at the reach with more intact beaver berms (Brazier et al., 2021). Because PALS are more porous than beaver berms or beaver dams, we expected to see reduced storage capacity at the relict beaver site, but potentially some similar physical characteristics (Wohl & Inamdar, 2025). Furthermore, we expected the untreated reach to show characteristics that may be more consistent with a transport reach, exhibiting less sedimentation, larger substrate, and less lentic habitat (Gomi et al., 2003; Hassan et al., 2005). We expected that these differences in the physical characteristics of each site would in turn drive variation in biological communities. More specifically, we predicted that increased habitat heterogeneity – due to large wood additions or natural beaver berms – would result in more spatially variable macroinvertebrate biomass throughout the reach, and increased overall richness as more lentic taxa gain suitable habitat (Mazza et al., 2024; Washko et al., 2020; Wohl et al., 2016). We also anticipated that large wood associated with LTPBR may provide increased habitat heterogeneity for fish, potentially leading to increased density (Herdrich et al., 2018; Riley & Fausch, 1995).

Methods

Study area

We evaluated stream characteristics in four study reaches within the Elkhorn Creek watershed, a tributary of the Cache la Poudre River in the Colorado Front Range of the Southern Rocky Mountains, USA (Fig. 1). The treatment reach, Upper Elkhorn Creek, was historically a beaver meadow with ponds but has not had active beaver since at least 2013 (Fig. S1). Between September 24 and October 8, 2022, the treatment reach received 12 post-assisted log structures (PALS) in an approximately 250 m reach. Most structures were installed in the main channel,

with one additional structure placed in the floodplain to account for new channel development and another in a relict channel that was formed after the main channel avulsed to the north after installation. The reach had four remnant beaver berms and many of the PALs were situated inside the channels that breached the relict berms (see Figs. S2, S3, S4 for aerial imagery of each reach).

In addition to the treatment reach, we surveyed a downstream reach named Lower Elkhorn that had not yet received any type of restoration treatment (hereafter the ‘untreated’ reach) and a tributary to Elkhorn Creek named Swamp Creek that had more intact beaver berms (hereafter the ‘relict beaver’ reach). Reaches were selected in an effort to minimize variation in floodplain characteristics and upstream burn severity, as well as to be in relatively close proximity to one another. The untreated reach was scheduled to receive future installation of PALs and had an unconfined floodplain with two relict beaver berms. We attempted to locate an upstream untreated reach above the treatment area but there were no suitable reaches with similar floodplain characteristics to the treatment reach. The relict beaver reach had three, more intact beaver berms and significant ponding of water compared to the treatment and untreated reaches, although beaver had not been active at the reach since prior to the 2020 wildfire. The characteristics of this reach were in several ways consistent with management goals for the treatment reach (e.g., more intact berms and greater floodplain connectivity) and we considered the reach representative of a natural beaver meadow that had experienced wildfire, despite the fact that it did not currently have active beaver. Because the berms were relatively intact, this reach was not prioritized for post-fire restoration activity. The relict beaver reach, however, had very low trout density, likely due to low discharge in late summer and fall, and possibly due in part to effects of the wildfire. As a result, we surveyed a fourth location without any restoration

called Middle Elkhorn Creek (hereafter the ‘fish control’ reach). This site was surveyed exclusively for trout population characteristics (i.e., density, size structure and diet). Middle Elkhorn was chosen based on comparable discharge, elevation, channel gradient, presence of two relict beaver berms, and stream size as the treatment reach, although the total area of the floodplain was smaller, and the channel was less complex.

Environmental factors

At the three main reaches (Upper Elkhorn, Lower Elkhorn, and Swamp) we used drone imagery from June 2024 to obtain data on characteristics of the stream channel and floodplain. Drone imagery was collected using a DJI Mavic 3 Multispectral drone with RTK correction. Images were collected at between 81m and 94m above ground level, with a front and side overlap of 80%. Orthoimages and digital surface models were processed using Agisoft Metashape software. The ground resolution of the resulting maps was between 2.07 cm/pix and 2.46 cm/pix. Six ground control points were collected at each site and used to improve the absolute spatial accuracy of resulting orthoimages and digital surface model. An Emlid RS2 base and rover RTK GPS were used to collect these points in addition to acting as a base station for our drone. We used ArcGIS Pro to classify habitat from drone imagery to obtain values for channel length, wetted channel area, sinuosity, and habitat areas. Wetted channel areas and habitat areas were digitized and extrapolated for area, and sinuosity for the main channel was calculated as total river length divided by straight line distance. Google Earth was substituted for drone imagery for Middle Elkhorn. Upstream watershed area was calculated with StreamStats (U.S. Geological Survey, 2019), which was then used to extract Differenced Normalized Burn Ratio (dNBR) and soil burn severity (SBS) raster data using the extract raster tool in ArcGIS Pro (Table 1).

To characterize differences in environmental variables between reaches, we collected data on water temperature, water chemistry, depth, substrate, wood, and riparian vegetation. Water temperature was recorded using seven HOBO Pendant temperature loggers per reach that were attached to the stream bottom in representative habitats with surface connectivity to the main channel. HOBO loggers were deployed from June to September and took a temperature measurement every 15 minutes. If loggers became exposed due to low streamflow, data collected after the logger was no longer submerged were eliminated from the dataset. Water chemistry data were obtained using grab samples that were collected in June and September at each reach. One sample was collected from just above and just below the reach to test for potential nutrient retention effects of the study reaches. Water samples were processed for dissolved organic carbon (DOC), total dissolved nitrogen (TDN), pH, specific conductivity (SC), sodium (Na), ammonium (NH₄), and nitrate (NO₃) (see Appendix for analytical methods). Remaining environmental measurements were collected in late June to early July following peak discharge. We took depth measurements (range = 37 to 73 measurements per reach) in the channel thalweg. Wolman pebble counts (Wolman, 1954) were completed at each reach using a gravelometer. We measured 50 pebbles taken from five random cross sections of each reach, primarily in lotic areas. Estimates of wood volume and wood surface area were obtained by counting wood pieces in the wetted channel at each reach and grouping each piece into visually estimated length bins of 0-25 cm, 26-50 cm, 50-100 cm, 100-200 cm, and >200 cm, and diameter bins of 0-5 cm, 6-10 cm, 11-15 cm, 16-20 cm, and >20 cm. Wetted surface area and volume of wood in each individual PALS at the treatment reach was estimated by taking the mean number of wetted wood pieces counted by four observers and then taking exact length and diameter measurements of 30 representative pieces. Lastly, we quantified composition of riparian vegetation by placing a

square-meter quadrat adjacent to the wetted stream edge. Percent cover of vegetation categories for grass, sedge, forbs, rush, shrubs, trees, dead/dry, and bare ground were recorded.

Basal resources

We characterized basal resources via measurements of benthic chlorophyll-a, periphyton biomass, fine particulate organic matter (FPOM) and coarse particulate organic matter (CPOM). Basal resource values were expressed as mass per unit area of stream bottom. Chlorophyll-a was quantified by scrubbing periphyton from a flat, top surface of randomly selected rocks into a collection dish which was then transferred into a Whirlpack and frozen prior to analysis. The area of each rock that periphyton was removed from was traced onto a datasheet and surface area was calculated based on the mass of a known area of the paper (Hauer & Lamberti, 2017). Periphyton samples were later thawed in a water bath and filtered through 0.7 μm glass-fiber filters, dissolved in 15 mL of acetone, centrifuged, and run on a fluorometer to obtain chlorophyll concentration in micrograms (Arar & Collins, 1997). To quantify floating algal mats that were present at some locations, we collected algal biomass samples using an aluminum can open on both ends (0.035 m^2). Floating algae mat samples were filtered through 0.7 μm glass-fiber filters, dried at 60°C for 24 hours, and combusted at 500°C for two hours to obtain ash-free dry mass (AFDM). We took additional periphyton measurements using a Benthotorch, summing values for green algae, diatoms, and cyanobacteria into one chlorophyll-a value per reading (Kahlert & McKie, 2014). We collected FPOM samples by placing the aluminum can (0.035 m^2) or a 5-gallon bottomless bucket (0.21 m^2) onto the substrate, mixing the substrate into the water column by hand, and removing 120 mL of water using a syringe (Reinert et al. 2022). Samples were placed into a 120 mL cup and stored in a cooler until they were moved to the freezer for storage until further processing. FPOM samples were filtered through an 0.7 μg glass-fiber filter

and combusted to obtain AFDM using the same protocol as for algal mats. Benthic CPOM was measured using material collected from Surber samples (Hauer & Lamberti, 2017; Reinert et al., 2022). After Surber samples were subsampled for macroinvertebrates, CPOM was air-dried in a fume hood and sieved through a 1 mm sieve. Particles larger than 1 mm were placed in a crucible and combusted to obtain AFDM using the above protocol.

Macroinvertebrate sampling

We quantified benthic density, biomass, composition, richness, and fluxes of macroinvertebrates into and out of the streams. We collected benthic macroinvertebrate samples in June from each reach. We stratified samples by habitat type to include collections from riffles, vegetated areas, lentic depositional areas, and on wood. Four sampling methods were used, depending on habitat type: Surber sampler, bottomless bucket, D-frame dipnet sweeps, and removal of insects from wood. The number of samples per habitat type varied depending on the relative habitat area at the reach (see Table S1 for exact sample numbers per reach). Benthic Surber samples were collected using a 0.09 m², 500 µm mesh Surber sampler in lotic areas void of riparian vegetation. A few samples from the untreated reach included a perennial aquatic plant (*Ranunculus* spp.) within the Surber area. Samples collected with a Surber sampler are hereafter referred to as “lotic” samples. Bucket samples were collected by placing a bottomless 5-gallon bucket (0.21 m²) approximately 10 cm into the substrate of depositional lentic areas that were part of the active channel, with no vegetation and substrate comprised of silt and sand. A 200 x 145 mm dipnet (250 µm mesh) was used to remove invertebrates from within the bucket until at least three sweeps revealed no additional invertebrates. Samples collected using the bucket method are referred to as “lentic” samples. Dipnet samples were collected using a 30.5 x 25.4 x 55.9 cm net (500 µm mesh) in primarily off-channel lentic ponds with dense riparian vegetation

(i.e. grasses and sedges) in or around the sample. A few samples from the treatment and untreated reach were lotic side channels with flow over dense vegetation. The dipnet was swept for one meter per sample (0.305 m² surface area sampled). Due to the large amount of vegetation present in these samples, dipnet samples are hereafter referred to as “vegetated” samples.

Invertebrates from wood were collected by removing individual wood pieces and then gently scrubbing them into a 5-gallon bucket using a soft-bristled brush. Each individual wood sample contained combined invertebrates collected from the surfaces of approximately five pieces of wood (range = 2 to 8 pieces per sample). After removing invertebrates, wood pieces were measured for length and mean diameter to obtain an estimated surface area and volume. All macroinvertebrate samples were stored in 80% ethanol for processing in the laboratory. Benthic invertebrate samples were subsampled (n = 200 individuals) using a 31 x 20 cm mesh tray (150 µm) evenly divided into 24 cells, and identified to family (Merritt & Cummins, 1996; Ward et al., 2002). Taxa that were large and rare to the sample were additionally included in the subsample. Subsamples were then scaled to the total sample using the formula:

$$\text{Total count} = \frac{\text{subcount} * 24}{\# \text{ cells counted}} + \text{large and rare taxa}$$

We measured inputs and exports of invertebrate biomass to the streams in June, July, and August. Samples were collected using five or six replicate emergence and pan traps per reach per date. Traps were placed in representative lotic and lentic areas of each reach. Emergence traps were 0.09 m² in area and had a PVC plastic frame with an attached 500 mL bottle of 80% ethanol to passively collect emergent insects (Cadmus et al., 2016). Pan traps were placed near the bank of the stream in areas with riparian vegetation. Pan traps measured 45 x 65 x 15 cm and contained stream water with a small amount of unscented dish soap. We collected the emergence

and pan samples approximately 72 hours after deployment. Emergence and pan samples were mostly identified to order and values were expressed as $\text{mg}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$.

Fish

We completed two-pass depletion surveys for brook trout in June and September of 2024 at the treatment, fish control, and untreated reaches using two Smith-Root LR-20B backpack electrofishers and a crew of six people. Each reach was split into sections using natural barriers and block nets to facilitate electroshocking. Block nets were utilized at the top and bottom of each reach and at the convergence of side and main channels within the reach. At each site, we surveyed the entire unconfined meadow, so the total stream length surveyed differed across reaches. In June, young-of-year fish under 50 mm were excluded from surveys due to catch inefficiency, while in September all fish were captured. All fish were measured for total length (mm) and wet mass (g). We nonlethally collected stomach contents on a subset of fish greater than 50 mm to determine diet composition. Fish for stomach contents collection were anesthetized with AQUI-S, lavaged with a squirt bottle or blunt 50 CC syringe, and stomach contents were filtered in the field and stored in 80% ethanol for processing in the lab. We identified diet contents to order and measured a subset of prey items (up to 10 per taxon per sample) to extrapolate prey biomass. To determine fish density, we divided the estimated number of fish per reach based on two-pass removal by the wetted area of the reach. We obtained wetted area from the treatment and untreated reaches using drone imagery, and with measurements of channel cross-sections and reach length for the fish control reach.

Data analyses

Environmental variables and basal resources were analyzed using Kruskal-Wallis (KW) tests and Dunn's Multiple Comparison post-hoc tests (MCT) to test for differences between sites

using the function *dunnTest* from the *DescTools* package in R (Signorell, 2025). Water chemistry was analyzed for differences using linear models with main effects for site and month, and likelihood ratio tests (LRTs) to test for interactions of site*month and site*position (i.e., upstream or downstream of the study reach) using the *lrtest* function in the *lmtest* package in R (Zeileis and Hothorn, 2002). Macroinvertebrate biomass was analyzed for main effects of site and habitat type using linear models and LRTs for interactions of site*habitat. We used PERMANOVA on macroinvertebrate count data to determine whether site, habitat type, or their interaction influenced community composition, using the *adonis* function from the *vegan* package in R, with Bray-Curtis dissimilarity between groups (Oksanen et al. 2025). We used linear models to analyze main effects of site and month for emergent insects and aquatic and terrestrial inputs and LRTs to test for interactions for site*month. Fish size structure, in terms of individual length and mass, were analyzed using generalized linear models (GLM) with a gamma distribution to account for right-skewed data. We used Tukey's Honestly Significant Difference (HSD) tests to further determine differences of means between groups. Because of elimination of young-of-year fish in the spring, fish data from the spring and fall were analyzed separately and not compared across seasons. Fish density was calculated using the *FSA* package to estimate total population counts based on two-pass removal estimates. Trout body condition was analyzed based on length-to-mass residuals for fish longer than 100 mm, using generalized linear models and LRTs for the interaction of site*season. To analyze diet composition, we used PERMANOVA analysis to test for interactions or main effects of site*month. Statistical analyses were completed using R ver. 4.4.2 (R Core Team, 2024).

Results

The treatment, relict beaver, and untreated reaches showed differences in physical characteristics, including wetted channel area, sinuosity, depth, substrate size, and wood volume (Table 1). Longer channel lengths showed greater sinuosity, with the highest sinuosity index of 1.58 at the relict beaver reach, 1.5 at the treatment reach, 1.4 at the fish control reach, and 1.3 at the untreated reach. Depth differed significantly across all three sites, with the median depth being over 2 times shallower in the relict beaver reach compared to the untreated and treatment reach (Kruskal-Wallis, $\chi^2 = 51.1$ $p < 0.0001$, Fig. 2a). The median substrate at the relict beaver reach was nearly 7 times smaller than that of the treatment reach (Dunn's MCT, $p = 0.061$, Fig. 2b) and 11 times smaller than substrate at the untreated reach (Dunn's MCT, $p = 0.014$, Fig. 2b). The treatment reach had over 4x greater estimated wood volume per unit wetted area than the other reaches (see Table S2 for surface areas).

Although mean water temperatures across the three reaches did not differ significantly (Kruskal-Wallis, $\chi^2 = 4.9$, $p = 0.09$, Fig. 2c), each reach showed different levels of heterogeneity in water temperatures over space (Figs. S5, S6). The treatment and relict beaver reaches showed high temperature heterogeneity (C.V. between means of loggers at each reach: treatment = 8.96, relict beaver = 13.29), while the untreated reach had more consistent temperatures throughout the reach (C.V. = 0.56) (Fig. S5).

Water chemistry differed between sites and over time. There was a significant interaction between site and month for NO_3 (LRT, site*month, $\chi^2 = 25.9$, $p < 0.0001$, Fig. S7) and TDN (LRT, site*month, $\chi^2 = 18.3$, $p < 0.0001$). The treatment and untreated reaches had 2x to 3x higher NO_3 and TDN than the relict beaver reach in the spring, but concentrations were similar across all sites in the fall (Fig. S7, Table S5). There was also a decrease in NO_3 from the upstream to downstream end of the relict beaver meadow that persisted in both spring and fall

(Fig. S7). Specific conductivity, Na, and NH₄ also differed across sites, showing the highest values at the relict beaver reach and lowest values at the treatment reach for all three metrics (Table S5, S6). DOC and Na differed across seasons (Table S6).

Basal resource standing stocks, including fine particulate organic matter and coarse particulate organic matter differed between sites. Median FPOM at the relict beaver reach was roughly 40 times greater than the treatment (Dunn's MCT, $p = 0.001$, Fig. 2d) and untreated (Dunn's MCT, $p = 0.0001$, Fig. 2d) reaches. CPOM was also highest at the relict beaver reach, but the difference was not statistically significant (Kruskal-Wallis, $\chi^2 = 1.2$, $p = 0.56$, Fig. 2e). Chlorophyll-a from Benthotorch measurements was highest at the treatment reach, followed by the untreated reach, and the relict beaver reach (Kruskal-Wallis, $\chi^2 = 5.6$, $p = 0.06$). Extracted chlorophyll-a showed the same relative pattern as the Benthotorch (Kruskal-Wallis, $\chi^2 = 3.8$, $p = 0.15$, Fig. 2f). Riparian vegetation composition was relatively similar between the three reaches (PERMANOVA, $F = 0.9$, $p = 0.45$, Fig. S8).

Macroinvertebrate community structure differed between habitat types, and for some metrics, between sites. Total taxonomic richness combined across all sample types was consistent between sites (42 taxa at the untreated reach, 43 taxa at both the treatment and relict beaver reaches). The effect of habitat type on macroinvertebrate biomass differed between sites (LRT, site* habitat, $\chi^2 = 16.5$, $p = 0.01$, Fig. 3). The untreated reach had the highest biomass from lotic samples, while the relict beaver reach had the highest biomass on wood samples. The treatment reach showed more similar biomass across habitat types and values were slightly lower than the other two reaches. On a per-sample basis, the relict beaver reach had the highest average biomass across habitat types at 1.97 g/m², followed by 1.42 g/m² at the untreated reach and 1.05 g/m² at the treatment reach. When scaled to the wetted areas of the habitat types, the relict beaver

reach still had the highest mean macroinvertebrate biomass (1.55 g/m²), followed by the treatment reach (1.29 g/m²), and the untreated reach (1.26 g/m²). Both site (PERMANOVA, $R^2 = 0.06$, $p = 0.001$, Fig. S9) and habitat type (PERMANOVA, $R^2 = 0.21$, $p = 0.001$, Fig. 4) significantly influenced macroinvertebrate community composition, though differences were more strongly correlated with habitat type than site. Unlike biomass, we did not find a significant site-by-habitat interaction for overall taxonomic composition (PERMANOVA, site*habitat, $R^2 = 0.05$, $p = 0.14$). Diptera and non-insect taxa (i.e., Ostracods, Oligochaeta, Bivalvia, Copepods, Amphipods) were associated with lentic and vegetated habitat. Taxa from orders Ephemeroptera, Plecoptera, and Trichoptera were typically found in lotic habitat; although one family within the Ephemeroptera, Siphonuridae, was strongly correlated with vegetated, off-channel habitats (Table S9). Community composition was most similar between lotic and wood habitats, and lentic and vegetated habitats (Fig. 4). Lentic, vegetated habitat showed the most distinction in taxonomic composition from other habitat types. The emergence of aquatic insects was highest in June, especially at the untreated reach, resulting in a nearly significant interaction of site and sampling time (LRT, site*month, $\chi^2 = 8.88$, $p = 0.06$, Fig. 5). Terrestrial inputs peaked in July (LRT, month, $\chi^2 = 15.3$, $p = 0.0005$, Fig. 5) but did not differ across sites (Table S10). Aquatic insect inputs did not differ across months or sites (Table S10).

The treatment reach had the highest brook trout density in both spring and fall (Fig. 6a, 6b). In spring, the density at the treatment reach was 19% higher than the fish control and 111% higher than the untreated reach (Fig. 6a). In fall, the density at the treatment reach was 38% higher than the fish control and 29% higher than the untreated reach (Fig. 6b). In spring, these relative patterns were the same when only considering fish above 90 mm or below 90 mm (Fig. S10). In fall, the treatment reach had twice the density of fish >90 mm as the untreated reach, but

roughly equal densities of fish < 90 mm (Fig. S10). The untreated reach had larger fish than the other two sites in spring (Tukey's HSD, $p < 0.0001$ for all pairwise combinations with untreated, Fig. 6c, Table S11). The treatment and fish control had nearly identical size distributions in spring. In fall, the treatment and untreated reach had smaller fish on average than the fish control (Tukey's HSD, $p < 0.01$ for all pairwise combinations with fish control, Fig. 6d, Table S11). Body condition of brook trout was relatively similar across sites and seasons, although we did observe a shift in average body condition at the untreated site from spring (slightly above average residuals) to fall (slightly below average residuals) (Fig. S11). This change resulted in a significant site-by-season interaction, but the magnitude of difference was small (LRT, $\chi^2 = 5.8$, $p < 0.0001$). Diets collected from a subset of fish from all sites in June and September varied in taxon composition according to site and month (PERMANOVA, site*season, $R^2 = 0.03$, $p = 0.001$, Fig. 7); most notably, consumption of Ephemeroptera at the treatment and untreated sites decreased from June to September, replaced primarily by Diptera and Hemiptera at the treatment reach and Coleoptera and Hemiptera at the untreated reach.

Discussion

In this study, we compared abiotic and biotic characteristics of stream reaches with and without LTPBR in a wildfire-affected catchment. Although LTPBR has rapidly gained popularity as a management practice, relatively few studies have examined ecological changes following LTPBR, especially in a post-wildfire context. Our findings suggest that the stream reach receiving LTBPR had a number of characteristics that were consistent with management goals, such as evidence of sediment storage, channel complexity, habitat heterogeneity, and a comparable or higher density of trout relative to the untreated sites. However, the treatment site also differed from the relict beaver site in a number of ways, suggesting that addition of PALS

did not recreate effects of natural beaver berms in several ways. Differences between the study reaches likely reflected a combination of treatment effects alongside pre-existing site differences. In the sections that follow, we discuss the similarities and differences between the reaches, and particularly the responses that were likely to have been affected by LTPBR relative to pre-existing site differences.

The treatment reach that received LTPBR had physical characteristics that were intermediate between the untreated reach and the relict beaver reach. Based on ongoing research and direct observations, the PALS at the treatment reach facilitated sediment storage and caused the stream to avulse north into a previously abandoned channel, indicating the treatments increased floodplain connectivity, water table height, stream channel complexity and likely reduced stream bank incision. Although our study did not quantify these changes from before to after treatment implementation, we can interpret the differences between sites in light of these observations. For instance, some results suggest the treatment reach may be functioning somewhere between the relict beaver reach and untreated reach in terms of capture and storage of sediment, organic matter, and water. The treatment reach had median sediment D_{50} values that were between the sediment sizes at the relict beaver reach and the untreated reach. The relatively more intact beaver berms at the relict beaver reach resulted in this site having finer sediment, higher levels of FPOM and CPOM, and greater area of lentic habitat compared to the other two reaches. Importantly, whether the treatment reach has potential to function similarly as the relict beaver reach following restoration depends on the pre-existing geomorphic context. Historical imagery from approximately 11 years prior to our study (Fig. S1) showed this site to have extensive ponds, suggesting it has potential to return to a similar state as the relict beaver reach. However, the relict beaver reach also had a more shallow gradient from top-to-bottom of the

reach, which likely contributed to its storage capacity. Prior studies that compared natural beaver dams with sites receiving LTPBR report some similarities to our findings in terms of lentic habitat, channel widening, and water table height (Bouwes et al., 2016; Munir & Westbrook, 2021; Scamardo et al., 2025); although differences between the functioning of human-built instream structures (e.g., PALS and BDAS) and natural beaver dams are also reported in previous studies (Scamardo et al., 2025; Wohl & Inamdar, 2025).

Heterogeneity in stream channel characteristics likely contributed to the differences in water temperatures between reaches. Although the overall mean temperature at each reach differed by less than 1°C, the level of variation in temperatures over time and space differed strongly between reaches. The relict beaver reach had the most variable temperatures, followed by the treatment reach. Channel features created from the pre-existing berms, in combination with addition of wood at the treatment site, increased water residence times, likely contributing to temperature heterogeneity by increasing water temperatures in the lower flow areas. Additionally, influences of groundwater likely contributed to the temperature regime of the study reaches. We noted evidence of springs at all three reaches. Although the untreated reach had extensive off-channel seeps, this site had relatively homogeneous temperatures in the stream channel, likely due to the lack of lentic habitats that had warmer temperatures at the other reaches. Higher groundwater tables and increased-surface groundwater exchange in areas with greater floodplain connection may have led to cooler pockets of water that contrasted with warmer, shallow ponds to create a more variable temperature regime in the other two reaches (Weber et al., 2017). Position of the treatment and relict beaver reach upstream of the untreated reach may also be an important consideration when interpreting water temperature patterns. Many studies have documented the temperature regime after installation of LTBPR, sometimes

reporting cooler temperatures due to increased water storage or rising groundwater levels (Scamardo et al., 2025). Our findings suggest that LTPBR may contribute to temperature heterogeneity that could provide increased opportunities for temperature-sensitive species to find preferable conditions (Bouwes et al., 2016; Reinert et al., 2022; Weber et al., 2017). More extensive temperature data over space and across seasons, as well as mapping of groundwater inputs, would be useful to more thoroughly document how the LTPBR at our study sites is affecting temperature regimes.

Differences in water chemistry between reaches – especially for nitrate – reflected the effects of wildfire, seasonality, and the role of beaver meadows. The high burn severity upstream of the Elkhorn Creek sites contributed to higher NO_3 and TDN, especially during peak discharge months in spring. Elevated nitrate can persist for many years following wildfire in Rocky Mountain streams (Rhoades et al., 2019) and it is generally higher during runoff than base flows (Rhoades et al., 2011). Additionally, beaver complexes act as a nitrogen sink by trapping nitrate upstream of berms (Lazar et al., 2015) which may explain why the relict beaver reach showed a decrease in NO_3 from upstream to downstream ends of the reach. This site was less severely burned upstream and had lower discharge, potentially explaining why it had lower NO_3 than the Elkhorn treatment and untreated sites. Interestingly, we did not observe evidence for a change in nitrate from above to below the treatment reach, potentially because this response may occur on longer time scales post-restoration, requiring longer-term monitoring. Ongoing research at other LTPBR sites in the Cameron Peak fire scar in our study region is documenting changes in water chemistry before and after restoration and should provide a clearer understanding of how stream treatments affect nutrient retention and processing.

Macroinvertebrate composition differed between habitat types, leading to subtle differences in average invertebrate biomass at the reach scale. Habitat type strongly influenced community composition, with a subset of taxa being associated with lotic hard substrates and wood, and another subset being associated with lentic soft substrate and vegetation. Specifically, most of the Ephemeroptera, Plecoptera, and Trichoptera that showed statistically significant habitat associations were positively correlated with lotic or wood habitat. Exceptions included Siphonuridae (Ephemeroptera) and Limnephilidae (Trichoptera), which are known to inhabit pools and stream edges (Ward et al., 2002). As expected, non-insects, such as ostracods, oligochaetes, clams, copepods, and amphipods, as well as flies (Diptera) were associated with vegetated or lentic habitat. Despite these habitat associations – and contrary to our expectations – we did not find differences in total macroinvertebrate richness between reaches. Prior studies have determined that additions of wood increase average invertebrate taxon richness and other measures of diversity (Benke & Wallace, 2003; Johnson et al., 2003; Wohl et al., 2016). These studies and others note that lentic regions may have lower biomass and richness than lotic regions, but addition of ponds from beavers or LTPBR increases the presence of taxa adapted to lentic habitats, increasing overall taxonomic richness at the reach scale (Corline et al., 2023; Washko et al., 2020). At larger spatial scales, other studies have found variation in the longitudinal gradient across a river network had greater impact on taxonomic composition than local physical habitat, providing a possible explanation for similarities in richness in our study considering the short distances and small elevational difference of less than 100 m between reaches (Finn & Poff, 2005). Furthermore, we sought each habitat type at each study reach and all three had some lentic habitat; if sampling had been constrained to the main channel, richness may have been lower at the untreated reach where most lentic and vegetated habitats were

located off-channel. Higher taxonomic resolution beyond family (i.e., identification to genus or species) could alter the results of our findings. Lastly, similarity in taxon richness between sites may indicate the recolonization of macroinvertebrate taxa post-disturbance, from both wildfire and restoration activities at the treatment site, although differences in biomass between sites may be related to these disturbance effects.

The abundance of macroinvertebrates on wood contributed significantly to the biomass at the relict beaver reach, and to a lesser extent, the treatment reach. At the relict beaver reach, biomass of macroinvertebrates was up to 5 times higher on wood relative to other habitat types. Old wood pieces that had been submerged for many years serve as habitat and provide food sources (i.e., periphyton) for many benthic macroinvertebrates and provide surfaces for invertebrates to attach when larger sediment may be scarce in depositional areas (Benke & Wallace, 2003; Johnson et al., 2003). Wood also traps additional organic materials that may be consumed or broken down by macroinvertebrates (Wohl et al., 2016). Similar to our findings, areas containing large wood often have higher invertebrate biomass and productivity in other studies (Benke & Wallace, 2003; Coe et al., 2009). When scaled to total habitat areas, mean biomass was greatest at the relict beaver reach likely due to the abundance of productive off-channel ponds, as well as the presence of wood that originated in the beaver berms. Although lentic regions had a lower biomass across all of our study sites, the addition of heterogeneous habitat types to a floodplain may raise biomass at a site by increasing overall habitat availability for both lotic and lentic species (Washko et al., 2020). Additionally, the lack of predation by trout at the relict beaver reach may have affected overall biomass of macroinvertebrates. That said, we suspect that habitat characteristics had more influence on macroinvertebrate biomass patterns (Nicola et al., 2010). Supporting this idea, the invertebrate biomass on lotic substrates

was highest at the untreated reach despite this site having high fish biomass compared to the relict beaver reach. The high biomass of invertebrates on hard lotic substrates at the untreated reach may also reflect the somewhat more stable discharge, especially in late summer and fall, due to the larger upstream watershed area.

Inputs and emergence of insects did not differ between reaches, but did vary over time. While water temperature is known to drive emergence in heterogeneous thermal habitats, in areas with consistent water temperature emergence may be driven more by weather patterns, potentially explaining the high amount of emergence from the untreated reach early in the summer season (Ivković et al., 2013). For example, higher air temperatures recorded in June (NOAA, 2024) may have triggered greater emergence overall, but especially at the untreated reach. Furthermore, higher emergence at the untreated reach could be linked to higher biomass of lotic macroinvertebrates at that reach. While it is common to see the highest biomass of terrestrial insect inputs during midsummer, daily fluctuations in weather, including wind, may affect inputs (Baxter et al., 2005). While similar vegetation composition and lack of canopy across the three sites may have contributed to similar terrestrial inputs across sites, weather patterns could partly explain some of why biomass varied across summer months. Some studies have found that greater abundances of wood and lentic areas increase emergence, although this was not apparent in our results (Baxter et al., 2005; Merten et al., 2014). Other studies suggest that lentic areas with emergent vegetation at the edge the stream channel lead to higher emergence, suggesting higher emergence in floodplains than confined stream reaches (McLaughlin & Harris, 1990; Venarsky et al., 2018). However, more replication across time and space would provide useful insight into how emergent insect biomass varies within and across

seasons (Corbet, 1964), as would coupling emergence with measurements of in-stream secondary production.

The density of brook trout at the treatment reach was slightly higher than at the other reaches. High density at the treatment reach may have resulted from variation in flow and depth that created a range of microhabitats for young and adult trout (i.e., riffles, deep plunge pools, shallow ponds). In the spring, the treatment reach had a high density of smaller fish likely due to lower stream flow and presence of slower-flowing side channels. In contrast, the untreated reach was characterized by a deeper channel, larger upstream watershed area (i.e., higher discharge), and uniform temperature that may have allowed for higher numbers of larger and older fish. However, we saw different patterns for body size and density across reaches in September due to lower baseflow discharge and the spawning season. Large areas of the treatment reach, particularly side channels, were no longer present in fall and contributed to a smaller fish habitat area despite higher numbers of fish. In addition, larger, spawning-sized fish may have moved upstream to the fish control and treatment reaches in fall, leaving more available habitat for smaller and young of year fish. Furthermore, presence of an upstream dam above the treatment reach may have increased fish numbers in fall if they were migrating from downstream. Benefits of LTPBR to salmonids vary across studies (Albertson et al., 2022; Bouwes et al., 2016; Hodge et al., 2025). Prior studies suggest that beaver dams positively affect brook trout overall, but effects may vary based on trout species (Chisholm et al., 1987; Lokteff et al., 2013). Despite some variable results regarding fish populations and LTPBR, the benefits of large wood on fish density, size-structure, and biomass are well documented. Fish may use wood from the PALS as shelter from predators, a source of shade and cooler water, refuge from fast streamflow, and a source for invertebrate prey (Benke & Wallace, 2003; Fausch, 1993; Fausch & Northcote, 1992;

Nagayama et al., 2012). Lastly, reaches with more variable temperature regimes may benefit temperature-sensitive species, such as cutthroat trout that are native to the study area. Increased thermal heterogeneity may provide fish the ability to move to warmer areas within their suitable temperature range, possibly leading to opportunities for faster growth of young-of-year fish, without compromising acceptable thermal tolerance for adult fish (Weber et al., 2017; Xu et al., 2010).

Longer-term monitoring, greater site replication, and especially data from before and after treatment installation, will be useful in documenting stream changes following LTPBR in wildfire-affected watersheds. This study was completed two years post-installation and lacks ecological pre-installation monitoring; a common shortcoming in many ecological restoration projects (Albertson et al., 2022; Reinert et al., 2022; Scamardo & Wohl, 2020). While additional treatment sites would have provided more information on the effects of LTPBR, logistical challenges of aligning research studies with the timing of treatment installation prevented us from having additional site replication. Likewise, our untreated reach, located downstream of the treatment and containing a larger upstream watershed area, was the only appropriate reference due to lack of unconfined floodplains upstream of the treatment and the need for an equivalently sized floodplain to the treatment reach. Difference in discharge between the sites could be a driver of some differences across sites rather than implementation of structures. Despite these study limitations, our results provide a useful temporal snapshot of ecological characteristics at the three study reaches and also provide a baseline for future monitoring at the downstream untreated site that is scheduled to receive LTPBR and for longer-term monitoring at the current treatment site.

Growing interest in applying LTPBR across diverse stream environments presents valuable opportunities for additional research and long-term monitoring studies. Continued ecological studies on macroinvertebrates and fish (e.g. community composition and growth, density, and survival) may help provide further insight to guide land managers when managing for specific ecological responses. Additionally, more research on fire behavior in proximity to LTPBR is needed. It is predicted that LTPBR projects should function similar to a beaver complex in the event of fire (Fairfax et al., 2024), potentially facilitating resilience against wildfire impacts at the watershed scale, in addition to mitigation of post-fire impacts. Further studies that link ecological and geomorphic properties will be crucial to understanding the efficacy of LTPBR in watersheds affected by wildfire.

Tables and Figures

Table 1. Channel properties, upstream drainage area, and burn severity for the four study reaches. Channel properties consisted of elevation, reach length, gradient, and sinuosity. Upstream watershed area, burned watershed area, percentage of burned watershed area, and stream order were calculated using StreamStats and ArcGIS Pro. The treatment, untreated, and relict beaver reach burn metrics were calculated using dNBR. The fish control burn severity was calculated using soil burn severity data.

Reach	Elevation (m)	Reach length (m)	Channel gradient (%)	Sinuosity index	Upstream watershed area (km ²)	Upstream burned watershed area (km ²)	Upstream burned %	Stream order
Treatment (Upper Elkhorn Creek)	2708	274.29	2.7	1.5	4.68	4.340	92.53	1
Relict Beaver (Swamp Creek)	2708	363.95	1.45	1.58	1.97	0.9	45.91	1
Untreated (Lower Elkhorn Creek)	2621	216.65	2.1	1.29	16.19	12.05	74.44	2
Fish Control (Middle Elkhorn Creek)	2664	153.47	2.6	1.4	5.26	4.67	88.8	1

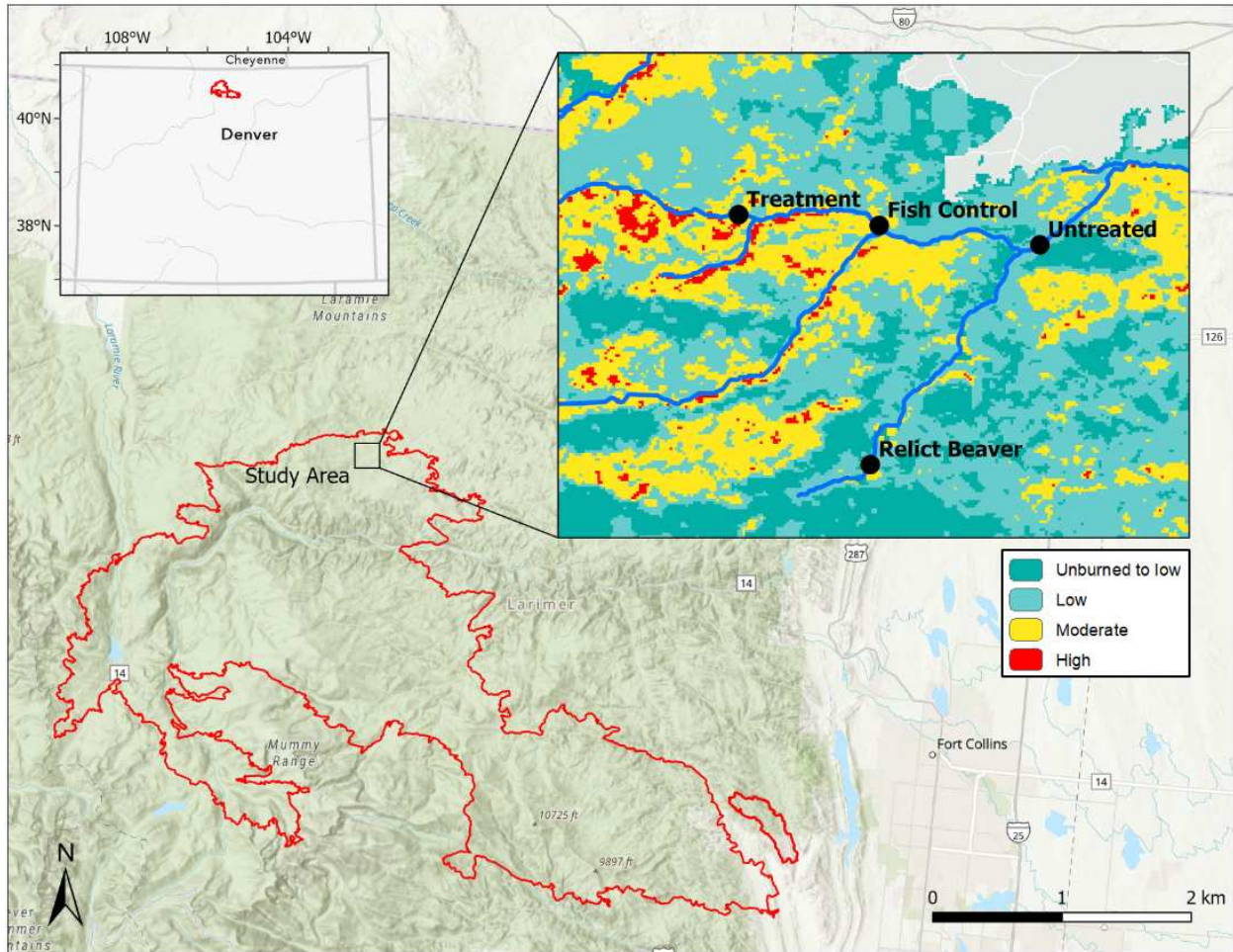


Figure 1. Map of the study reaches within the Cameron Peak Fire boundary, located within the Cache la Poudre Watershed in Northern Colorado, USA. The upper-left panel shows the fire perimeter within Colorado. The upper-right panel shows each of the four study reaches within the fire perimeter, their position on Elkhorn and Swamp Creeks, and burn severity metrics. Burn severity for the study area ranges from unburned to high burn severity, listed in the legend below the inset map, using soil burn severity raster data.

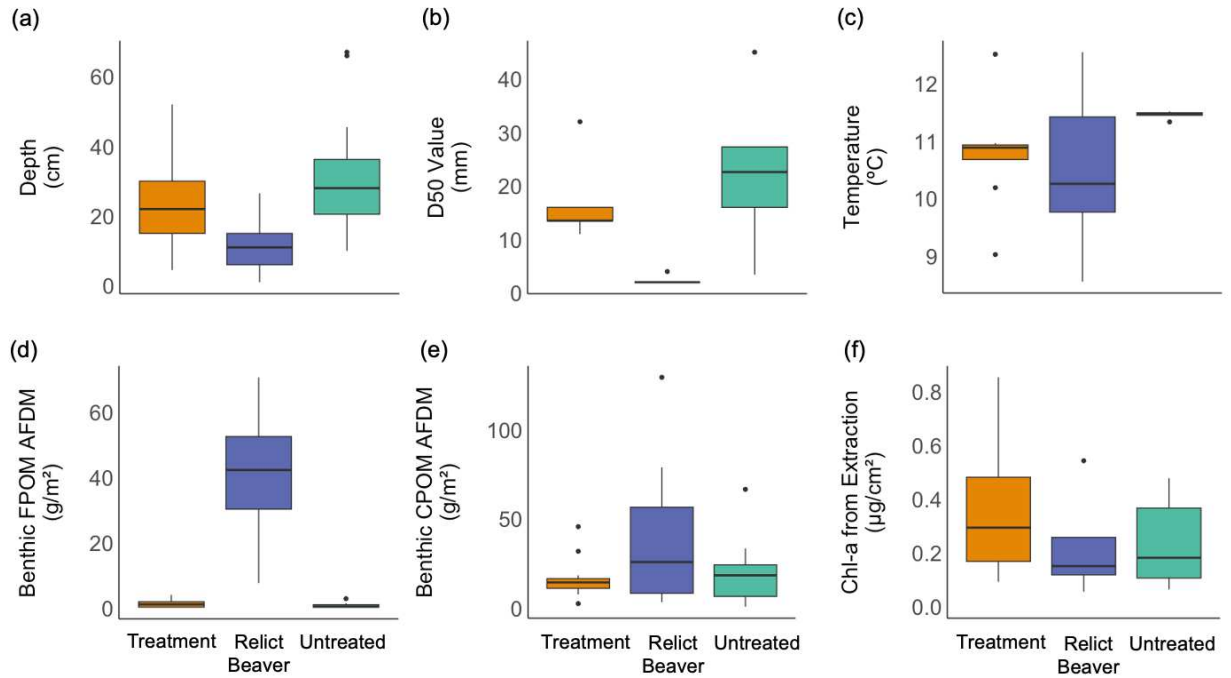


Figure 2. Environmental characteristics at the three main study reaches including water depth (a), median particle size of substrate (b), and temperature (c). Basal resources are shown on the bottom row, including fine particulate organic matter (FPOM) ash free dry mass (e), coarse particulate organic matter (CPOM) ash free dry mass (f), and chlorophyll-a extracted from periphyton (d).

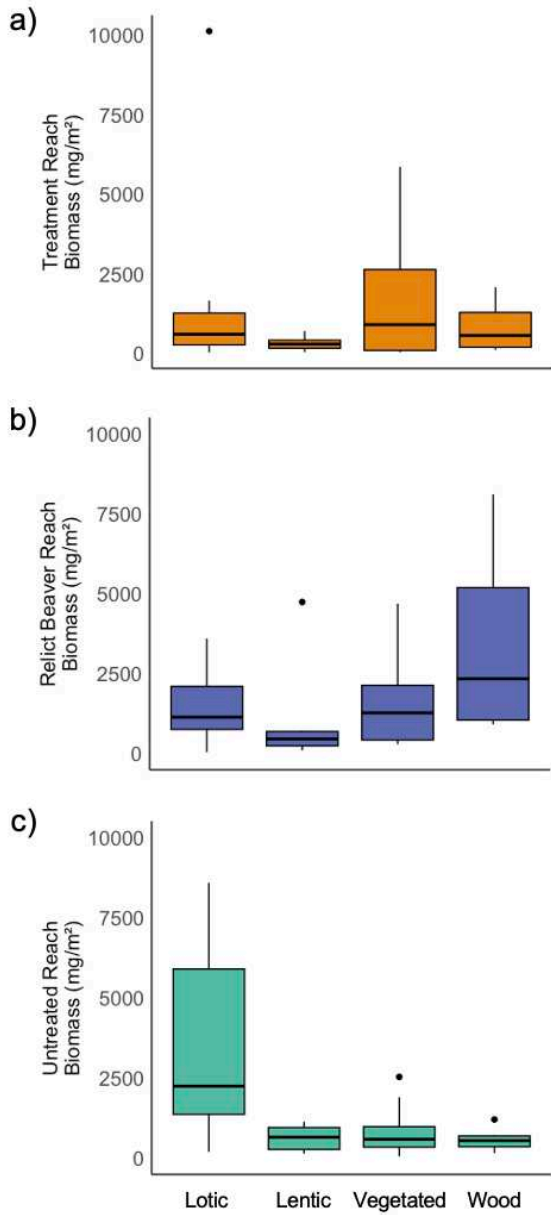


Figure 3. Benthic macroinvertebrate biomass (mg/m²) of each habitat type from the treatment (a), relict beaver (b), and untreated reaches (c). Each habitat type was sampled using a specific method: lotic regions using Surber samplers, lentic using bucket samples, vegetated areas using dipnet sweeps, and wood using wood brushes from known surface and volume of wood pieces.

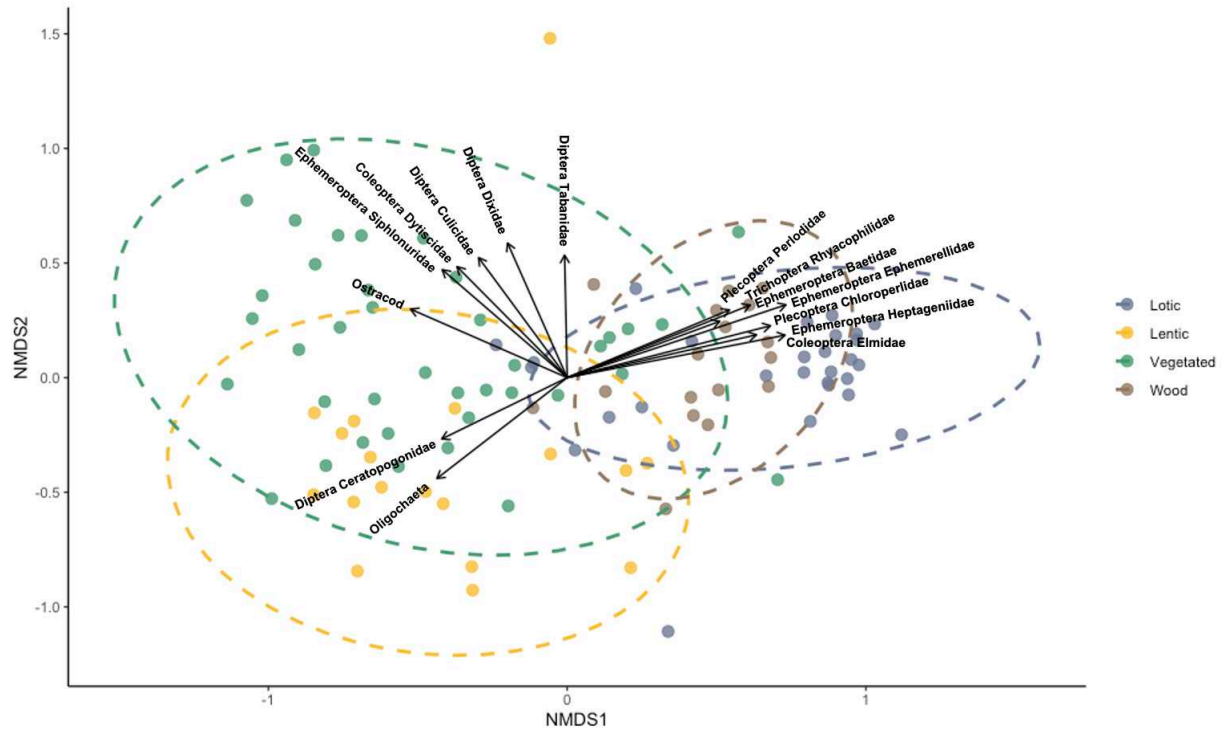


Figure 4. NMDS plot of community composition of benthic macroinvertebrates across four different habitat types: lotic, lentic, vegetated, and wood. Each point in the plot represents composition of an individual sample based on taxon composition, colored to represent its respective habitat. Distance between points reflect similarity between sample composition, where a shorter distance indicates more similar taxa. Each vector shows the direction and strength of correlation of individual taxa with the NMDS axes. Larger arrows indicate stronger relationships. See Table S9 for all habitat associations for specific taxa.

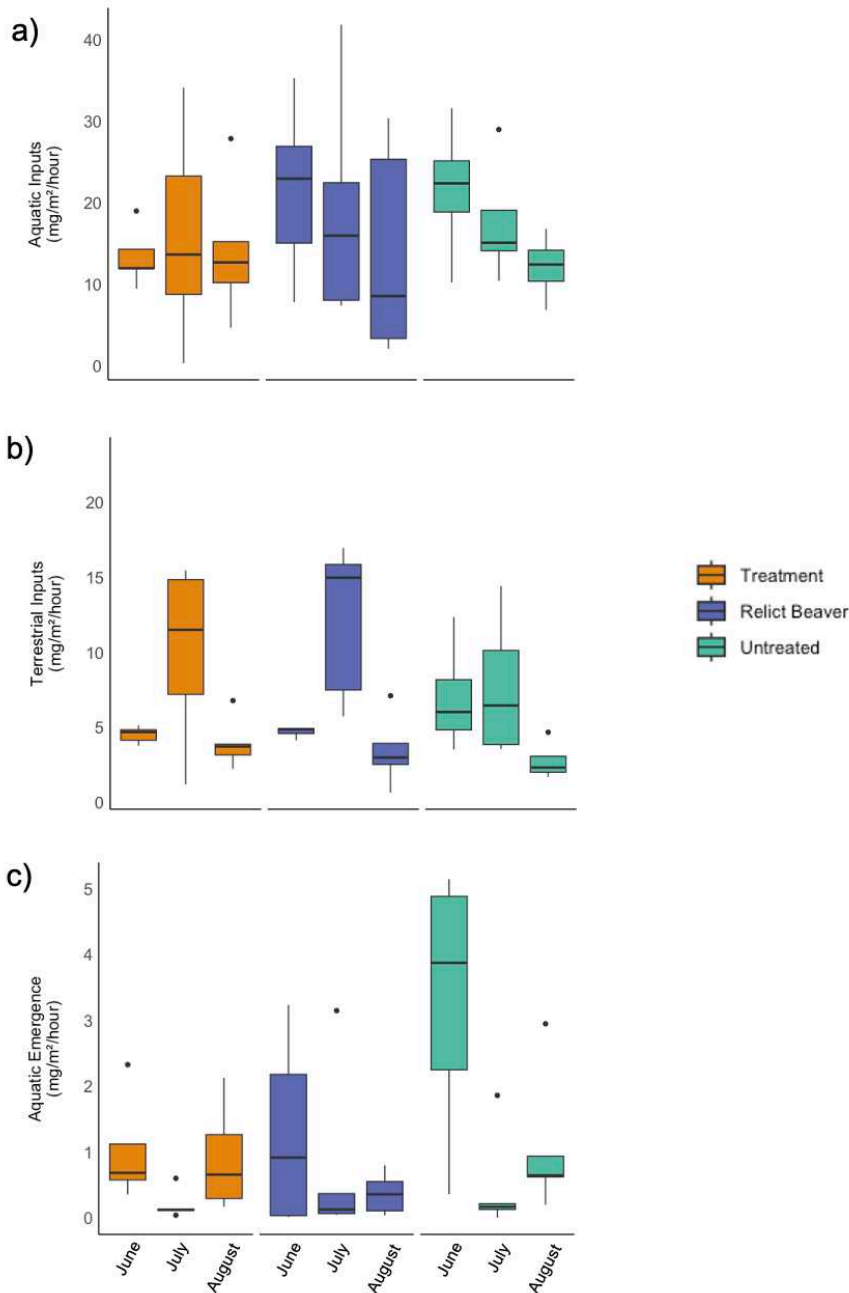


Figure 5. Biomass fluxes for aquatic inputs (a), terrestrial inputs (b), and emergent insects (c), to streams in June, July, and August at the three main reaches: treatment, relict beaver, and untreated, depicted in the legend. Biomass is represented as mg/m^2 entering and leaving the stream per hour. Aquatic and terrestrial inputs were collected via pan traps along the stream margins. Aquatic inputs represent insects that emerged from the stream as adults and later reentered the stream. Emergent insects were collected via emergence traps as the insects emerged as adults from the stream. Note different y-axes between plots.

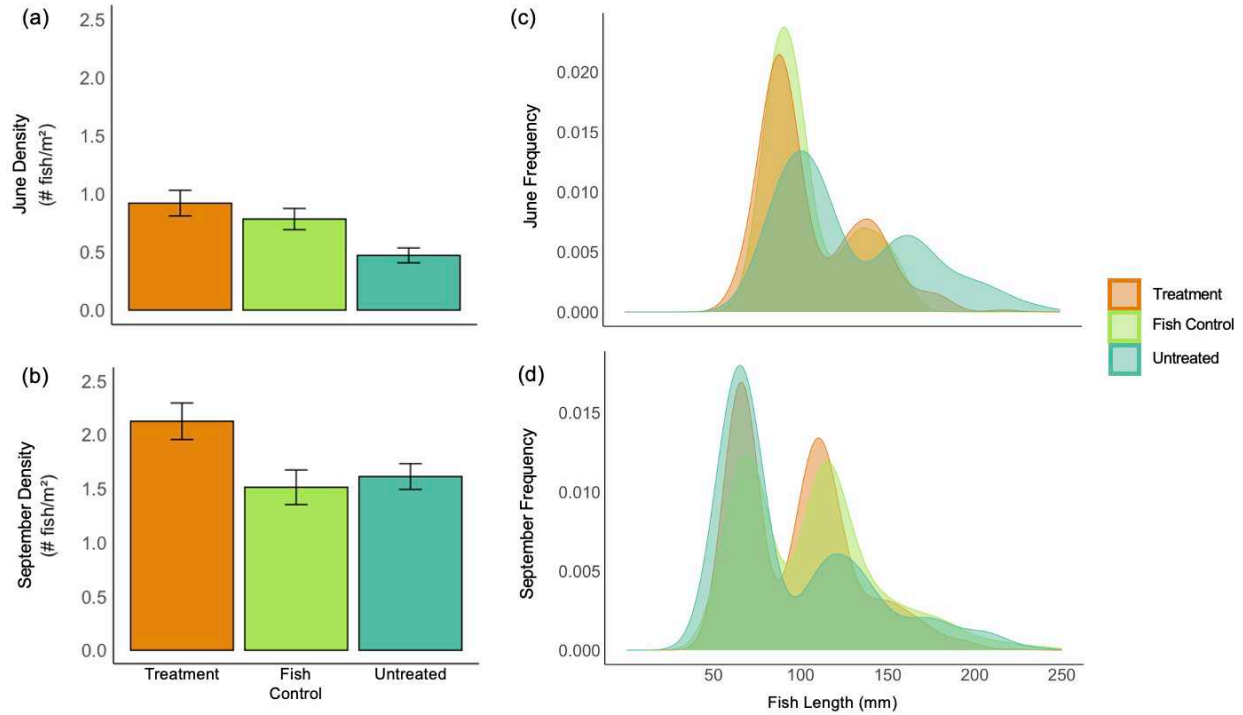


Figure 6. Brook trout density (i.e., the number of fish per square meter of wetted area) in spring (a) and fall (b) for the three reaches containing fish. Additionally, size frequency density plots of brook trout in spring (c) and fall (d) for the treatment, fish control, and untreated reaches is shown on the right panels. The shaded curves are the probability density functions showing relative distributions of sizes.

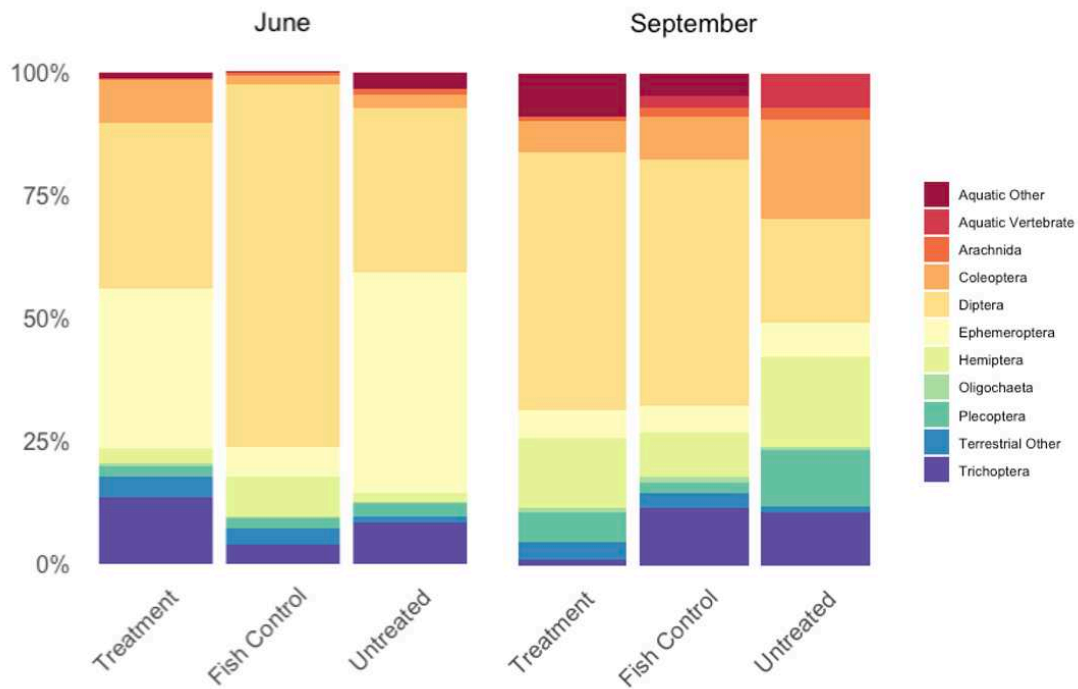


Figure 7. Proportions of different taxa identified from brook trout stomach contents from the three reaches containing fish. Samples were collected in June and September at each reach. Colors correspond to invertebrate orders shown in the legend at right.

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APPENDIX

Water chemistry analysis – Water samples were collected in high-density polyethylene plastic bottles, after triple-rinsing bottles in stream water, then stored cold and filtered through 0.45 μm pore-size glass fiber filters (Millipore Corp, Burlington, MA). All bottles were triple washed with deionized water (Specific Conductivity $\text{SC} < 1.0 \mu\text{S}/\text{cm}$), prior to use. Dominant cation (Na , NH_4) and anion (NO_3) concentrations were determined by ion chromatography (Thermo-Fisher Corporation, Waltham, MA, USA) within 72 hours of collection. Detection limits were 0.01 mg/L for all ions. Specific conductivity (SC) and pH were measured on unfiltered subsamples (Mettler Toledo, Columbus, OH, USA). Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) concentrations were quantitated using high-temperature combustion catalytic oxidation on a total organic C/N analyzer after 2M HCl treatment to remove mineral C (TOC- V_{CPN} Shimadzu Corporation, Columbia, MD). Detection limits for DOC and TDN were 0.04 and 0.01 mg L^{-1} , respectively.



Figure S1. Google Earth imagery of the treatment site taken in October of 2013 (a), and August of 2019 (b).

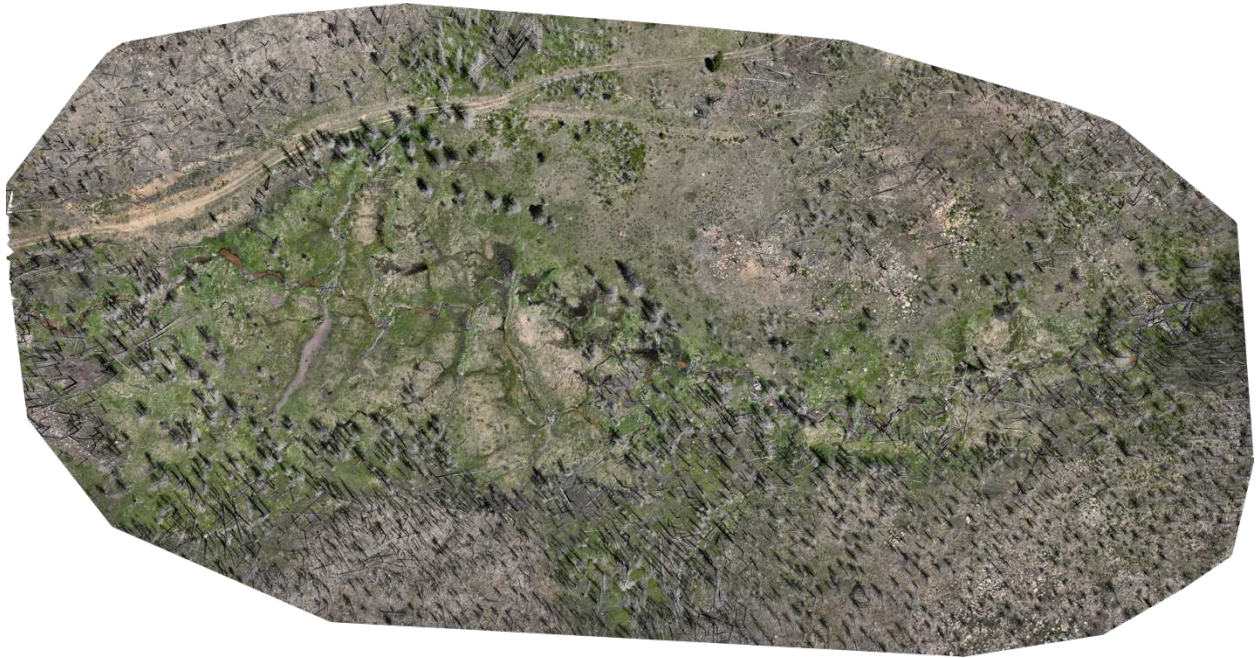


Figure S2. Aerial imagery of the treatment reach. The flow path of the stream is from left to right across the image.



Figure S3. Aerial imagery of the relict beaver reach. The flow path of the stream is from lower left to top right across the image.

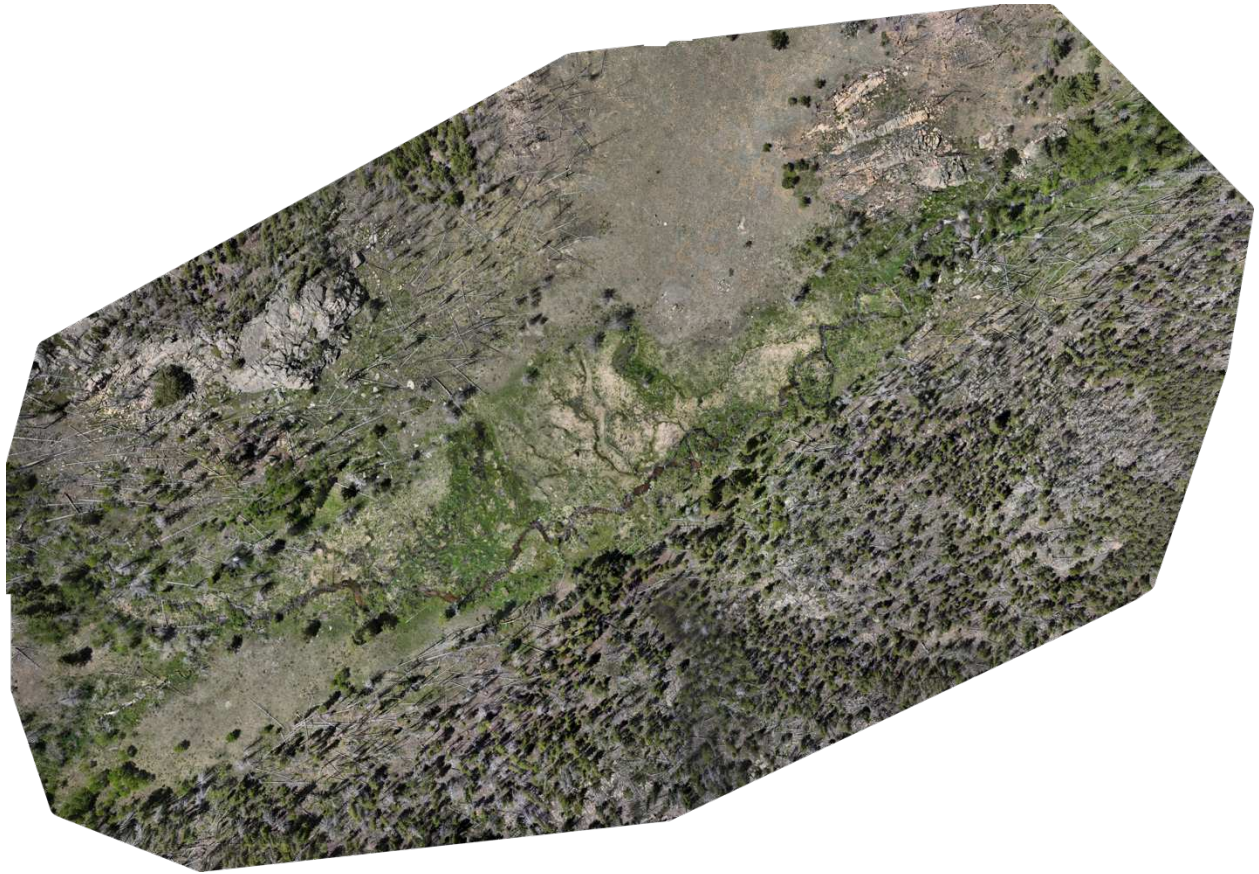


Figure S4. Aerial imagery of the untreated reach. The flow path of the stream is from left to right across the image.

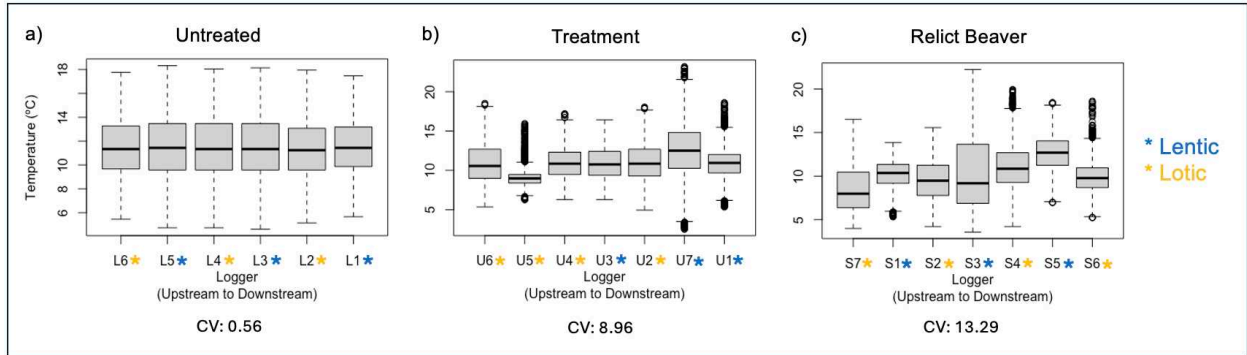


Figure S5. Temperature ranges (°C) across the untreated (a), treatment (b) and relict beaver reach (c). Loggers are ordered from most upstream (left) to downstream (right). Colored stars on the x-axis indicate if each logger was placed in a lotic or lentic habitat, which were all connected to the main channel. Coefficient of variation (C.V.) between means are listed under each plot. Data consist of individual temperature measurements taken from June to September every 15 minutes. The top and bottom edges of the box represent 25-75% of the data with the center of the box representing the median of the data. Bars show the range of data with outliers represented by circles.

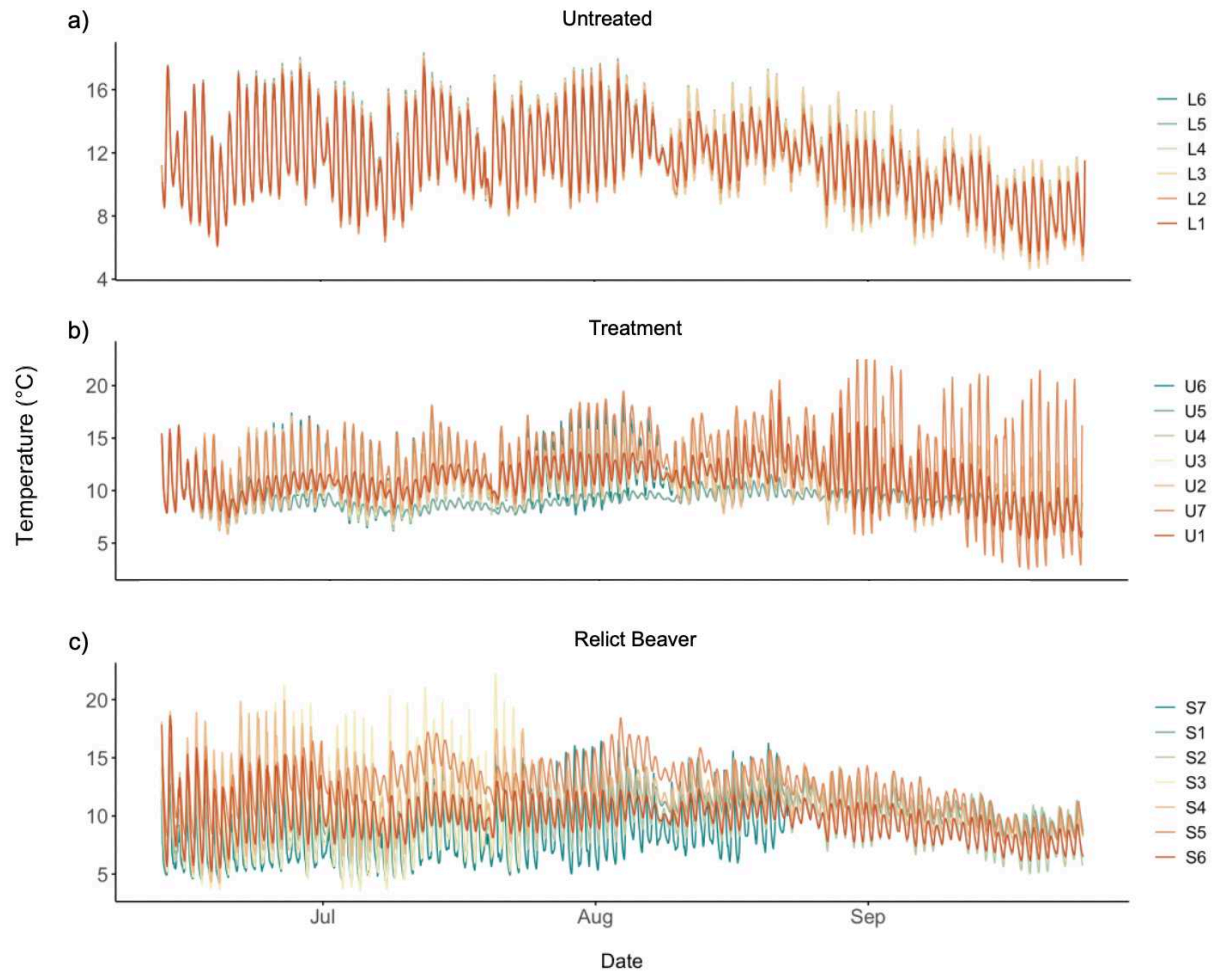


Figure S6. Temperature time series from individual loggers from the untreated reach (a), treatment reach (b), and relict beaver reach (c). Individual temperature loggers are ordered from most upstream (blue) to most downstream (red) in the legend.

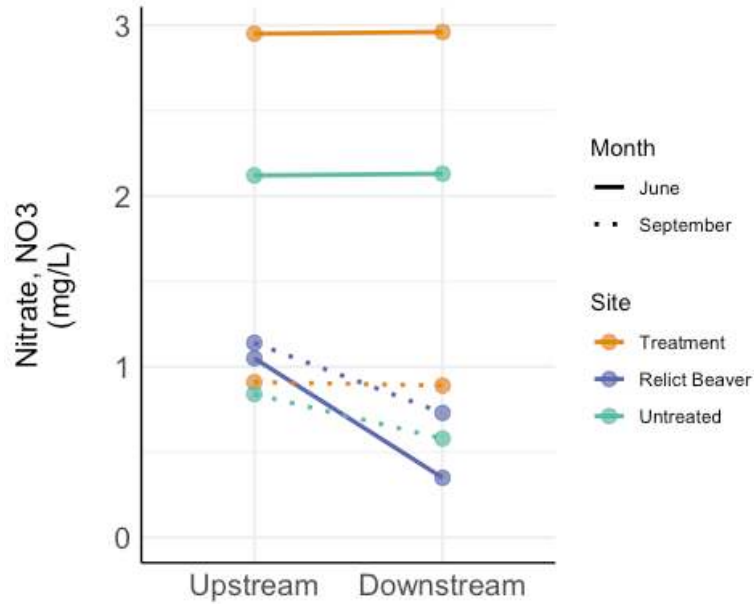


Figure S7. Nitrate concentrations (mg/L) upstream and downstream of each study reach in June vs. September. Each line connects the upstream sample to the downstream sample. Samples collected in June are represented by a solid line and samples collected in September are represented by a dotted line. Sites are shown in different colors.

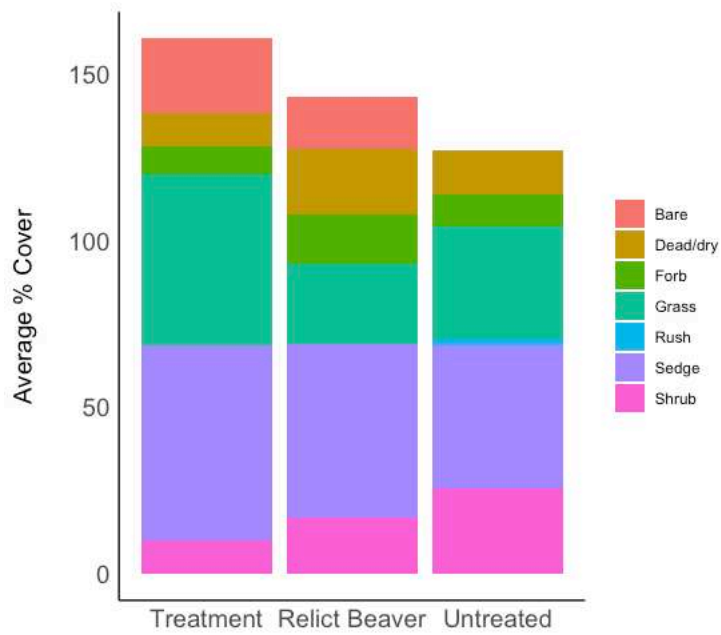


Figure S8. The proportion of vegetation cover at the treatment, relict beaver, and untreated reach. Vegetation types consisted of bare, dead/dry, forbs, grasses, rushes, sedges, and shrubs. Overlapping vegetation in the vertical dimension results in a coverage over 100%.

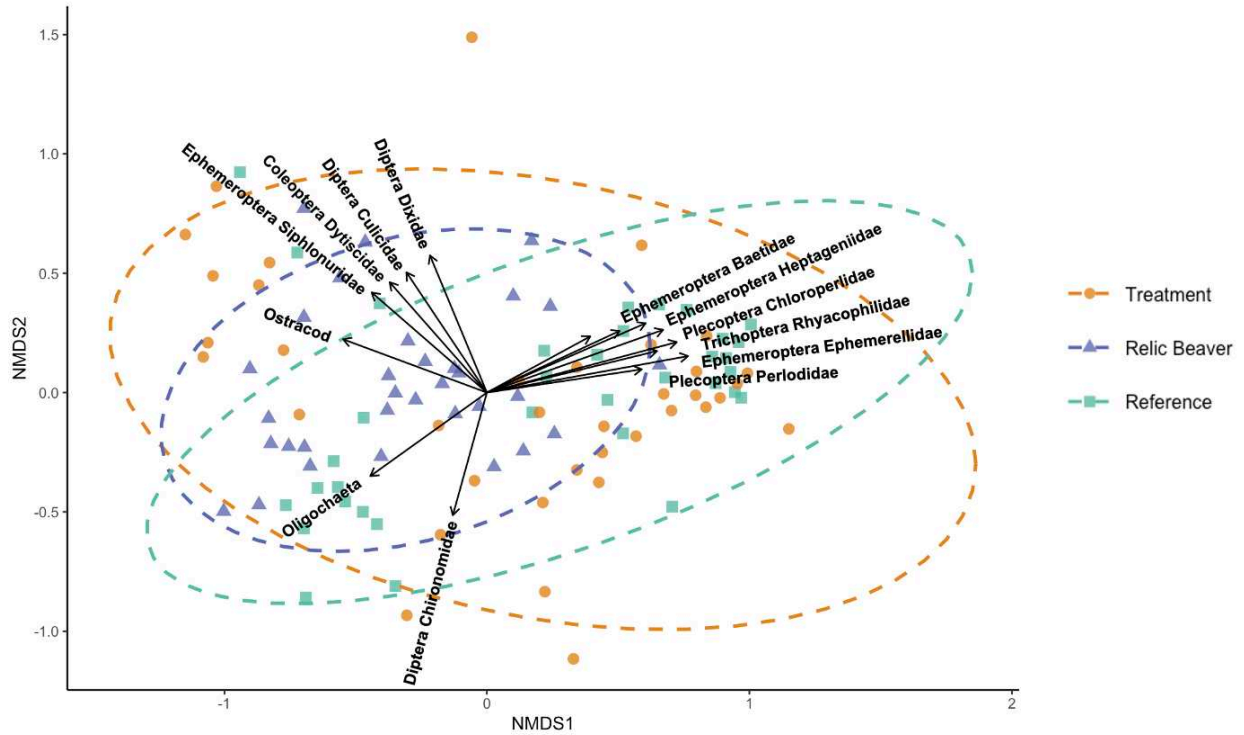


Figure S9. NMDS plot of community composition of benthic macroinvertebrates across the three primary study reaches. Each point in the plot represents composition of an individual sample based on taxon composition, colored to represent its respective reach. Distance between points reflect similarity between sample composition, where a shorter distance indicates more similar taxon composition. Each vector shows the direction and strength of correlation of individual taxa with the NMDS axes. Larger arrows indicate stronger relationships.

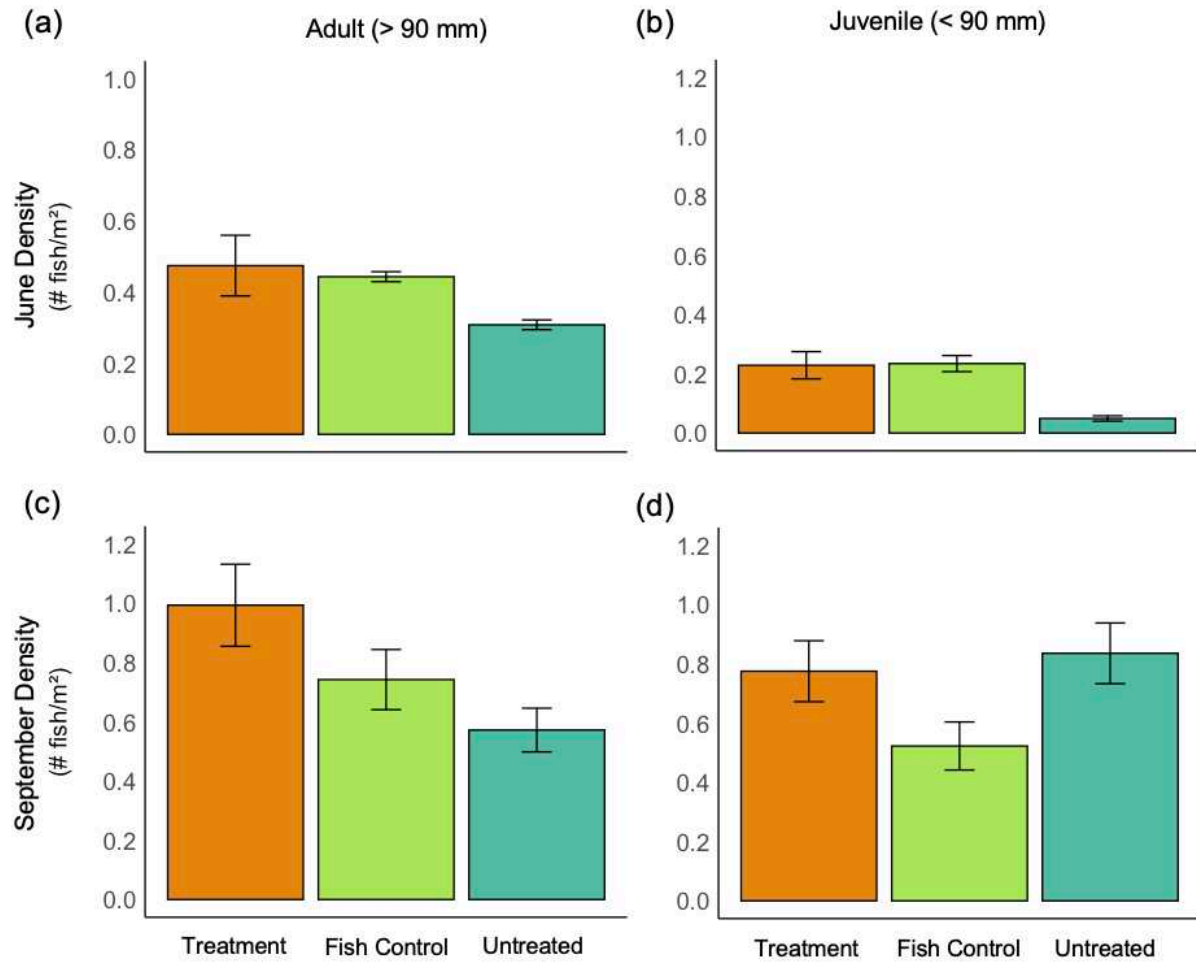


Figure S10. Brook trout density across seasons for large (>90 mm) brook trout in spring (a) and fall (c) and for small (<90 mm) fish in spring (b) and fall (d).

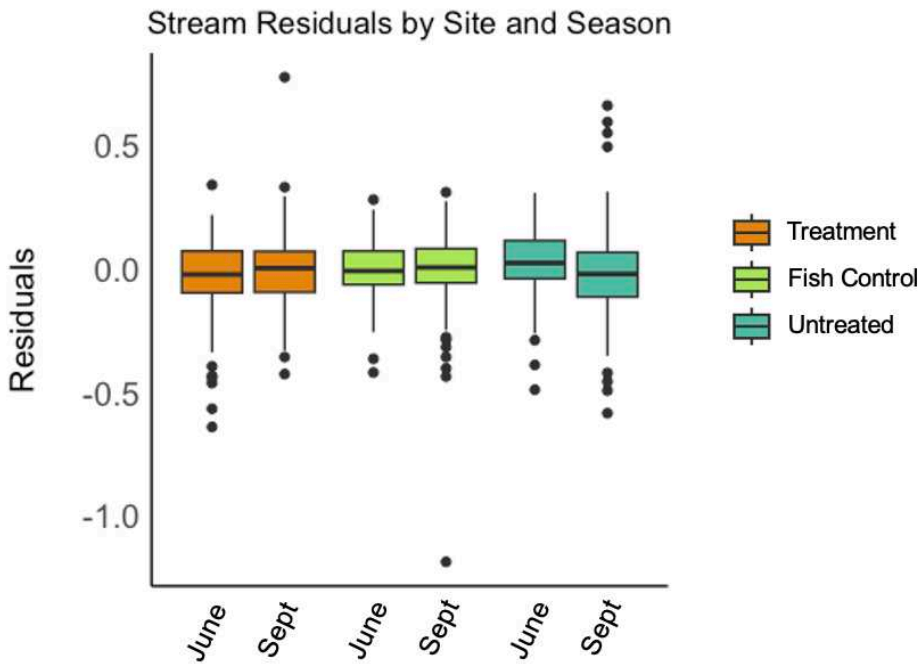


Figure S11. Trout body condition based on body condition residuals for fish greater than 100 mm. Residuals over zero indicate a heavier bodyweight, whereas below zero indicate a lighter weight. Residuals are shown for each site for June and September.

Table S1. Number of samples collected at each reach by sample type.

	Treatment	Relict Beaver	Untreated	Fish Control
Surber (BMI)	11	7	11	n/a
Bucket (BMI)	6	6	6	n/a
Dipnet (BMI)	13	14	6	n/a
Wood (BMI)	6	5	6	n/a
Pebbles	250	250	250	n/a
Algae (rocks)	22	4	20	n/a
Algae (mats)	0	10	3	n/a
Benthotorch	20	3	20	n/a
Vegetation plots	12	12	12	n/a
Depth	73	37	40	n/a
FPOM	10	10	10	n/a
CPOM	11	7	11	n/a
Pan traps	15	15	15	n/a
Emergence traps	15	18	15	n/a
# Fish caught (spring)	299	n/a	146	168
# Fish caught (fall)	617	n/a	549	336
Lavage (spring)	108	n/a	61	60
Lavage (fall)	30	n/a	30	30

Table S2. Total wood volume and surface area from the treatment, relict beaver, and untreated reach.

	Treatment	Relict Beaver	Untreated
Total volume (m ³)	4.53	0.829	0.955
Total surface area (m ²)	206	35.8	40.3

Table S3. Area (m²) of each habitat type at the three reaches.

	Treatment	Relict Beaver	Untreated
Lotic	317	257	376
Lentic	88	1322	211
Vegetated	476	2802	1717
Wood	206	35.8	40.3

Table S4. Overall and pairwise comparison p-values for environmental and basal resources from Kruskal-Wallis (KW) nonparametric tests and Dunn's post-hoc tests.

	Temperature (KW)	Depth (KW + Dunns)	D50 (KW + Dunns)	Chl-a Extraction (KW)	Chl-a Benthotorch (KW)	FPOM (KW + Dunns)	CPOM (KW)
Overall p-value	0.09	< 0.0001	0.01	0.1	0.06	< 0.0001	0.56
Treatment-Relict Beaver	n/a	< 0.0001	0.06	n/a	n/a	0.001	n/a
Treatment- Untreated	n/a	0.06	1	n/a	n/a	1	n/a
Untreated -Relict-Beaver	n/a	< 0.0001	0.01	n/a	n/a	0.0001	n/a

Table S5. Raw values of water chemistry variables. Water samples were collected upstream and downstream of each study reach in June and September. Analytes included dissolved organic carbon, total dissolved nitrogen, pH, specific conductivity, sodium, ammonium, and nitrate.

Site	Month	Stream Position	DOC mg/L	TDN mg/L	pH	SC uS/cm	Na mg/L	NH ₄ mg/L	NO ₃ mg/L
Treatment	June	Upstream	3.24	0.77	7.16	39.76	2.34	0.01	2.95
Treatment	June	Downstream	3.52	0.76	7.13	44.38	2.34	0.01	2.96
Relict beaver	June	Upstream	2.59	0.31	7.23	67.28	3.80	0.03	1.05
Relict beaver	June	Downstream	5.66	0.22	7.22	59.75	3.72	0.02	0.35
Untreated	June	Upstream	3.54	0.62	7.25	56.73	2.79	0.01	2.12
Untreated	June	Downstream	3.38	0.61	7.15	50.89	2.90	0.02	2.13
Treatment	September	Upstream	1.46	0.29	7.22	48.54	2.94	0.01	0.91
Treatment	September	Downstream	1.52	0.43	6.76	41.02	2.97	0.00	0.89
Relict beaver	September	Upstream	2.01	0.36	7.57	70.28	4.59	0.01	1.14
Relict beaver	September	Downstream	2.56	0.19	7.14	59.83	3.67	0.03	0.73
Untreated	September	Upstream	1.50	0.27	7.15	48.37	3.03	0.00	0.84
Untreated	September	Downstream	1.86	0.25	7.55	60.95	3.28	0.01	0.58

Table S6. Interaction and main effect p-values for water chemistry variables between site and month from likelihood ratio tests.

	NO ₃	DOC	TDN	pH	SC	Na	NH ₄
INTERACTION LRT ~ site*month ~ site + month	< 0.0001	0.99	< 0.0001	0.33	0.95	0.53	0.78
MAIN EFFECT LRT ~ site ~ site + month	n/a	0.0003	n/a	0.67	0.5	0.003	0.068
MAIN EFFECT LRT ~ month ~ site + month	n/a	0.24	n/a	0.16	< 0.0001	< 0.0001	0.008

Table S7. Interaction and main effect p-values for benthic biomass between site and habitat using likelihood ratio tests.

	Benthic biomass p-value
INTERACTION LRT ~ site*habitat ~ site + habitat	0.009
MAIN EFFECT LRT ~ site ~ site + habitat	0.03
MAIN EFFECT LRT ~ habitat ~ site + habitat	0.33

Table S8. PERMANOVA p-values for site, habitat, and overall for benthic macroinvertebrate community composition represented by the NMDS plot.

	Site R ²	Site p-value	Habitat R ²	Habitat p-value	Overall p-value
PERMANOVA Site*Habitat	0.06	0.001	0.21200	0.001	0.114

Table S9. NMDS1 values relate to position on the x-axis while NMDS 2 relate to position on the y-axis of the NMDS plot in the main text. Taxa with positive NMDS1 values move to the right of the plot, shown in the NMDS plot as lotic, and negative values stay towards the left of the plot, and lean lentic. Only significant taxa with $p < 0.05$ are shown.

Taxa	NMDS1	NMDS2	p-value
Ostracod	-0.37	0.15	0.002
Oligochaeta	-0.3	-0.23	0.001
Ephemeroptera Siphonuridae	-0.29	0.28	0.001
Diptera Ceratopogonidae	-0.28	-0.05	0.01
Coleoptera Dytiscidae	-0.25	0.31	0.002
Diptera Culicidae	-0.2	0.34	0.001
Bivalvia Sphaeriidae	-0.18	-0.21	0.013
Copepod	-0.18	-0.23	0.013
Diptera Dixidae	-0.14	0.38	0.001
Amphipod	-0.13	0.21	0.038
Trichoptera Limnephilidae	-0.11	0.27	0.019
Diptera Chironomidae	-0.09	-0.34	0.003
Snail	-0.09	0.22	0.035
Diptera Tabanidae	-0.01	0.36	0.01
Trichoptera Pupa	0.16	0.22	0.02
Trichoptera Uenoidae	0.21	0.12	0.042
Diptera Empididae	0.24	0.07	0.046
Plecoptera Pteronarcyidae	0.26	0.13	0.014
Trichoptera Lepidostomatidae	0.26	0.16	0.006
Ephemeroptera Baetidae	0.34	0.17	0.001
Plecoptera Perlodidae	0.39	0.06	0.001
Ephemeroptera Heptageniidae	0.4	0.19	0.001
Trichoptera Rhyacophilidae	0.43	0.12	0.001
Plecoptera Chloroperlidae	0.45	0.18	0.001
Coleoptera Elmidae	0.48	0.14	0.001
Ephemeroptera Ephemerellidae	0.51	0.1	0.001

Table S10. Interaction and main effect p-values for site and month for emergent insects, terrestrial inputs, and aquatic inputs using likelihood ratio tests.

	Aquatic emergence (mg/m ² /hour)	Terrestrial input (mg/m ² /hour)	Aquatic input (mg/m ² /hour)
INTERACTION LRT ~ site*month ~ site + month	0.06	0.57	0.77
MAIN EFFECT LRT ~ site ~ site + month	0.002721	0.0005	0.3
MAIN EFFECT LRT ~ month ~ site + month	0.06	0.3	0.53

Table S11. P-values for fish size (millimeters) obtained from generalized linear models with a gamma distribution between sites and overall.

	Spring	Fall
Treatment-Fish Control	0.99	0.01
Treatment- Untreated	< 0.0001	0.6
Fish Control - Untreated	< 0.0001	0.0006
Overall site	< 0.0001	0.0007

Table S12. PERMANOVA p-values for site, season, and overall for trout diet composition.

	Site R ²	Site p-value	Season R ²	Season p-value	Overall p-value
PERMANOVA Site*Season	0.04	0.001	0.11	0.001	0.001