Freshwater Biology

Beavers alter stream macroinvertebrate communities in northeastern Utah

Journal:	*Freshwater Biology*
Manuscript ID	FWB-P-Jul-19-0378.R1
Manuscript Type:	Standard Paper
Date Submitted by the Author:	19-Sep-2019
Complete List of Authors:	Washko, Susan; University of Arizona, School of Natural Resources and the Environment; Utah State University, Department of Watershed Sciences Roper, Brett; USDA Forest Service, 2Fish and Aquatic Ecology Unit, Forestry Sciences Lab Atwood, Trisha; Utah State University, Department of Watershed Sciences
Keywords:	Running water / rivers / streams < Habitat, Community < Level of Organisation, Invertebrates < Taxonomic Group / Assemblage, Other species interactions < Process / Approach / Methods, Ecosystem < Level of Organisation

Title: Beavers alter stream macroinvertebrate communities in northeastern Utah

Running title: Beavers alter stream communities

Authors: Washko, Susan[1,a*], Brett Roper[2], Trisha Atwood[1]

[1]Department of Watershed Sciences and The Ecology Center, Utah State University, Logan, UT, 84341
[2]USDA Forest Service, National Stream and Aquatic Ecology Center, 860 North 1200 East, Logan, UT 84321.
*Corresponding author: Susan Washko, washko.susan@gmail.com, School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721

Keywords: beaver, stream, macroinvertebrates, functional feeding group, mobility group

Footnotes: [a] Present address School of Natural Resources and the Environment, University of Arizona, Tucson, AZ

SUMMARY

1. Understanding changes in macroinvertebrate communities is important because they play a large role in stream ecosystem functioning, and they are an important food resource for fish. Beaver-induced changes to stream morphology could alter macroinvertebrate communities, which in turn could affect food webs and ecosystem function. However, studies investigating the effects of North American beaver activities on macroinvertebrates are rare in the intermountain west, an area with high potential for beaver-assisted restoration.
2. The aim of this study was to quantify differences in the macroinvertebrate community between unaltered segments of streams and within beaver ponds in northeastern Utah, USA. We assessed macroinvertebrate species richness, biomass, density, functional feeding group (FFG) composition, mobility group (MG) composition, and macroinvertebrate habitat characteristics to test the hypothesis that macroinvertebrate communities will differ among habitat types (undammed stream segments and beaver ponds) in beaver-occupied streams.
3. Beaver pond communities significantly differed from lotic reach communities in many ways. Beaver ponds were less diverse with 25% fewer species. Although there was variability among streams, in general beaver ponds had 75% fewer individuals and 90% lower total macroinvertebrate biomass compared to lotic reaches.
4. Regarding FFGs, beaver ponds contained more engulfers, while lotic reaches contained more scrapers, filterers, and gatherers. For MGs, beaver ponds had more sprawlers, while lotic reaches had more clingers. Swimmers were also more prevalent in lotic reaches, though this is likely due to the abundance of *Baetis* within lotic reaches. More beaver pond taxa were classified as lentic-dwelling insects, while more lotic reach taxa were categorized as preferring lotic habitats.
5. The creation of ponds by beavers fundamentally altered the macroinvertebrate community in northeastern Utah streams. Such changes to stream macroinvertebrate communities suggests that recolonization of beavers across North America may be altering stream functioning and food webs. Our study highlights the need to further investigate the effects of beaver recolonization on stream communities.

INTRODUCTION

Overexploitation of the North American beaver (*Castor canadensis*) from ~1600-1900 brought this species to the brink of extinction. However, declines in the fur trade, stricter trapping regulations, and beaver reintroduction programs has helped this species return to most of its former range (Baker & Hill, 2003). Because beavers are ecosystem engineers with the capacity to alter both physical and chemical characteristics of aquatic ecosystems (Naiman, Melillo & Hobbie, 1986; Smith *et al.*, 1991; Gurnell, 1998; Correll, Jordan & Weller, 2000; Wohl, 2013; Laurel & Wohl, 2019), their expanding populations will undoubtedly influence the aquatic communities residing in the rivers and streams that they recolonize.

Research investigating the effects of North American beaver on aquatic ecosystems has largely focused on physiochemical changes to the river/stream system or on fish. In general, previous research has suggested that beavers are beneficial for stream habitat heterogeneity and fish habitat (Pringle *et al.*, 1988; Rolauffs, Hering & Lohse, 2001; Rosell *et al.*, 2005; Bush & Wissinger, 2016; Law, Mclean & Willby, 2016; Laurel & Wohl, 2019), and as a result, agencies are using beavers as a natural solution for stream and riparian restoration (Gibson & Olden, 2014; Pollock *et al.*, 2014; Pilliod *et al.*, 2018).

However, results have been mixed for beaver effects on stream macroinvertebrates. Several studies have indicated a decrease in macroinvertebrate species richness within beaver ponds compared to lotic segments (Gard, 1961; McDowell & Naiman, 1986; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Strzelec, Białek & Spyra, 2018). There is also a trend for differences in macroinvertebrate taxa community composition between beaver ponds and lotic reaches (McDowell & Naiman, 1986; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Malison *et al.*, 2014; Law *et al.*, 2016; Strzelec *et al.*, 2018). Density results seem to be site-dependent for whether density is higher within beaver ponds (McDowell & Naiman, 1986), not statistically different between lotic habitats and beaver ponds (Rolauffs *et al.*, 2001; Anderson & Rosemond, 2007; Law *et al.*, 2016), or higher within the lotic segments (Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Strzelec *et al.*, 2018). Even studies comparing macroinvertebrate densities between natural pools and lotic reaches have shown site-dependent effects (Logan and Booker 1983, Herbst et al. 2018). Biomass (g/m^2) tends to be higher in beaver ponds than streams, although there are fewer studies on this factor (Gard, 1961; McDowell & Naiman, 1986; Anderson & Rosemond, 2007). Lastly, the beaver dam itself is a habitat with a unique macroinvertebrate assemblage (Clifford, Wiley & Casey, 1993), and beaver ponds can affect macroinvertebrates downstream due to hydrologic changes altering stream temperature and nutrients (Fuller & Peckarsky, 2011a b). Most information about beaver effects on macroinvertebrates have come from studies on the Eurasian beaver (*Castor fiber*) in European streams, followed by studies from North America and then a couple on invasive North American beavers in South American streams. Surprisingly, few studies have been conducted on the effects of North American beaver recolonization on stream macroinvertebrate communities in North American streams of the Intermountain West, despite that this region has undergone extensive beaver recolonization and utilizes beaver-assisted restoration.

The functional integrity of a stream is heavily dependent on its macroinvertebrate community. Macroinvertebrates control detritus processing and nutrient cycling in streams, influence stream primary productivity, and are a major food source for higher trophic level vertebrates like fish (Wallace & Webster, 1996; Heino, 2005). Studies comparing macroinvertebrate communities between streams (Heino, 2005) and between habitat types (e.g., natural pools versus lotic reaches) within a stream (Logan & Brooker, 1983; Herbst *et al.*, 2018) show that many physical and chemical factors such as water velocity, substrate size, nutrient concentrations, and the availability of allochthonous and autochthonous food resources drive differences in the colonization of stream macroinvertebrates. Furthermore, trait characteristics that reflect a species' adaptations to its environment influence its functional role. Thus, the development and presence of beaver dams, which alter physical and chemical characteristics of streams, will have consequences for the types and functional characteristics of macroinvertebrates that can colonize streams where beavers are present (Anderson and Rosemond, 2010, Strzelec *et al. 2018*).

Physical changes to a stream due to the formation of beaver ponds should influence the macroinvertebrate community as it changes the necessary traits for maneuvering through the environment (i.e., mobility group; MGs). As water pools behind a beaver dam, the stream's shape forms a wide pond, characterized by slower, deeper water that might benefit swimming taxa that are excluded from fast-moving lotic reaches (Mackay, 1992; Stout, Majerova & Neilson, 2017). Additionally, the substrate size shifts from gravel or cobble in undammed sections to fine sediments within the beaver ponds (Levine & Meyer, 2014; Strzelec *et al.*, 2018). Sediment grain size is known to be a strong habitat filter influencing macroinvertebrate communities in streams (Mackay, 1992; Rabení, Doisy & Zweig, 2005; Bo *et al.*, 2007). Size of sediment influences the size of interstitial spaces that macroinvertebrates can occupy. Thus, finer sediments behind beaver ponds may select for macroinvertebrates that can cling to fine particles or burrow in the sediment (Mackay, 1992).

Both physical and chemical changes as a result of beaver ponds can also influence how macroinvertebrates acquire food (i.e., functional feeding groups; FFGs) (Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). Beaver ponds act as important sinks for nutrients (Westbrook, Cooper & Baker, 2006; Lazar *et al.*, 2015), which can stimulate *in situ* primary production (Coleman & Dahm, 1990), potentially promoting grazers. However, studies on the effect of Eurasian beaver on macroinvertebrates in European streams found that grazers declined in beaver ponds (Law et al. 2016). This may be because the substrate size has decreased within the beaver pond, making large grazing surfaces rare (Levine & Meyer, 2014; Strzelec *et al.*, 2018). Also, beaver ponds are large sinks for organic matter, and leaching of dissolved organic carbon can color the water like tea (Kwick & Carter, 1975; Cirmo & Driscoll, 1993; Vehkaoja *et al.*, 2015), inhibiting light penetration and primary production. Conversely, the organic matter entering the pond could be utilized by collector and shredder taxa. However, studies on Eurasian beaver found mixed results for these FFGs, with beaver ponds decreasing shredders in Polish streams and increasing collectors and shredders in Scottish streams. The major consensus from this European literature, as well as one study done on the effects of invasive *C. canadensis* on South American streams, is that predator taxa increase (Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). This increase in predator taxa may be due to enhanced prey availability (Harthun, 1999). Prey drifting into beaver ponds cannot continue to drift further to escape predation because water velocity in the pond is too slow, likely increasing the ability of predatory macroinvertebrates to capture prey (Martin & Knight, 1989; Thorp & Covich, 2001).

The aim of our study was to quantify differences in the macroinvertebrate community between stream lotic reaches and within beaver ponds in northeastern Utah. Understanding the taxa composition of beaver ponds in arid western regions is crucial because stream communities are important for the biodiversity of arid ecoregions (Gibson & Olden, 2014), and because beaver populations are increasing as a result of natural dispersal and their use in stream restoration projects (Small, Frey & Gard, 2016). Our aim is to compare beaver ponds with lotic reaches to better understand how macroinvertebrate taxa of stream reaches changes when beaver ponds occupy habitat that was formerly lotic. We predict that macroinvertebrate communities will differ between lotic reaches and beaver ponds within beaver-occupied streams in multiple ways. In beaver ponds relative to lotic reaches, we expect **1)** a higher biomass and density of macroinvertebrates, and **2)** lower species richness through a lack of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa. Further, we expect **3)** more collectors and shredders due to increases in detritus and fine particulate organic matter in beaver ponds, **4)** more predators, and **5)** more swimmers and burrowers due to slow, deep water, and abundant soft sediment in ponds.

METHODS

Study Sites

This study took place in northeastern Utah in three beaver-inhabited streams; Right Hand Fork, Spawn Creek, and Temple Fork (Figure 1). All streams are tributaries to the Logan River and are located within the Wasatch-Cache National Forest. The three streams are in the Semiarid Foothills ecoregion just below the Wasatch Montane Zone ecoregion, between approximately 1,500 and 1,900 meters elevation (Table 1). Riparian communities in the Semiarid Foothills are characterized by sagebrush, grama grass, pinyon, juniper, and maple-oak scrub (Woods *et al.*, 2001). Although the three stream systems are relatively close to one another in the watershed, they vary from one another in several physical and biological characteristics (Table 1). Right Hand Fork drains a watershed area of ~64 km^2, has a mean width of 3.9 m, a gradient 0.027 m m $^{-1}$, and is more canyon-confined than the other two streams (Meredith, Budy & Thiede, 2015). In addition, Right Hand Fork has an abundance of submerged macrophytes and its fish community is dominated by Bonneville Cutthroat trout (*Oncorhynchus clarkii utah*), and lacks invasive brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and rainbow trout (*Oncorhynchus mykiss*). Temple Fork drains a watershed area of ~25 km^{2,} has an average width of 4.0 m, a gradient of 0.030 m m $^{-1}$ (Meredith *et al.*, 2015). Temple Fork generally lacks the submerged macrophytes observed at Right Hand Fork, and its fish community contains Bonneville Cutthroat trout, invasive brown trout, and very small populations of brook and rainbow trout. Spawn Creek has a mean watershed area of 15 km^2, has an average width of 1.8 m, and a gradient of 0.053 m m $^{-1}$ (Meredith *et al.*, 2015). Spawn Creek also lacks extensive macrophyte populations and its fish community is similar to that at Temple Fork. Spawn Creek is also surrounded by a 67-ha cattle exclusion fence. We selected these three streams because they are the main tributaries of the Logan River, and contained active beaver at the time of the study.

Two habitat types were sampled within each of the streams: i) lotic segments directly upstream of sampled beaver ponds, which were characterized by shallow depths, cobble substrate, and fast to moderate water flow (Wheaton *et al.*, 2015; Stout *et al.*, 2017), and ii) beaver ponds directly behind an in-stream beaver dam (Figure S1). Ponds chosen within a stream were single ponds (i.e. not part of a multi-pond complex) that were less than six years old and had not breached during the spring runoff. Five pairs of beaver ponds and lotic reaches were sampled at each of the three streams. One sample was taken at each designated beaver pond and each lotic reach (total samples = 30, one was compromised and omitted, changing the total number of samples to 29).

Environmental Characteristics

Characteristics measured within each sampling location of each stream to illustrate habitat differences included elevation, water temperature, dissolved oxygen, flow/velocity, and substrate grain size. Elevation was extracted via Google Earth imagery for each sampling location. Water temperature was measured using a Thermochron® iButtons® (Model DS1920, Maxim Integrated, San Jose, CA, USA) every half hour from July to September 2017. Stream flow was measured in the spot of sample collection via a Flo-Mate portable velocity flow meter (Hach Company, Frederick, MD, USA) in one afternoon during September 2017. Dissolved oxygen measurements were taken every half hour in September 2017 with miniDOT dissolved oxygen sensors (PME, Inc., Vista, CA, USA). Grain size measurements followed the protocol designed by Wolman (1954), and were collected in July 2018. Water depth was measured across each habitat (lotic reach or beaver pond) sampled on a grid system (i.e. one measurement per square meter across the length and width of the pond) during September 2017. Surface area was measured using aerial photographs taken in October 2017. Photos included a meterstick as a reference, and ImageJ was used to calculate areas from the photos. The same five beaver ponds and lotic reaches at each steam were sampled for environmental characteristics. The average values for the five beaver ponds and for the five lotic reaches at each stream were analyzed using analyses of variance (ANOVA).

Multiple environmental characteristics differed between beaver ponds and lotic reaches (Table 1). The average grain size was 95% smaller in beaver ponds (habitat: $F_{1,24} = 66.421$, $p < 0.001$), and the difference is likely underestimated because all grains smaller than the smallest gravelometer section were classified into the general category of < 2 mm. The average water velocity was 78.3% lower in beaver ponds (habitat: $F_{1,54} = 67.119$, $p < 0.001$), and the average beaver pond depth was 37.8% deeper than the average lotic reach depth (habitat: $F_{1,67} = 8.526$, $p < 0.001$). Characteristics that differed between individual streams included temperature (stream: $F_{1,48} = 230.833$, $p < 0.001$), dissolved oxygen (stream: $F_{1,18} = 25.812$, $p < 0.001$), elevation (stream: $F_{1,24} = 616.285$, $p < 0.001$), and pond surface area (stream: $F_{1,24} = 8.605$, $p = 0.0015$). Temple Fork was approximately 2°C colder than Spawn Creek and Right Hand Fork. Right Hand Fork was over 150 meters lower in elevation than the other two streams, and approximately 0.5 mg/L lower in dissolved oxygen. Pond surface area was not different from lotic reach surface area, but average surface area values were higher in Temple Fork. We found no interactions between habitat and stream for any environmental characteristics (all p-values > 0.05). These data illustrate the differences between the habitats sampled in this study.

Macroinvertebrate Sampling Procedure

Benthic macroinvertebrate samples were collected in July 2017. A single macroinvertebrate sample was collected from each lotic reach and each beaver pond within Right Hand Fork, Temple Fork, and Spawn Creek. We chose to sample only a single location in each pond and lotic habitat to reduce disturbance. Macroinvertebrates from lotic reaches were collected using surber samplers (total sample area 0.093 m^2) with a mesh size of 250 μm (Lancaster & Hildrew, 1993). Macroinvertebrates from beaver ponds were collected using a sweep net, also of mesh size of 250 μm, by sweeping the net along a one-meter segment of the pond (total sample area 0.305m^2; Sarnelle *et al.*, 1998; Muzaffar & Colbo, 2002; Wissinger, Perchik & Klemmer, 2018). Both surber and sweep samples covered a known area and a sediment depth of ~2 cm. Beaver pond habitats were sampled mid-depth in areas of deposited fine sediment. Pond tails, dam structures, and other habitat types within the pond were not sampled; sample sites were chosen due to fine sediment areas being the most common and abundant feature (i.e. constituted a large area) among our beaver pond habitats (Figure S1). To directly compare surber and sweep net samples, macroinvertebrate data was standardized to one square meter. Macroinvertebrate collections were fixed in 95% ethanol and transported to the laboratory where they were identified to genus when possible, otherwise to family, both of which are acceptable taxonomic resolutions for determining functional groups (Bailey, Norris & Reynoldson, 2001). To estimate macroinvertebrate biomass of each genus or family, each sample was divided into taxa groupings, dried at 60°C to a constant weight and weighed. Individual taxa group weights were summed by sample for overall biomass.

We report macroinvertebrate results in both biomass and density as functional dominance can occur as a result of a species being either numerically dominant or as a result of their relatively large body size (Lecerf & Richardson, 2011; Atwood, Hammill & Richardson, 2014). In this study, we aimed to capture any analogous functional community structure, through either a density effect or a biomass effect.

Macroinvertebrates were assigned to a functional feeding group (FFG), mobility group (MG), and lotic/lentic habitat categories using Merritt, Cummins, and Berg (2008). Although more than one functional group may have been listed per taxa, only the primary group was utilized in our study.

Statistical Analyses

To determine the effects of beaver dams on macroinvertebrate communities, multiple metrics were compared between beaver ponds and lotic reaches across our three stream systems (Right Hand Fork, Temple Fork, and Spawn Creek). Metrics included species richness, macroinvertebrate density (# organisms per m^2), macroinvertebrate biomass (dry weight of each taxa type in the sample per m^2), and the biomass and density of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa, each FFG in the community, each MG in the community, and lentic and lotic insects as classified in Merritt et al. (2008). We used linear mixed effects models through the 'lme' function in the 'nlme' package (Pinheiro *et al.*, 2018) in R to test for differences in each metric between habitats. Mixed effects models included the random effect of site identification and fixed effects of habitat and stream. Total density and biomass models included an additional random effect, which was an identifier of the paired beaver ponds and lotic reaches (n=28 for tests with paired habitats). We then ran the models for each metric through analyses of variance (ANOVA) to compare between pond and lotic reach habitats. All metrics were either log-transformed or square root-transformed prior to running the ANOVA to meet normality assumptions. If a significant interaction between stream and habitat occurred in our ANOVA test, we used Tukey contrasts multiple comparisons of means to determine which stream's ponds and lotic reaches were significantly different.

Community composition in terms of taxa present, FFGs and MGs were compared between beaver ponds and lotic reaches. All three metrics were quantified using both density and biomass. FFG biomass and density were calculated by combining the biomass or density of all taxa classified as each FFG in the sample. The same technique was used for MGs. Community compositions were assessed with nonmetric multidimensional scaling (NMDS) ordinations through the 'vegan' package (Oksanen *et al.*, 2017) in R. To compare community composition between beaver ponds and lotic reaches, we used permutational multivariate analysis of variance (PERMANOVA) via the 'adonis' function within the 'vegan' package in R. Stream was set as a block in the PERMANOVA. To determine which specific groups of macroinvertebrates were driving observed differences between pond and lotic reach communities, we used the similarity percentages test, 'simper.' The 'simper' function within the 'vegan' package uses Bray-Curtis dissimilarities to determine species differences between groups. All statistical analyses were completed using the statistical program R (R Core Team, 2017).

RESULTS

Overall Macroinvertebrate Availability

Macroinvertebrate density was 75% higher in lotic reaches than in beaver ponds ($F_{1, 23}$ = 15.005, p = 0.001; Figure 2a), but overall model significance was driven by large differences at Right Hand Fork only (Tukey's HSD, $p < 0.001$). Similarly, macroinvertebrate biomass was 90% higher in lotic reaches ($F_{1, 23}$ = 34.872, $p < 0.001$; Figure 2b). However, this result was driven by differences between biomass in beaver ponds and lotic reaches in Temple Fork (Tukey's HSD, p

< 0.001) and Right Hand Fork (Tukey's HSD, $p < 0.001$); beaver ponds and lotic reaches at Spawn Creek did not differ in macroinvertebrate biomass.

Taxa Richness & Composition

Overall, beaver ponds were less taxa-rich compared to lotic reaches, with 25% fewer taxa than lotic reaches ($F_{1, 23} = 16.621$, $p < 0.001$). This pattern was similar and significant at all streams (i.e. there was not a significant interaction between habitat and stream). A list of taxa present and their functional group designations is included in the supplementary materials (Table S1).

NMDS and PERMANOVA tests demonstrated that the taxonomic composition of macroinvertebrates in terms of density (i.e. taxa present and their respective densities) differed significantly between beaver ponds and lotic reaches ($F_{1, 23} = 9.716$, $p < 0.001$; Figure 2c). A similarity percentages test ('simper') attributed the differences in community composition to *Baetis,* Ephemerellidae, and Elmidae larvae, which were 99%, 99%, and 97% higher in abundance in lotic reaches, respectively, as well as Chironomidae larvae and snails, which were 338% and 77% higher in beaver ponds.

The taxonomic composition in terms of biomass (i.e. taxa present and their respective biomasses) also significantly differed between beaver ponds and lotic reaches ($F_{1, 23} = 10.984$, $p < 0.001$; Figure 2d). Dissimilarity in the community composition between beaver ponds and lotic reaches was driven by a suite of mayfly taxa (98% higher), *Oligophleobodes* caddisflies (99% higher), Elmidae larvae (97% higher), and *Hesperoperla pacifica* (100% higher) being more abundant in lotic reaches, whereas *Psychoglypha* (100% higher) and *Lepidostoma* (88% higher) caddisflies and Chironomidae larvae (60% higher) dominated beaver ponds.

Lentic/Lotic Classification

Density

The density of lotic taxa was 83% higher in lotic reaches ($F_{1, 23} = 23.664$, $p < 0.001$; Figure 3a), though overall model significance was driven by differences solely at Right Hand Fork (Tukey's HSD, $p < 0.001$). The density of lentic taxa was 72% higher in beaver ponds ($F_{1, 23} = 16.728$, $p < 0.001$), though was only different in Spawn Creek (Tukey's HSD, $p < 0.001$) and Temple Fork (Tukey's HSD, $p < 0.001$). Lastly, the density of taxa classified as both lentic and lotic did not differ between beaver ponds and lotic reaches at any stream.

Biomass

The biomass of lotic taxa was 94% higher in lotic reaches ($F_{1, 23} = 43.764$, $p < 0.001$; Figure 3b), but overall model significance was driven by differences at Temple Fork (Tukey's HSD, $p < 0.001$) and Right Hand Fork (Tukey's HSD, $p = 0.002$). Lentic taxa biomass was 71% higher in beaver ponds ($F_{1, 23} = 11.045$, $p = 0.003$), however, differences only occurred at Temple Fork (Tukey's HSD, $p = 0.001$). Biomass of taxa classified as both lentic and lotic was 82% higher in lotic reaches ($F_{1, 23} = 6.652$, $p = 0.017$) overall, but was driven by differences only at Right Hand Fork (Tukey's HSD, $p < 0.001$).

EPT

Density

The quantity of EPT taxa differed between beaver ponds and lotic reaches. EPT density was 98% higher in lotic reaches than in beaver ponds ($F_{1, 23} = 56.845$, $p < 0.001$; Figure 3c), and the pattern was significant at all streams. Within EPT, Ephemeroptera density was 99% higher in lotic reaches ($F_{1, 23} = 18.964$, $p < 0.001$; Figure 3c), and was significant at all streams. Plecoptera density was 96% higher in lotic reaches ($F_{1, 23} = 21.870$, $p < 0.001$), but overall model significance was driven by large differences at Right Hand Fork (Tukey's HSD, $p < 0.001$). Similarly, Trichoptera density was 89% higher in lotic reaches ($F_{1, 23} = 53.740$, $p < 0.001$), but the pattern was driven by large differences only between beaver ponds and lotic reaches at Temple Fork (Tukey's HSD, $p < 0.001$).

Biomass

The biomass of EPT also differed between beaver ponds and lotic reaches. Overall, EPT biomass was 95% higher in lotic reaches ($F_{1, 23} = 16.621$, $p < 0.001$; Figure 3d), though this result was driven by differences at Right Hand Fork (Tukey's HSD, $p <0.001$) and Temple Fork (Tukey's HSD, $p < 0.001$). EPT density was not different between beaver ponds and lotic reaches at Spawn Creek. Within EPT, Ephemeroptera biomass was 98% higher in lotic reaches ($F_{1, 23} = 49.414$, $p < 0.001$; Figure 3d), but was not significantly different at Spawn Creek. Plecoptera biomass was 99% higher in lotic reaches ($F_{1, 23} = 14.472$, $p < 0.001$), but overall model significance was driven by differences at Right Hand Fork only (Tukey's HSD, $p < 0.001$). Finally, Trichoptera biomass was 91% higher in lotic reaches ($F_{1, 23} = 40.062$, $p < 0.001$), but differences only occurred between beaver ponds and lotic reaches at Temple Fork (Tukey's HSD, $p < 0.001$).

Functional Feeding Groups

When testing for differences in density between each individual feeding type (engulfer, filterer, gatherer, piercer, scraper, shredder), we found that only some feeding groups were different between beaver ponds and lotic reaches, and some only at certain streams. Significant types are reported below, while all results are included in the supplementary materials (Table S2).

Density

The overall composition of FFGs (i.e. the FFGs present and their densities) was different between beaver ponds and lotic reaches ($F_{1, 23} = 5.217$, $p = 0.003$, Figure 4a). According to 'simper,' these differences were driven by gatherers and scrapers in lotic reaches. Using mixed effects models and ANOVAs, FFGs with different densities between beaver ponds and lotic reaches are as follows. Filterer density was 74% higher in lotic reaches compared to beaver ponds at all streams ($F_{1, 23} = 5.289$, $p = 0.031$). Gatherer densities were also higher in lotic reaches ($F_{1, 23} = 10.876$, $p = 0.003$) by 75%, though this pattern was driven by differences only at Right Hand Fork (Tukey's HSD, $p < 0.001$). Shredder density was 83% higher in lotic reaches ($F_{1, 23} = 7.972$, $p = 0.010$), but only significantly differed at Right Hand Fork (Tukey's HSD, $p < 0.001$). Scraper density was 90% higher in lotic reaches ($F_{1, 23} = 61.180$, $p < 0.001$), and was driven by differences at Temple Fork (Tukey's HSD, $p < 0.001$) and Right Hand Fork (Tukey's HSD, $p < 0.001$); scraper density was not different between beaver ponds and lotic reaches at Spawn Creek.

Biomass

The composition of FFGs based on biomass (i.e. the FFGs present and their respective biomasses) was also different between beaver ponds and lotic reaches (habitat: $F_{1, 23} = 12.488$, p

< 0.001, Figure 4b), 'Simper' outputs attributed this difference to scrapers and gatherers. FFGs with significantly different biomass between beaver ponds and lotic reaches are as follows. Engulfers were 91% higher in beaver ponds ($F_{1, 23} = 8.733$, $p = 0.007$), but this trend was driven by differences at Right Hand Fork only (Tukey's HSD, $p < 0.001$). Filterers were 99% higher in lotic reaches ($F_{1, 23} = 17.378$, $p < 0.001$), with the trend holding at all streams. Gatherer biomass was 82% higher in lotic reaches ($F_{1, 23} = 23.496$, $p < 0.001$), once again driven by differences only at Right Hand Fork (Tukey's HSD, $p < 0.001$). Scraper biomass was almost 100% higher in lotic reaches ($F_{1, 23} = 87.562$, $p < 0.001$), and was driven by differences at both Temple Fork (Tukey's HSD, $p < 0.001$) and Right Hand Fork (Tukey's HSD, $p = 0.038$); scraper biomass was not different between beaver ponds and lotic reaches at Spawn Creek.

Mobility Groups

When testing for differences in density between each individual mobility group (burrower, climber, clinger, skater, sprawler, swimmer) using mixed effects models, only some groups were significantly different between beaver ponds and lotic reaches, and some only at certain streams. Significant types are reported here, while all results can be seen in the supplementary materials (Table S2).

Density

The composition of MGs (i.e. the MGs present and their densities) was different between beaver ponds and lotic reaches ($F_{1, 23} = 11.669$, $p < 0.001$, Figure 4c). 'Simper' outputs determined that this was due to clingers, burrowers, and swimmers. Using mixed effects models and ANOVAs, MGs with significantly different densities between beaver ponds and lotic reaches are as follows. Clingers were 95% higher in lotic reaches ($F_{1, 23} = 105.844$, $p < 0.001$), and differences occurred at all streams. Sprawler density was 74% higher in beaver ponds ($F_{1, 23} = 15.342$, $p < 0.001$), though overall model significance was driven by differences at Right Hand Fork (Tukey's HSD, $p < 0.001$) and Temple Fork (Tukey's HSD, $p = 0.020$); sprawler density was not significantly different between beaver ponds and lotic reaches at Spawn Creek. Swimmer density was 96% higher in lotic reaches ($F_{1, 23} = 29.194$, $p < 0.001$), and differences occurred at all streams.

Biomass

Similar to our density results, we found that the composition of MGs using biomass (i.e. the MGs present and their biomasses) was also significantly affected by habitat type (habitat: $F_{1, 23} = 18.423$, $p < 0.001$, Figure 4d). According to 'simper' outputs, clingers and swimmers drove this pattern. Using mixed effects models and ANOVAs, MGs with significantly different biomass between beaver ponds and lotic reaches are as follows. Clingers were almost 100% higher in lotic reaches ($F_{1, 23} = 197.860$, $p < 0.001$), and differed at all streams. Swimmer density was 87% higher in lotic reaches ($F_{1, 23} = 13.357$, $p = 0.001$), and was significant in all streams.

DISCUSSION

Our results demonstrate that the macroinvertebrate community of beaver ponds is significantly different from that of lotic reaches. Overall, we observed that beaver ponds had lower species richness, biomass, and density of macroinvertebrates compared to lotic reaches, though biomass and density were not always significantly different between habitats at each stream. Our study also demonstrated that the community composition, dominant functional feeding groups, and dominant mobility groups differed between beaver ponds and lotic reaches. However, whether the trends were expressed in terms of macroinvertebrate biomass or density varied among streams. Overall, our results suggest that beavers, and their effects on habitat through the building of dams, restructure macroinvertebrate communities but exactly how this restructuring is manifested differs among streams. Context-dependent differences in the effects of beaver dams on macroinvertebrate communities may influence the results of stream restoration using beaver. As a result, to help better inform beaver restoration future studies should examine the mechanisms behind beaver-mediated effects on macroinvertebrates.

Biomass and Density

Our study found mixed results for the effects of beaver ponds on both density and biomass. In terms of density, only Right Hand Fork showed a statistically significant difference between beaver ponds and lotic reaches. However, the overall trend for all three streams was a higher average density in lotic reaches compared to beaver ponds. Past studies on the effects of beavers on the density of macroinvertebrates have also found mixed results, with some studies reporting an increase in ponds and others a decrease (Rupp, 1955; Huey & Wolfrum, 1956; Gard, 1961; McDowell & Naiman, 1986; Rolauffs *et al.*, 2001; Anderson & Rosemond, 2010; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016; Strzelec *et al.*, 2018). In terms of macroinvertebrate biomass, we found that all three streams had an average higher biomass in lotic reaches compared to beaver ponds, although this was not statistically significant in Spawn Creek. These results differ from past studies which found that beaver ponds generally had higher biomass of macroinvertebrates compared to lotic reaches (Gard, 1961; McDowell & Naiman, 1986; Anderson & Rosemond, 2010), or showed no difference in biomass (Rolauffs *et al.*, 2001). Our results for biomass are, however, congruent with studies that compared natural pools with lotic reaches (Logan & Brooker, 1983; Herbst *et al.*, 2018).

In our stream systems, fine sediments in beaver ponds may preclude the colonization of many stream invertebrates, as interstitial spaces are less available (Bo *et al.*, 2007; Strzelec *et al.*, 2018) and oxygen concentrations may be lower (Wood & Armitage, 1997). We found that on average sediment size was 17-23 times larger in lotic reaches than in ponds (Table 1). The significantly smaller sediment size in ponds may select for smaller individuals that inherently weigh less, reducing overall biomass in beaver ponds. Additionally, the diversity of gravel sizes in ponds is low, which may constrain the number of niches available to colonizing macroinvertebrates. This idea is further supported by the fact that we saw 25% fewer genera/families of macroinvertebrates in beaver ponds compared to streams, a finding that was also documented in Polish streams recolonized by Eurasian beaver (Strzelec *et al.*, 2018). When the surface area of our lotic zones were compared with the surface areas of our beaver ponds, we found no significant difference (Table 1). This data suggests that for the areas we sampled the total abundance and biomass of macroinvertebrates is not likely to greater in beaver ponds. However, in some systems, large beaver ponds may add significantly to stream surface area and macroinvertebrate habitat. If the added area of the ponds is greater than the difference in biomass or densities, than ponds may contain a higher absolute abundance or biomass of macroinvertebrates than lotic systems. However, considering that macroinvertebrates are a major food source for fish, lower densities and biomass of macroinvertebrates per unit area combined with a larger search area in ponds may mean that these pond habitats are poor foraging ground for fish. To date, however, few studies have looked at whether fish are using pond habitats for foraging.

Lentic/Lotic Classification

Beaver pond taxa were different from lotic reach taxa in their habitat classifications using both biomass and density. Organisms in beaver ponds were decidedly lentic, while the lotic reach taxa were lotic. This is not surprising due to the differences in habitat structure and flow characteristics. However, beaver ponds did not include some of the more common taxa associated with completely lentic habitats (e.g., lakes and ponds). Very few Hemipterans were found in beaver ponds, and Odonates were completely absent. Beaver ponds were also devoid of other wetland taxa such as *Callibaetis*, Megalopterans, and Isopods. This was despite the fact that potential source wetlands are common in the Cache National Forest.

Functional Feeding Group Differences

Beaver ponds differed from lotic reaches for several FFGs, although which FFG contributed to the differences varied between biomass and density. First, beaver ponds contained less biomass and density of scrapers, which primarily feed on periphyton. The same trends were observed in many other studies (McDowell & Naiman, 1986; Hering *et al.*, 2001; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012).While the fine sediments of beaver ponds can support periphyton (Coleman & Dahm, 1990), fine grains are likely to be too small for scraping taxa to manipulate. Thus, scraper colonization in beaver ponds is likely to be low.

Second, beaver ponds also contained fewer filter-feeding taxa than lotic reaches. These results are supported by the majority of existing literature on beaver pond macroinvertebrates (Margolis, Raesly & Shumway, 2001; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). We hypothesize that the higher density and biomass of filterers in lotic reaches in our study may stem from faster water velocity that increases suspended food particles (Wallace, Webster & Meyer, 1995). Lotic reaches in our study had water velocities 2.5-17 times faster than in ponds.

Third, beaver ponds largely did not contain more predators compared to lotic reaches; only Right Hand Fork demonstrated higher engulfer biomass in beaver ponds than lotic reaches. Higher prevalence of predators in beaver ponds compared to lotic reaches is noted within past studies from all beaver-occupied continents (McDowell & Naiman, 1986; Harthun, 1999; Anderson & Rosemond, 2007; Arndt & Domdei, 2011; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). Although the mechanism behind a dominance of predators in beaver ponds is unknown, it is speculated that the physical environment of ponds may be beneficial to predators. Specifically, slower water velocity and finer sediments with little interstitial space may help predators capture prey that drift into the pond from upstream sections or fall into the pond from the riparian zone. It is unclear why our results for predator taxa are not congruent with other studies. However, as our ponds were relatively young (less than 6 years old), larger-bodied predatory taxa with more complex life cycles may not have been able to establish stable populations (Mackay, 1992). Future studies should investigate the effect of pond age on macroinvertebrate communities.

Fourth, shredders were also more prominent in beaver ponds in terms of density, but not biomass. The large amount of organic matter such as terrestrial leaves that become trapped behind beaver ponds may help support high densities of detritivorous macroinvertebrates (Hodkinson, 1975; Butler & Malanson, 1995). Though the trend was only significant at one stream, it was the stream with the greatest canopy cover (personal observation). Higher densities of shredders in ponds may suggest that these habitats are hotspots for allochthonous organic matter processing.

Finally, lotic reaches had higher density and biomass of gatherers. This trend was the opposite of previous work, which noted increased gatherer importance within beaver ponds (McDowell & Naiman, 1986; Hering *et al.*, 2001; Anderson & Rosemond, 2007; Pliūraitė & Kesminas, 2012; Law *et al.*, 2016). Higher gatherer density in lotic reaches may reflect a difference in the type of organic matter trapped by different substrate sizes within stream habitats in northern Utah. FFG and resource acquisition are traits that have been found to be highly associated with ecosystem functioning (Wallace & Webster, 1996). Differences between lotic reaches and beaver ponds in the dominance of FFGs found in our study suggests that these two habitats may function differently, especially in terms of organic matter processing.

Mobility Group Differences

Beaver ponds also differed from lotic reaches for several MGs. Beaver ponds contained higher densities and biomass of burrowers, which are known to inhabit fine sediment (Rabení *et al.*, 2005). Sprawlers were also more prevalent in beaver ponds by density. Sprawlers are associated with fine sediment and litter (Johnson, Breneman & Richards, 2003; Gillies, Hose & Turak, 2009), and may move and forage well in small interstitial spaces (Richards *et al.*, 1997), making sprawlers well-adapted for inhabiting the fine sediments and organic matter within beaver ponds. Conversely, lotic reaches contained higher densities and biomass of clingers. Clingers are adapted to withstand flowing water in erosional areas, and heavily rely on interstitial spaces for refuge (Johnson *et al.*, 2003; Rabení *et al.*, 2005). The low quantity of gravel substrate for both clinging and hiding within beaver ponds in our study system likely made clinging taxa ill-equipped to tolerate ponded conditions.

Surprisingly, swimmer density was higher in lotic reaches than in beaver ponds. This pattern was likely driven by the dominance of *Baetis* in lotic reaches. *Baetis* on average accounted for 98% and 95% of swimmers in lotic reaches by density and biomass respectively, with the remainder of the swimmers in lotic reaches represented by only three other taxa. Contrarily, there were at least eight types of swimming taxa in beaver ponds (small Dytiscidae larvae were only identified to family, therefore likely underestimated), and *Baetis* accounted for only 38% of beaver pond swimmers by density, and 46% of swimmers by biomass. Although a beaver pond may be more conducive to swimming taxa due to the low water velocity and increased depth, *Baetis* may simply be well adapted to swimming through more turbulent conditions, allowing them to be abundant in lotic reaches. Differences in MGs likely indicate differences in structural resource types within ponds (Heino, 2005), which can demonstrate habitat heterogeneity for the streams that contain beaver ponds (Pringle *et al.*, 1988; Rolauffs *et al.*, 2001; Bush & Wissinger, 2016; Law *et al.*, 2016).

Conclusion

Results from our study suggest that the addition of lentic habitat to stream systems can negatively influence macroinvertebrate biomass and density per unit area, and change community composition and functional traits of macroinvertebrates. Such changes to the community composition suggest that beaver ponds may function differently than non-ponded segments, and that streams containing beaver may function differently than those without. Changes in the quantity of macroinvertebrates can further alter ecosystem functions in ecosystems that receive subsidies from streams, such as emerging adult insects to riparian species (Marcarelli *et al.*, 2011). Understanding how beaver ponds affect macroinvertebrate communities is important to gauging changes to the system instigated by beavers.

Although ponds contained lower species richness compared to lotic reaches, overall stream diversity may have been increased by beaver ponds considering the Dytiscid beetles, *Siphlonurus* mayflies, *Psychoglypha* caddisflies, and other taxa not recorded in lotic reaches. However, studies have suggested that beaver ponds do not increase species diversity, but rather increase habitat availability for lentic species already occurring in natural pools (Anderson *et al.*, 2014). Regardless, the beaver ponds in these streams contained taxa not found in lotic reaches.

To fully understand the effects of beaver ponds on overall stream biodiversity, future studies should sample across a diversity of habitats, including natural pools. Understanding the effects of beavers on macroinvertebrates is important for predicting changes in stream communities and ecosystem functions as a result of the rewilding of beavers in North America. Results from our study suggests that the macroinvertebrate communities can drastically change as a result of beaver pond construction, and such changes may have consequences for fish and other macroinvertebrate predators, as well as ecosystem functioning.

Acknowledgments

We extend our thanks to Dylan Anderson and Rachel Chamberlain for fieldwork assistance, and to Audree Provard and Colten Elkin for laboratory sample processing assistance. This project was funded by a USDA Forest Service grant (#16-CS-11132422-318) to TBA, and an Ecology Center grant and National Science Foundation Graduate Research Fellowship to SW.

Conflict of Interest

We claim no conflict of interest.

Data Availability Statement

Data available on request from the authors.

References

Anderson C.B. & Rosemond A.D. (2010) Beaver invasion alters terrestrial subsidies to subantarctic stream food webs. *Hydrobiologia* **652**, 349–361.

Anderson C.B. & Rosemond A.D. (2007) Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia* **154**, 141–153.

Anderson C.B., Vanessa Lencinas M., Wallem P.K., Valenzuela A.E.J., Simanonok M.P. & Martínez Pastur G. (2014) Engineering by an invasive species alters landscape-level ecosystem function, but does not affect biodiversity in freshwater systems. *Diversity and Distributions* **20**, 214–222.

Arndt E. & Domdei J. (2011) Influence of beaver ponds on the macroinvertebrate benthic community in lowland brooks. *Polish Journal of Ecology* **59**, 799–811.

Atwood T.B., Hammill E. & Richardson J.S. (2014) Trophic-level dependent effects on CO2 emissions from experimental stream ecosystems. *Global Change Biology* **20**, 3386–3396.

Bailey R.C., Norris R.H. & Reynoldson T.B. (2001) Taxonomic resolution of benthic macroinvertebrate communities in bioassessments. *Journal of the North American Benthological Society* **20**, 280–286.

Baker B.W. & Hill E.P. (2003) Beaver (Castor canadensis). In: *Wild Mammals of North America: Biology, Management, and Conservation*, Second Edi. (Eds G.A. Feldhamer, B.C. Thompson & J.A. Chapman), pp. 288–310. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Bo T., Fenoglio S., Malacarne G., Pessino M. & Sgariboldi F. (2007) Effects of clogging on stream macroinvertebrates: An experimental approach. *Limnologica* **37**, 186–192.

Bush B.M. & Wissinger S.A. (2016) Invertebrates in Beaver-Created Wetlands and Ponds. pp. 411–449. Springer International Publishing.

Butler D.R. & Malanson G.P. (1995) Sedimentation rates and patterns in beaver ponds in a mountain environment. *Geomorphology* **13**, 255–269.

Cirmo C.P. & Driscoll C.T. (1993) Beaver pond biogeochemistry: Acid neutralizing capacity generation in a headwater wetland. *Wetlands* **13**, 277–292.

Clifford H.F., Wiley G.M. & Casey R.J. (1993) Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. *Canadian Journal of Zoology* **71**, 1439–1447.

Coleman R.L. & Dahm C.N. (1990) Stream geomorphology: Effects on periphyton standing crop and primary production. *Journal of the North American Benthological Society* **9**, 293–302.

Correll D.L., Jordan T.E. & Weller D.E. (2000) Beaver pond biogeochemical effects in the Maryland Coastal Plain. *Biogeochemistry* **49**, 217–239.

Fuller M.R. & Peckarsky B.L. (2011a) Does the morphology of beaver ponds alter downstream ecosystems? *Hydrobiologia* **668**, 35–48.

Fuller M.R. & Peckarsky B.L. (2011b) Ecosystem engineering by beavers affects mayfly life histories. *Freshwater Biology* **56**, 969–979.

Gard R. (1961) Effects of beaver on trout in Sagehen Creek, California. *The Journal of Wildlife Management* **25**, 221–242.

Gibson P.P. & Olden J.D. (2014) Ecology, management, and conservation implications of North American beaver (Castor canadensis) in dryland streams. *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**, 391–409.

Gillies C.L., Hose G.C. & Turak E. (2009) What do qualitative rapid assessment collections of macroinvertebrates represent? A comparison with extensive quantitative sampling. *Environmental Monitoring and Assessment* **149**, 99–112.

Gurnell A.M. (1998) The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography* **22**, 167–189.

Harthun M. (1999) The infuence of the European beaver (Castor fiber albicus) on the biodiversity (Odonata, Mollusca, Trichoptera, Ephemeroptera, Diptera) of brooks in Hesse (Germany). *Limnologica* **29**, 449–464.

Heino J. (2005) Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. *Freshwater Biology* **50**, 1578–1587.

Herbst D.B., Cooper S.D., Medhurst R.B., Wiseman S.W. & Hunsaker C.T. (2018) A comparison of the taxonomic and trait structure of macroinvertebrate communities between the riffles and pools of montane headwater streams. *Hydrobiologia* **820**, 115–133.

Hering D., Gerhard M., Kiel E., Ehlert T. & Pottgiesser T. (2001) Review study on near-natural conditions of Central European mountain streams, with particular reference to debris and beaver dams: Results of the “REG meeting” 2000. *Limnologica - Ecology and Management* *of Inland Waters* **31**, 81–92.

Hodkinson I.D. (1975) Dry weight loss and chemical changes in vascular plant litter of terrestrial origin, occurring in a beaver pond ecosystem. *Journal of Ecology* **63**, 131–142.

Huey W.S. & Wolfrum W.H. (1956) Beaver-trout relations in New Mexico. *The Progressive Fish-Culturist* **18**, 70–74.

Johnson L.B., Breneman D.H. & Richards C. (2003) Macroinvertebrate community structure and function associated with large wood in low gradient streams. *River Research and Applications* **19**, 199–218.

Kwick J.K. & Carter J.C.H. (1975) Population dynamics of limnetic cladocera in a beaver pond. *Journal of the Fisheries Research Board of Canada* **32**, 341–346.

Lancaster J. & Hildrew A.G. (1993) Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society* **12**, 385–393.

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

Law A., Mclean F. & Willby N.J. (2016) Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshwater Biology* **61**, 486–499.

Lazar J.G., Addy K., Gold A.J., Groffman P.M., McKinney R.A. & Kellogg D.Q. (2015) Beaver ponds: Resurgent nitrogen sinks for rural watersheds in the northeastern United States. *Journal of Environment Quality* **44**, 1684–1693.

Lecerf A. & Richardson J.S. (2011) Assessing the functional importance of large-bodied invertebrates in experimental headwater streams. *Oikos* **120**, 950–960.

Levine R. & Meyer G.A. (2014) Beaver dams and channel sediment dynamics on Odell Creek, Centennial Valley, Montana, USA. *Geomorphology* **205**, 51–64.

Logan P. & Brooker M.P. (1983) The macroinvertebrate faunas of riffles and pools. *Water Research* **17**, 263–270.

Mackay R.J. (1992) Colonization by lotic macroinvertebrates: A review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 617–628.

Malison R.L., Lorang M.S., Whited D.C. & Stanford J.A. (2014) Beavers (Castor canadensis) influence habitat for juvenile salmon in a large Alaskan river floodplain. *Freshwater Biology* **59**, 1229–1246.

Marcarelli A.M., Baxter C. V., Mineau M.M. & Hall R.O.J. (2011) Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* **92**, 1215–1225.

Margolis B.E., Raesly R.L. & Shumway D.L. (2001) The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. **21**, 554–563.

Martin J.C. & Knight A.W. (1989) The effect of long pools on the drift of macro-invertebrates in a mountain stream. *Hydrobiologia* **185**, 63–70.

McDowell D.M. & Naiman R.J. (1986) Structure and function of a benthic invertebrate stream community as influenced by beaver (Castor canadensis). *Oecologia* **68**, 481–489.

Meredith C.S., Budy P. & Thiede G.P. (2015) Predation on native sculpin by exotic brown trout exceeds that by native cutthroat trout within a mountain watershed (Logan, UT, USA). *Ecology of Freshwater Fish* **24**, 133–147.

Merritt R.W., Cummins K.W. & Berg M.B. (2008) *An introduction to the aquatic insects of North America*, 4th edn. Kendall Hunt Publishing, Dubuque, Iowa, USA.

Muzaffar S.B. & Colbo M.H. (2002) The effects of sampling technique on the ecological characterization of shallow, benthic macroinvertebrate communities in two Newfoundland ponds. *Hydrobiologia* **477**, 31–39.

Naiman R.J., Melillo J.M. & Hobbie J.E. (1986) Ecosystem alteration of boreal forest streams by beaver (Castor canadensis). *Ecology* **67**, 1254–1269.

Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlinn D., *et al.* (2017) vegan: Community Ecology Package.

Pilliod D.S., Rohde A.T., Charnley S., Davee R.R., Dunham J.B., Gosnell H., *et al.* (2018) Survey of beaver-related restoration practices in rangeland streams of the western USA. *Environmental Management* **61**, 58–68.

Pinheiro J., Bates D., DebRoy S., Sarkar D. & R Core Team (2018) nlme: Linear and nonlinear mixed effects models.

Pliūraitė V. & Kesminas V. (2012) Ecological impact of Eurasian beaver (*Castor fiber*) activity on macroinvertebrate communities in Lithuanian trout streams. *Central European Journal of Biology* **7**, 101–114.

Pollock M.M., Beechie T.J., Wheaton J.M., Jordan C.E., Bouwes N., Weber N., *et al.* (2014) Using beaver dams to restore incised stream ecosystems. *BioScience* **64**, 279–290.

Pringle C.M., Naiman R.J., Bretschko G., Karr J.R., Oswood M.W., Webster J.R., *et al.* (1988) Patch dynamics in lotic systems: The stream as a mosaic. *Journal of the North American Benthological Society* **7**, 503–524.

R Core Team (2017) R: A language and environment for statistical computing.

Rabení C.F., Doisy K.E. & Zweig L.D. (2005) Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences* **67**, 395–402.

Richards C., Haro R.J., Johnson L.B. & Host G.E. (1997) Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology* **37**, 219–230.

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

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

Rupp R.S. (1955) Beaver-trout relationship in the headwaters of Sunkhaze Stream, Maine. *Transactions of the American Fisheries Society* **84**, 75–85.

Sarnelle O., Cooper S.D., Wiseman S. & Mavuti K.M. (1998) The relationship between nutrients and trophic-level biomass in turbid tropical ponds. *Freshwater Biology* **40**, 65–75.

Small B.A., Frey J.K. & Gard C.C. (2016) Livestock grazing limits beaver restoration in northern New Mexico. *Restoration Ecology* **24**, 646–655.

Smith M.E., Driscoll C.T., Wyskowski B.J. & Brooks C.M. (1991) Modification of stream ecosystem structure and function by beaver (Castor canadensis) in the Adirondack Mountains, New York. *Canadian Journal of Zoology* **69**, 55–61.

Stout T.L., Majerova M. & Neilson B.T. (2017) Impacts of beaver dams on channel hydraulics and substrate characteristics in a mountain stream. *Ecohydrology* **10**, 1–13.

Strzelec M., Białek K. & Spyra A. (2018) Activity of beavers as an ecological factor that affects the benthos of small rivers - a case study in the Żylica River (Poland). *Biologia* **73**, 577–588.

Thorp J.H. & Covich A.P. (2001) *Ecology and Classification of North American Freshwater Invertebrates*, 2nd edn. (Eds J.H. Thorp & A.P. Covich), Academic Press, San Diego, CA.

Vehkaoja M., Nummi P., Rask M., Tulonen T. & Arvola L. (2015) Spatiotemporal dynamics of boreal landscapes with ecosystem engineers: beavers influence the biogeochemistry of small lakes. *Biogeochemistry* **124**, 405–415.

Wallace J.B. & Webster J.R. (1996) The Role of Macroinvertebrates in Stream Ecosystem Function. *Annual Review of Entomology* **41**, 115–139.

Wallace J.B., Webster J.R. & Meyer J.L. (1995) Influence of log additions on physical and biotic characteristics of a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2120–2137.

Westbrook C.J., Cooper D.J. & Baker B.W. (2006) Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. *Water Resources Research* **42**, W06404.

Wheaton J.M., Fryirs K.A., Brierley G., Bangen S.G., Bouwes N. & O'Brien G. (2015) Geomorphic mapping and taxonomy of fluvial landforms. *Geomorphology* **248**, 273–295.

Wissinger S.A., Perchik M.E. & Klemmer A.J. (2018) Role of animal detritivores in the breakdown of emergent plant detritus in temporary ponds. *Freshwater Science* **37**, 826–835.

Wohl E. (2013) Landscape-scale carbon storage associated with beaver dams. *Geophysical Research Letters* **40**, 3631–3636.

Wolman M.G. (1954) A method of sampling coarse river-bed material. *Transactions - American Geophysical Union* **35**, 951–956.

Wood P.J. & Armitage P.D. (1997) Biological effects of fine sediment in the lotic environment. *Environmental Management* **21**, 203–217.

Woods A.J., Lammers D.A., Bryce S.A., Omernik J.M., Denton R.L., Domeier M., *et al.* (2001) *Ecoregions of Utah (color poster with map, descriptive text, summary tables, and photographs)*. Reston, Virgnia, USA.

Table 1. Environmental characteristics of streams and habitats sampled for summer 2017 (mean ± standard error). Replicates were for the whole stream, not within each pond/reach.

	Right Hand Fork		**Spawn Creek**		**Temple Fork**	
Environment	*Lotic reaches*	*Beaver Ponds*	*Lotic reaches*	*Beaver Ponds*	*Lotic reaches*	*Beaver Ponds*
Elevation (m)	1710 ± 3	1709 ± 3	1883 ± 5	1883 ± 5	1871 ± 8	1870 ± 8
Temperature (°C)	8.34 ± 0.39	8.66 ± 0.50	6.21 ± 0.26	6.21 ± 0.27	5.33 ± 0.09	5.40 ± 0.08
DO (mg/L)	9.00 ± 0.16	8.83 ± 0.32	9.70 ± 0.08	9.70 ± 0.05	10.04 ± 0.04	9.89 ± 0.02
Flow (m/s)	0.28 ± 0.05	0.11 ± 0.04	0.24 ± 0.04	0.06 ± 0.01	0.34 ± 0.06	0.02 ± 0.01
Grain Size (mm)	34.60 ± 9.14	< 2.00 ± 0	41.72 ± 6.99	< 2.00 ± 0	45.52 ± 8.34	< 2.00 ± 0
Depth (cm)	25.1 ± 1.0	35.2 ± 1.0	20.6 ± 10.0	38.0 ± 3.0	30.2 ± 2.0	39.5 ± 4.0
Surface Area (m^2)	89.96 ± 44.3	132.12 ± 74.2	73.08 ± 18.9	115.08 ± 23.9	848.20 ± 456.3	259.17 ± 61.9

Figure Captions

Figure 1. A map of study reaches within Right Hand Fork, Spawn Creek, and Temple Fork. All streams are tributaries to the Logan River, located in the Cache National Forest in northeastern Utah, USA. Blue lines indicate streams and orange lines indicate study reaches within streams.

Figure 2. Differences in community structure measured by density (number of organisms per m^2) and by biomass (grams of organisms per m^2) for lotic reach and beaver pond habitats: a) total macroinvertebrate density by habitat type (beaver ponds or lotic reaches) in each stream, b) total macroinvertebrate biomass within beaver ponds and lotic reaches in each stream c) nonmetric multidimensional scaling (NMDS) plot illustrating how beaver ponds differ from lotic reaches in terms of macroinvertebrate taxa present and their densities (stress 0.15), d) NMDS plot of macroinvertebrate taxa and their biomasses (stress 0.11). Each point represents a lotic reach (triangle) or beaver pond (circle) community for each of the three streams studied (Right Hand Fork (RHF) = grey, Temple Fork (Temple) = black, and Spawn Creek (Spawn) = white). The closer together the symbols are in the NMDS plot, the more similar the community composition. Asterisks above bars represent significantly higher values between the noted bar and its neighboring bar in that stream.

Figure 3. Differences in community composition in terms of macroinvertebrate habitat preference classifications (lentic, lotic, or both) and in terms of quantity of Ephemeroptera, Plecoptera, and Trichoptera (EPT): a) density of macroinvertebrates classified as lentic, lotic, and both in beaver ponds and lotic reaches at each stream, b) biomass of macroinvertebrates classified as lentic, lotic, c) density of EPT taxa in beaver ponds and lotic reaches at each stream, d) biomass of EPT taxa. Asterisks above bars represent significantly higher values between the noted bar and its corresponding bar (the other bar of the same color) in that stream.

Figure 4. Differences in Functional Feeding Groups (FFGs) and Mobility Groups (MGs) of macroinvertebrates between beaver ponds and lotic reaches. Composition differences are measured by comparing functional groups present and their respective biomasses or densities per m^2: a) FFG composition by density (stress 0.20; actual position of points in space may vary as stress is high), b) FFG composition by biomass (stress 0.09), c) MG composition by density (stress 0.17), and d) MG composition by biomass (stress 0.11). Symbols closer together represent more functionally similar communities. Each point represents a lotic reach (triangle) or beaver pond (circle) community for each of the three streams studied (Right Hand Fork (RHF) = grey, Temple Fork (Temple) = black, and Spawn Creek (Spawn) = white).

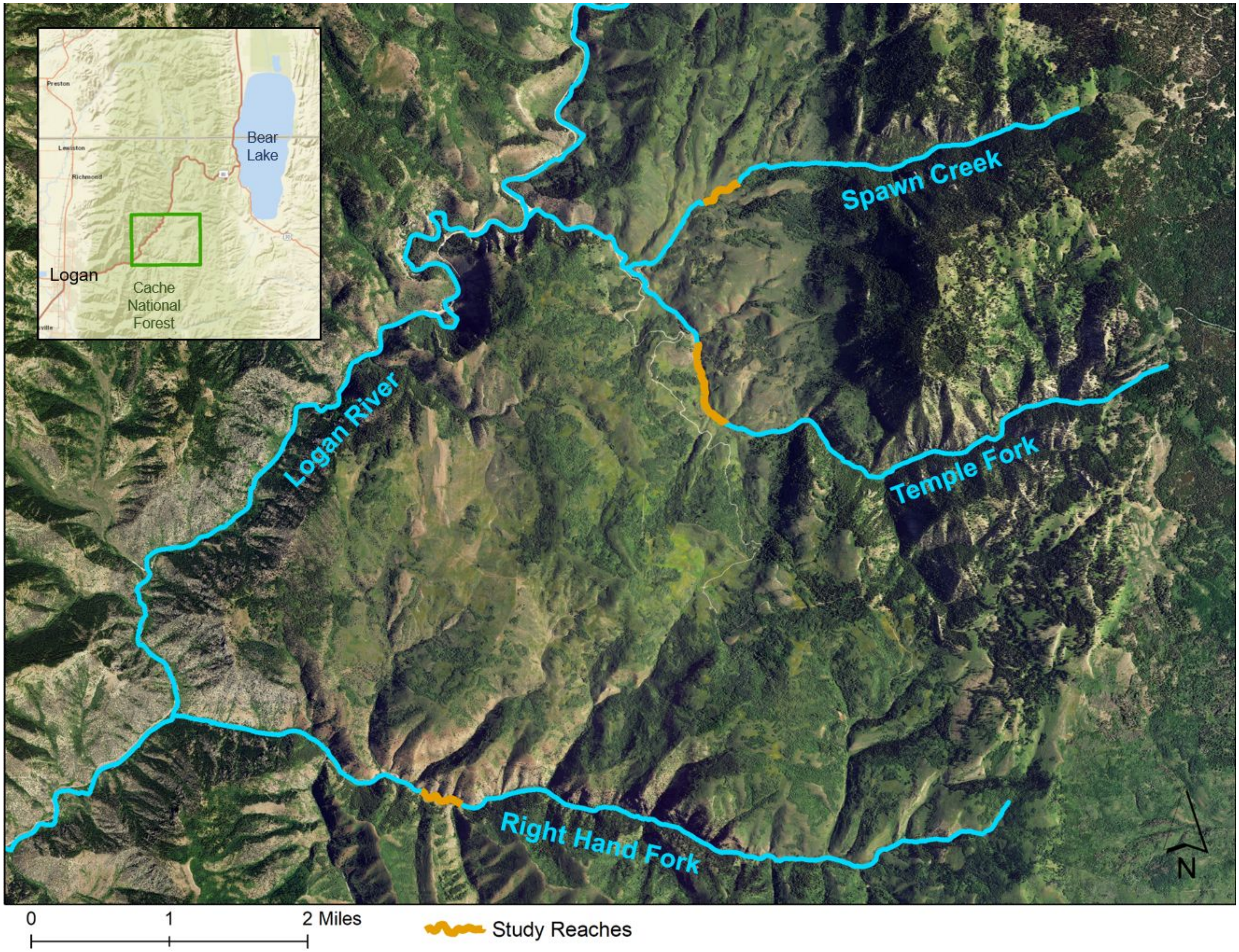
Preston
Lewiston
Richmond
Bear Lake
Logan
Cache National Forest
Logan River
Spawn Creek
Temple Fork
Right Hand Fork
N
0
1
2 Miles
Study Reaches

Figure 1.

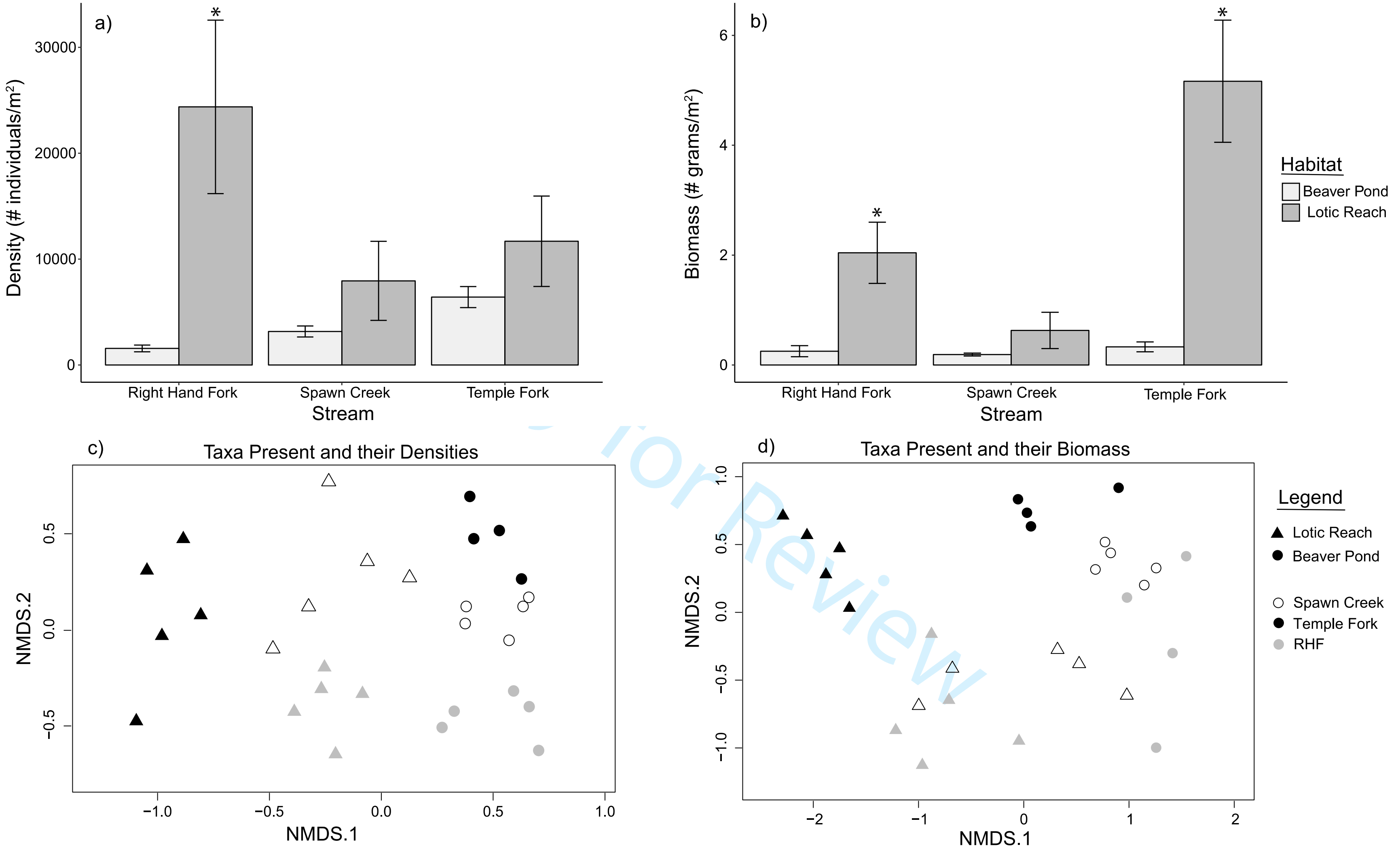
a)
Density (# individuals/m²)
30000
20000
10000
0
*
Right Hand Fork
Spawn Creek
Temple Fork
Stream
b)
Biomass (# grams/m²)
6
4
2
0
*
*
Right Hand Fork
Spawn Creek
Temple Fork
Stream
Habitat
Beaver Pond
Lotic Reach
c)
Taxa Present and their Densities
NMDS.2
0.5
0.0
−0.5
−1.0
−0.5
0.0
0.5
1.0
NMDS.1
d)
Taxa Present and their Biomass
NMDS.2
1.0
0.5
0.0
−0.5
−1.0
−2
−1
0
1
2
NMDS.1
Legend
▲ Lotic Reach
● Beaver Pond
○ Spawn Creek
● Temple Fork
● RHF

Figure 2.

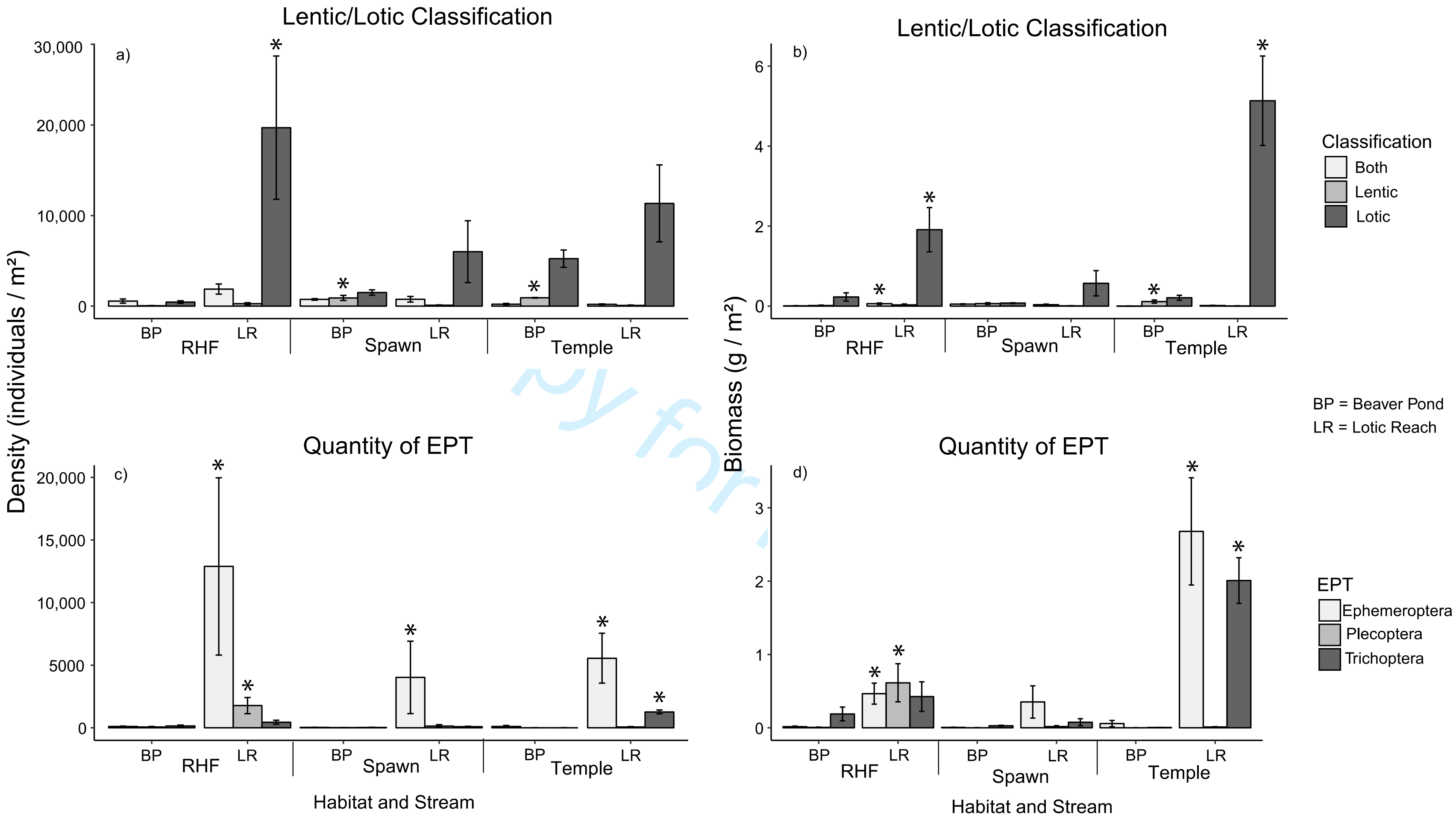
Lentic/Lotic Classification
a)
Density (individuals / m²)
30,000
20,000
10,000
0
*
BP
LR
RHF
Spawn
Temple
Lentic/Lotic Classification
b)
Biomass (g / m²)
6
4
2
0
Classification
Both
Lentic
Lotic
BP = Beaver Pond
LR = Lotic Reach
Quantity of EPT
c)
20,000
15,000
10,000
5000
0
Habitat and Stream
Quantity of EPT
d)
3
2
1
0
EPT
Ephemeroptera
Plecoptera
Trichoptera

Figure 3.

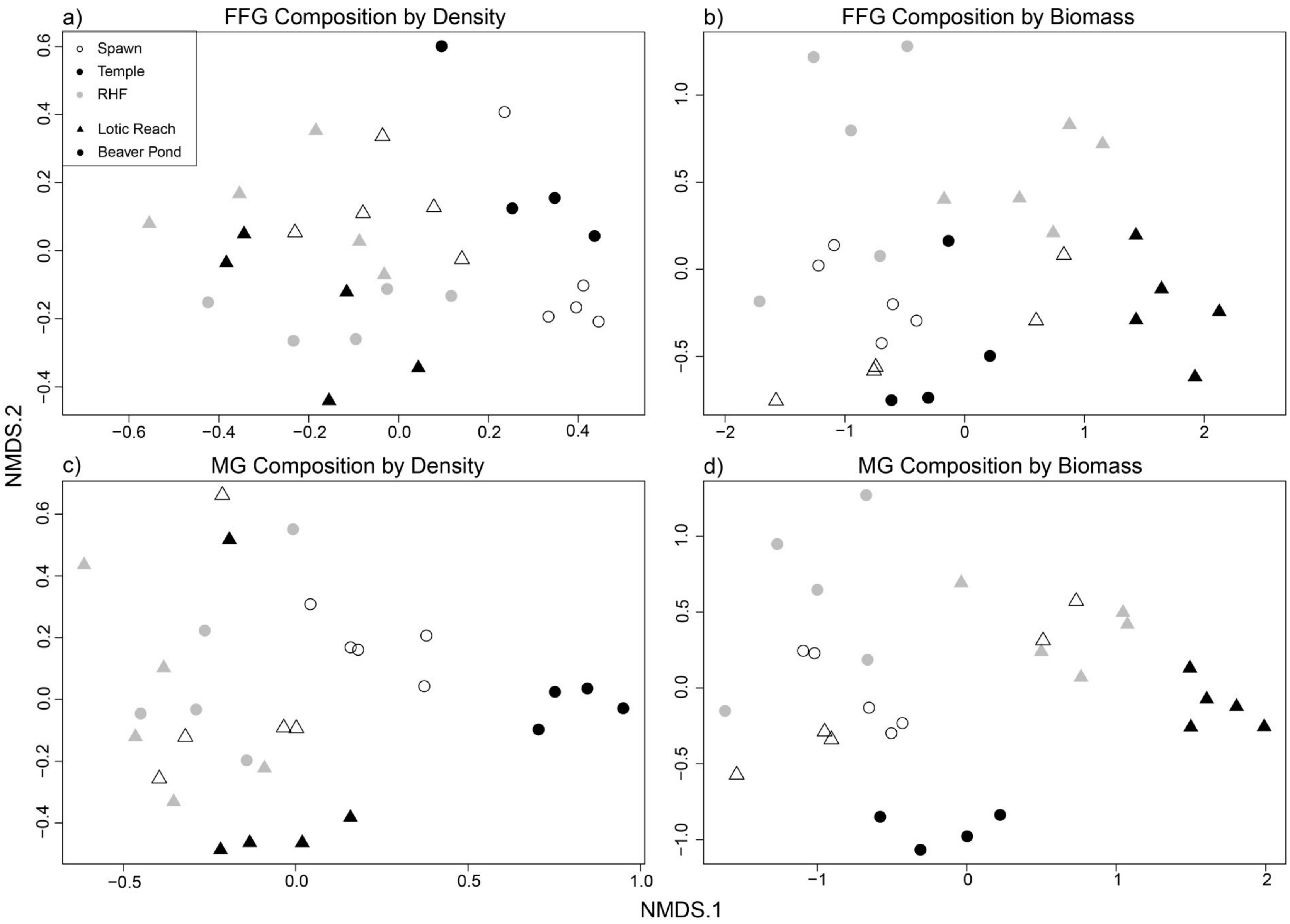
a)
FFG Composition by Density
○ Spawn
● Temple
● RHF
▲ Lotic Reach
● Beaver Pond
b)
FFG Composition by Biomass
c)
MG Composition by Density
d)
MG Composition by Biomass
NMDS.2
NMDS.1
−0.6
−0.4
−0.2
0.0
0.2
0.4
0.6
−2
−1
0
1
2
−0.5
0.5
1.0
−1.0

Figure 4.

Supplementary Items

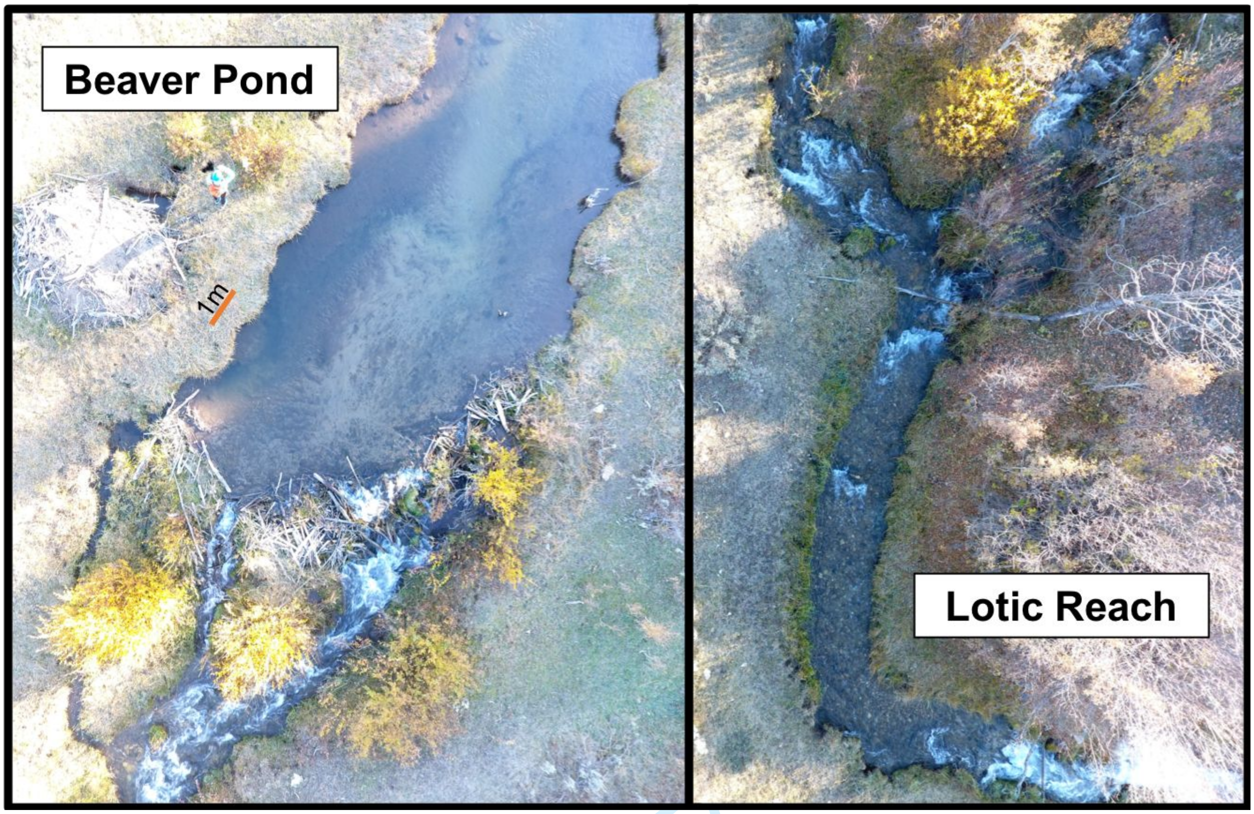

Figure S1. Examples of beaver ponds and lotic reaches used in this study.

Table S1. List of taxa sampled and their Functional Feeding Group (FFG) and Mobility Group (MG) assignments (based on taxa tables in Ode, 2003; Merritt, Cummins & Berg, 2008). Although many macroinvertebrates belong to multiple FFGs, only the first listed was used.

Class/Order	Family	Genus & species (if possible)	FFG	MG
Amphipoda	Hyalellidae	*Hyalella*	shredders	swimmer
Bivalvia	unidentified	*unidentified*	filter	burrower
Coleoptera	Curculionidae	*unidentified*	shredders	clinger
Coleoptera	Dytiscidae	*Oreodytes*	piercer	swimmer
Coleoptera	Dytiscidae	*Stictotarsus larvae*	piercer	swimmer
Coleoptera	Dytiscidae	*Tropisternus larvae*	piercer	swimmer
Coleoptera	Dytiscidae	*unidentified larvae*	piercer	swimmer
Coleoptera	Elmidae	*Cleptelmis adult*	gatherer	clinger
Coleoptera	Elmidae	*Elmidae larvae*	gatherer	clinger
Coleoptera	Elmidae	*Heterlimnius corpulentus adult*	gatherer	clinger
Coleoptera	Elmidae	*Narpusconcolor adult*	gatherer	clinger
Coleoptera	Elmidae	*Optioservus adult*	scraper	clinger

Coleoptera	Gyrinidae	*Gyrinus*	engulfer	swimmer
Coleoptera	Haliplidae	*Ametor*	gatherer	clinger
Coleoptera	Haliplidae	*Haliplidae larvae*	piercer	climber
Coleoptera	Helophoridae	*Helophorus*	shredder	climber
Collembola	unidentified	*unidentified*	gatherer	skater
Diptera	Ceratopogonidae	*Probezzia*	engulfer	burrower
Diptera	Chironomidae	*Chironominae*	gatherer	burrower
Diptera	Chironomidae	*Orthocladiinae*	gatherer	burrower
Diptera	Chironomidae	*Tanypodinae*	engulfer	sprawler
Diptera	Dixidae	*Dixa*	gatherer	swimmer
Diptera	Empididae	*Chelifera*	piercer	sprawler
Diptera	Empididae	*Clinocera*	piercer	clinger
Diptera	Empididae	*Neoplasta*	piercer	sprawler
Diptera	Empididae	*Wiedemannia*	piercer	clinger
Diptera	Limoniidae	*Hesperoconopa*	gatherer	burrower
Diptera	Muscidae	*unidentified*	piercer	sprawler
Diptera	Psychodidae	*Pericoma*	gatherer	burrower
Diptera	Simuliidae	*Simulium*	filter	clinger
Diptera	Simuliidae	*Twinnia*	scraper	clinger
Diptera	Stratiomyidae	*Caloparyphus*	gatherer	sprawler
Diptera	Stratiomyidae	*Stratiomys*	gatherer	sprawler
Diptera	Tabanidae	*unidentified*	piercer	sprawler
Diptera	Tipulidae	*Antocha*	gatherer	clinger
Diptera	Tipulidae	*Dicranota*	engulfer	sprawler
Diptera	Tipulidae	*Tipula*	shredder	burrower
Diptera	unidentified	*unidentified*	gatherer	sprawler
Ephemeroptera	Baetidae	*Baetis*	gatherer	swimmer
Ephemeroptera	Baetidae	*Cinygmula*	scraper	clinger
Ephemeroptera	Baetidae	*Rhithrogena*	scraper	clinger
Ephemeroptera	Baetidae	*Siphlonurus*	gatherer	swimmer
Ephemeroptera	Ephemerellidae	*Drunella coloradensis*	scraper	clinger
Ephemeroptera	Ephemerellidae	*Drunella dodsii*	scraper	clinger
Ephemeroptera	Ephemerellidae	*Drunella grandis*	scraper	clinger
Ephemeroptera	Ephemerellidae	*Ephemerella tibalis*	gatherer	clinger
Ephemeroptera	Ephemerellidae	*Serratella*	gatherer	clinger
Ephemeroptera	Paraleptophlebidae	*Paraleptophlebia*	gatherer	clinger
Gastropoda	unidentified	*unidentified*	scraper	clinger
Hemiptera	Gerridae	*unidentified*	piercer	skater
Oligochaeta	unidentified	*unidentified*	gatherer	burrower
Ostracoda	unidentified	*unidentified*	gatherer	burrower

Plecoptera	Chloroperlidae	*Sweltsa*	engulfer	clinger
Plecoptera	Nemouridae	*Malenka*	shredder	sprawler
Plecoptera	Nemouridae	*Zapada*	shredder	sprawler
Plecoptera	Perlidae	*Hesperoperla pacifica*	engulfer	clinger
Trichoptera	Brachycentridae	*Brachycentrus*	gatherer	clinger
Trichoptera	Brachycentridae	*Micrasema*	shredder	clinger
Trichoptera	Glossosomatidae	*Glossosoma*	scraper	clinger
Trichoptera	Hydropsychidae	*Arctopsyche*	gatherer	clinger
Trichoptera	Hydroptilidae	*Hydroptila*	piercer	clinger
Trichoptera	Lepidostomatidae	*Lepidostoma*	shredder	climber
Trichoptera	Limnephilidae	*Psychoglypha*	shredder	sprawler
Trichoptera	Rhyacophilidae	*Rhyacophila brunnea-vemna*	engulfer	clinger
Trichoptera	Rhyacophilidae	*Rhyacophila hyalinata*	engulfer	clinger
Trichoptera	Rhyacophilidae	*Rhyacophila verrula*	scraper	clinger
Trichoptera	Rhyacophilidae	*Rhyacophila volfixa*	engulfer	clinger
Trichoptera	Uenoidae	*Neothremma*	scraper	clinger
Trichoptera	Uenoidae	*Oligophlebodes*	scraper	clinger
Trombidiformes	Hydrachnidiae	*unidentified*	parasite	sprawler
Turbellaria	unidentified	*unidentified*	engulfer	clinger

Merritt R.W., Cummins K.W. & Berg M.B. (2008) *An introduction to the aquatic insects of North America*, 4th edn. Kendall Hunt Publishing, Dubuque, Iowa, USA.

Ode P. (2003) *List of Californian Macroinvertebrate Taxa and Standard Taxonomic Effort*. Rancho Cordova, CA.

Table S2. All statistical results.

Metric	**Transformation**	**DF**	**Habitat F-Stat, P-value**	**Stream ID F-Stat, P-value**	**Habitat:Stream F-Stat, P-value**	**Tukey comparison for significant Habitat:Stream**
Total Biomass	log	23	34.872, <0.001	9.118, 0.0012	4.804, 0.0181	p < 0.001 at Temple and RHF
Total Density	log	23	15.005, <0.001	2.328, 0.1200	6.405, 0.0062	p < 0.001 at RHF only
Total Richness	NA	23	16.621, 0.0005	2.236, 0.130	0.662, 0.526	
EPT Density	**Transformation**	**DF**	**Habitat F-Stat, P-value**	**Stream ID F-Stat, P-value**	**Habitat:Stream F-Stat, P-value**	**Tukey comparison for significant Habitat:Stream**
total EPT	log	23	56.845, <0.001	4.060, 0.0309	1.499, 0.2443	
Ephemeroptera	sqrt	23	18.964, 0.0002	1.100, 0.3499	0.734, 0.4907	
Plecoptera	sqrt	23	21.870, <0.001	15.487, <0.001	7.204, 0.0037	p < 0.001 at RHF
Trichoptera	sqrt	23	53.740, <0.001	14.442, <0.001	21.309, <0.001	p < 0.001 at Temple
EPT Biomass	**Transformation**	**DF**	**Habitat F-Stat, P-value**	**Stream ID F-Stat, P-value**	**Habitat:Stream F-Stat, P-value**	**Tukey comparison for significant Habitat:Stream**
total EPT	log	23	16.621, <0.001	9.118, 0.0012	4.804, 0.0181	p < 0.001 at RHF and Temple
Ephemeroptera	sqrt	23	49.414, <0.001	13.437, <0.001	8.201, <0.001	p = 0.052 at RHF, p < 0.001 at Temple
Plecoptera	sqrt	23	14.472, <0.001	10.646, <0.001	7.614, 0.0029	p < 0.001 at RHF only
Trichoptera	sqrt	23	40.062, <0.001	17.084, <0.001	24.335, <0.001	p < 0.001 at Temple only
FFG Density	**Transformation**	**DF**	**Habitat F-Stat, P-value**	**Stream ID F-Stat, P-value**	**Habitat:Stream F-Stat, P-value**	**Tukey comparison for significant Habitat:Stream**
engulfer	sqrt	23	0.504, 0.4849	12.692, <0.001	16.249, <0.001	
filterer	sqrt	23	5.289, 0.0309	3.045, 0.0671	0.192, 0.8262	
gatherer	log	23	10.876, 0.0031	2.388, 0.1142	8.316, 0.0019	p < 0.001 at RHF only
piercer	sqrt	23	0.006, 0.9369	0.145, 0.8661	1.365, 0.2753	
scraper	sqrt	23	61.18, <0.001	14.306, <0.001	5.929, 0.0084	p < 0.001 at Temple & RHF
shredder	sqrt	23	7.971, 0.0096	13.757, <0.001	6.525, 0.0057	p < 0.001 at RHF only
FFG Biomass	**Transformation**	**DF**	**Habitat F-Stat, P-value**	**Stream ID F-Stat, P-value**	**Habitat:Stream F-Stat, P-value**	**Tukey comparison for significant Habitat:Stream**
engulfer	sqrt	23	8.733, 0.0071	2.957, 0.072	6.176, 0.0071	p < 0.001 at RHF only
filterer	sqrt	23	17.378, <0.001	1.427, 0.2605	1.787, 0.190	
gatherer	log	23	23.496, <0.001	4.281, 0.0263	4.781, 0.0184	p < 0.001 at RHF only
piercer	sqrt	23	87.562, 0.4548	0.026, 0.9741	0.829, 0.4491	
scraper	sqrt	23	87.562, <0.001	34.488, <0.001	27.675, <0.001	p = 0.038 at RHF, p < 0.001 at Temple
shredder	sqrt	23	0.698, 0.4119	7.877, 0.0025	0.677, 0.5182	

MG Density	Transformation	DF	Habitat F-Stat, P-value	Stream ID F-Stat, P-value	Habitat:Stream F-Stat, P-value	Tukey comparison for significant Habitat:Stream
burrower	log	23	0.069, 0.7952	5.866, 0.0087	4.304. 0.0258	
climber	sqrt	23	0.0094, 0.9235	3.918, 0.0343	1.895, 0.1731	
clinger	log	23	105.844, < 0.001	12.682, < 0.001	0.0029	p < 0.001 at all 3 streams
skater	sqrt	23	1.712, 0.2035	0.203, 0.8177	0.004, 0.9959	
sprawler	log	23	15.342, < 0.001	29.365, < 0.001	8.729, 0.0015	p < 0.001 at RHF, p = 0.02 at Temple
swimmer	log	23	29.194, < 0.001	2.502, 0.1039	1.465, 0.2518	

MG Biomass	Transformation	DF	Habitat F-Stat, P-value	Stream ID F-Stat, P-value	Habitat:Stream F-Stat, P-value	Tukey comparison for significant Habitat:Stream
burrower	log	23	2.967, 0.0984	10.314, < 0.001	5.271, 0.0131	
climber	sqrt	23	0.992, 0.3295	4.820, 0.0178	2.943, 0.0728	
clinger	log	23	197.860, < 0.001	3.681, 0.041	10.860, < 0.001	p < 0.001 at all 3 streams
skater	sqrt	23	0.043, 0.8375	0.270, 0.7655	0.979, 0.3909	
sprawler	log	23	0.074, 0.7887	20.116, < 0.001	2.987, 0.0703	
swimmer	log	23	13.357, 0.0013	0.620, 0.5469	0.876, 0.43	

Lotic/Lentic Density	Transformation	DF	Habitat F-Stat, P-value	Stream ID F-Stat, P-value	Habitat:Stream F-Stat, P-value	Tukey comparison for significant Habitat:Stream
Both LL	log	23	0.728, 0.4024	10.800, < 0.001	2.267, 0.1263	
Lentic	sqrt	23	16.728, < 0.001	5.905, 0.0085	14.760, < 0.001	p < 0.001 in Spawn and Temple
Lotic	log	23	23.664, < 0.001	4.482, 0.0227	7.460, 0.0032	p < 0.001 in RHF only

Lotic/Lentic Biomass	Transformation	DF	Habitat F-Stat, P-value	Stream ID F-Stat, P-value	Habitat:Stream F-Stat, P-value	Tukey comparison for significant Habitat:Stream
Both LL	log	23	6.652, 0.0168	8.022, 0.0023	9.496, 0.001	p < 0.001 at RHF only
Lentic	sqrt	23	11.045, 0.0030	1.350, 0.2791	5.650, 0.0101	p = 0.001 at Temple
Lotic	log	23	43.764, < 0.001	9.978, < 0.001	3.129, 0.0628	p < 0.001 at Temple, p = 0.002 at RHF