

Evaluating differences in water temperature and macroinvertebrate communities in BDA ponds, stream pools, and beaver dam ponds

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Abstract

Beaver Dam Analogues (BDAs) are human-made structures mimicking beaver dams and are implemented in restoration projects to slow flow, aggrade sediment, and reconnect streams to floodplains or create wetland conditions. Despite the recent popularity of this technique, very little monitoring occurs at BDA sites. This study involved surveying and measuring beaver augmented BDA ponds, BDA ponds, and stream pools to assess differences in temperature and macroinvertebrate communities as an evaluation of how successful BDA installation has been. For each type of lentic habitat, we measured six different sites to get an accurate composition of the ecosystem for our data. Using temperature loggers and d-nets, we measured each restoration site over a period of 10 days. We found that the BDA ponds were comparable to beaver augmented BDA ponds in temperature, though the beaver-augmented ponds had a slightly lower mean daily maximum. In contrast, stream pools had a wide range of temperature fluctuation, with the lowest mean daily minimum and the highest mean daily maximum. The invertebrate community composition of each site was significantly different, with more lentic taxa in ponded sites than stream sites. The beaver-augmented BDA pond community was a more constrained subset of the BDA pond community, indicating that as those ponds change with beaver augmentation, the inhabiting invertebrates may be shifting towards more wetland-obligate taxa. These results suggest that BDA-based wetland restoration projects may require beaver to be successful or shorten the timeline to success.

Introduction

The American beaver (*Castor canadensis*) is the largest rodent in North America (Baker and Hill 2003). Beaver have been the focus of numerous scientific studies, highlighted because of their unique ability to create dams. This same function has helped them earn the respective labels of keystone species and ecosystem engineers (Baker and Hill 2003). Beaver dams help to create heterogeneous aquatic areas by building dams that restrict the water flow and create pools, fundamentally changing the ecosystem and shifting how all types of organic and inorganic material flow through (Naiman et al 1984). Before European settlers arrived in North America, the beaver population occupied wetland and riparian habitats from coast to coast, and numbered between 60-400 million (Baker and Hill 2003). Though the population was decimated by fur trappers in the 1700s, public concern has led to a continent-wide recovery (Baker and Hill 2003). However, due to stream degradation, some habitats that historically would have benefitted from beaver are no longer able to host the species. Stream degradation in the western United States has decreased base flows, increased peak flows, and caused a loss for the aquatic and riparian

habitats that beaver helped flourish (Bosworth et al 2025).

Fortunately, an alternative exists, which rehabilitates streams while preparing them for future beaver inhabitation. Beaver dam analogues (BDAs) are semi-permeable and inexpensive channel-spanning structures made of willows, grass, sand, and mud that mimic beaver dams and their effects on these wetland habitats (Pollock et al 2014). There is evidence that restoration techniques involving BDAs increase water retention without increasing temperatures because they facilitate an interaction with cooler groundwater (Bouwes 2016). Installation of BDAs also facilitates increased stream channel width, number of pools, side-channel area, and riparian plant growth, meaning that it creates diverse habitats similarly to beaver dams (Bouwes 2016). In a study involving BDAs and their subsequent ponds, it was found that BDAs and beaver dams both modify hydrology in similar ways (Munir & Westbrook 2021). In fact, all three BDA configurations created an upstream pool that was effective in mimicking the hydrological functions that beaver dams perform. BDAs help to accelerate ecosystem recovery, but are not intended to be a permanent structure; instead, the success of the BDA is dependent upon a future where beaver maintain the system, which could take many years. Therefore, placement of these structures is critical, and numerous studies have shown that multiple placements will increase system resilience, in addition to aquatic and habitat benefits (Wade et al 2020; Munir & Westbrook 2021).

One aquatic habitat benefit of beaver damming is a mosaic of stream temperatures, the heterogeneity of which can support a variety of aquatic species (Majerova et al 2015). For example, Bouwes et al. found that juvenile trout require warmer patches for development, and BDAs provide habitats with many temperatures (2016). As climate change causes the temperatures to rise in montane streams (Isaak et al 2017), beaver dams and BDAs can create warm or cool refugia. Beaver dam ponds remain cool in the summer and avoid freezing in the winter, allowing for a heterogenous climate (Bouwes et al 2016). Beaver dams can also aid both cooling and warming downstream (Majerova et al 2015). Beaver dams can create cooler downstream temperatures because the hydraulic head of the pond itself pushes groundwater out below the pond. This increases mayfly growth by providing cooler habitat (Fuller & Peckarsky 2011). Stream biodiversity is similarly boosted because of the addition of ponded habitats. With the heterogeneity of the beaver dam temperatures, mayflies and other stream insects who use water temperature as a cue for emergence may have their phenology altered when beaver dams are present. These variations allow for better individual fitness and population growth (Fuller and Peckarsky 2011). Beaver dams enhance the landscape diversity by adding a lentic habitat (Washko et al. 2022), changing the temperature and the success of different invertebrate and fish populations.

The objective of this research is to compare how beaver ponds, BDA ponds, and stream pools differ in their temperature regimes and macroinvertebrate communities. By collecting this data, we can address the much larger question of how BDAs fit in as an effective conservation strategy. Specifically, we will address i) the average water temperatures at two depths, ii) the range of temperature fluctuations during the day, and iii) the difference between macroinvertebrate communities. I expect that BDAs are able to effectively recreate the temperature effects of natural beaver dams and will house similar macroinvertebrates, and therefore will be a significant restoration method. I expect to see this because previous studies have shown that BDAs are able to mimic the hydrological conditions of beaver dams and other

work has suggested that aquatic invertebrates in BDA-altered habitats may be similar to those in beaver pond habitats (Croll 2025). This work is important to the management of aquatic ecosystems, especially where restoration and reintroduction of beaver is being considered.

Methods

Study Area

The proposed study area is Trail Creek, a creek located in the headwaters of the Gunnison Basin near Gunnison, Colorado, USA. Trail Creek is located in an alpine-montane wet meadow at around 10,000ft in elevation. The stream is a 2nd order tributary that's surrounded by pine forests and sagebrush. Trail Creek used to be naturally maintained by beaver, however, once beaver were heavily trapped, their dams fell into disrepair. The managers of the Trail Creek system have begun to use low-tech restoration techniques to slow the flow of water through the Taylor River watershed and restore the natural ecosystem (EcoMetrics 2021). Upstream, the natural beaver dams have filled with sediment, breached, and are no longer being maintained. In the untreated reach, stream pools are currently the dominant lentic habitat type. Downstream, over 200 BDAs have been installed (EcoMetrics 2021), and beaver are slowly colonizing the installed BDAs and adding to their structure (Susan Washko personal observation).

Within the BDA treatment reach, we chose six BDA ponds that have generic hydrology (i.e. singular channels and no islands) to control variation in pond type. For the stream pools, we chose six upstream locations with pools of varying depth (all at least 40 cm deep). For the beaver dams, we chose six BDAs that were augmented by beaver along the same channel (Figure 1).



Figure 1. Map of research site, including 6 stream pools, 6 BDA ponds, and 6 augmented BDA ponds.

Sampling

Sampling took place from July 9th until July 31st. Six of each type of restoration method were chosen: six BDA ponds, six beaver augmented BDA ponds, and six stream pools. At each of these sites, two temperature loggers were installed to measure water temperature every half hour. Of the two sensors, one was placed at 40 cm depth, and one at 10 cm depth. Additionally, the sensors were placed close to the primary dam structure. This provided a range of temperatures. Due to a limited number of loggers, three ponds/pools of each treatment type had loggers for one week. Then, a different set of three pools/ponds from each treatment had loggers installed for seven days. Temperature loggers were encased in mesh bags and strapped to rebar with zip ties.

Aquatic invertebrate communities were sampled in each of the six sites of each treatment. We swept a d-net across 1 meter for 10 seconds to gather the invertebrates and gathered data on both river right and river left to survey. In the stream pools, we only took one sample, but in the beaver augmented BDA ponds and the BDA ponds, we took two. This occurred in a random area of the pond shoreline in the thawleg and not on the dam structure. In the field, we identified the family of the vertebrate and counted each individual macroinvertebrate in a pan pondside to assess community composition across treatments, returning invertebrates to the water upon completion. Following this, we used the USGS Taylor River temperature gauge to create a complete diagram of the temperature fluctuations by treatment type across the 3 weeks, since we

had different samples of each treatment type across 3 different weeks.

Statistical Analysis

All statistics were completed in RStudio (R Team 2025). For the community composition analysis, we calculated the invertebrate species richness (*specnumber* function in the ‘vegan’ package; Oksanen et al 2025). Next, we used the Shapiro-Wilk test (*shapiro.test* function) to find the normality of the data, which was normally distributed. Following this, we used an ANOVA (*aov* function) to compare the invertebrate species richness to the treatment type. We then used Non-metric Multidimensional Scaling or “NMDS” (*nmds* function) to visualize the community data from the macroinvertebrate surveys. We applied permanova (*adonis2* function in the ‘vegan’ package) to test for significant differences in community composition by treatment. Finally, we used the pairwise permanova (*pairwise.adonis* function in the ‘vegan’ package) test to find the significant differences between treatments.

For temperature analyses, we started by completing the incomplete temperature records (because each pond only had a logger for a week) by modeling against the USGS Taylor River gaging site temperature logger to predict the Trail Creek temperatures in each site (*lm* function).

Results

Invertebrate Community Analysis

We found that community composition does vary by treatment (PERMANOVA, $F_{2,27} = 9.1894$, $p < 0.001$). In fact, all treatments were significantly different from one another. BDA ponds were different from beaver-augmented BDA ponds (Pairwise Adonis, $p = 0.002$), BDA ponds were different from stream pools (Pairwise Adonis, $p = 0.001$), and beaver-augmented BDA ponds were different from stream pools (Pairwise Adonis, $p = 0.001$). The stream pools clustered to the left side of the graph with very little overlap with either pond habitat. However, the beaver-augmented BDA ponds fall within the BDA ponds. This overlap indicates that they share taxa, but the beaver-augmented sites seem to be a subset of the BDA community. A dispersion test revealed differences in dispersion (or distance to centroid) by treatment (ANOVA, $F_{2,27} = 15.613$, $p < 0.001$), where the beaver-augmented ponds have lower dispersion than the stream pools (TukeyHSD, $p < 0.001$) and the BDA ponds (TukeyHSD, $p < 0.001$), while BDAs and stream pools did not differ in dispersion. NMDS stress was 0.1540.

The indicator taxa analysis showed that mites ($p = 0.0297$) and Chironomidae ($p = 0.0297$) were significant in augmented BDA ponds. The analysis also showed that Cladocera ($p = 0.0149$), Dytiscidae larvae ($p = 0.0149$), and Leptophlebiidae ($p = 0.0149$) were significant in beaver ponds. Finally, Elmidae larvae ($p = 0.0150$), Ceratopogonidae ($p = 0.0150$), Tabanidae ($p = 0.0150$), Tipulidae ($p = 0.0297$), and *Brachycentrus* ($p = 0.0150$) were significant in stream pools.

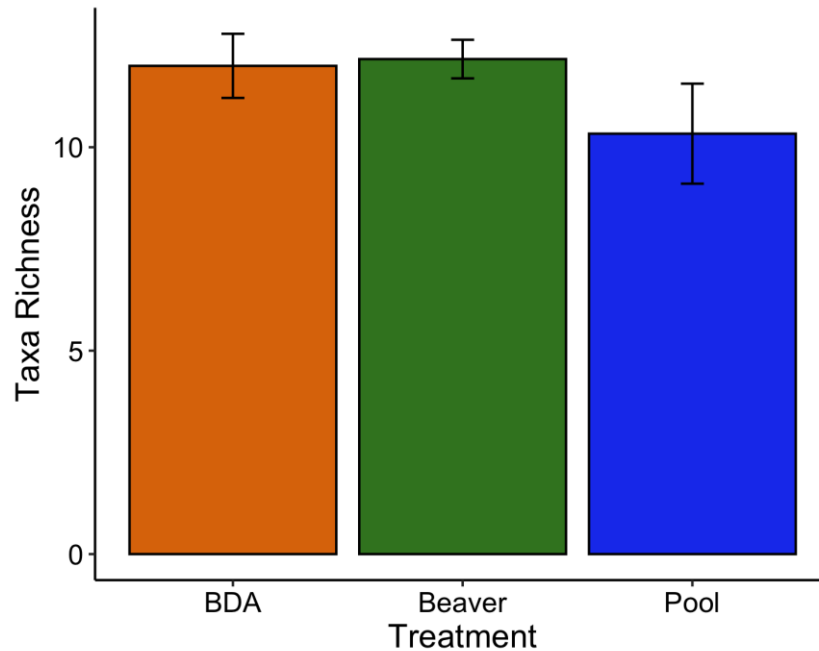


Figure 2. Species richness by treatment type.

Temperature Analysis

While analyzing temperature data, we found no significant difference between the loggers at 10cm and 40cm in any treatment. Thus, we proceeded to omit depth as a variable in analyses with treatment. Stream pools had the largest temperature swings during the day, often shifting more than 10 degrees throughout the day. With the completed data, we used a Kruskal-Wallis test to compare both the mean temperature ($p = 0.9266$) and the temperature variance ($p = 0.003011$). We found that the relationship between mean temp and pond treatment is significant (KW, $X = 180.12$, $df = 2$, $p < 0.001$). The BDA ponds had a much smaller temperature range, and the augmented BDA ponds had the smallest temperature range (Figure 4). Likely due to this wide range of temperatures, stream pools had the highest mean daily maximum temperature (Kruskal Wallis, $X = 3.2481$, $df = 2$, $p = 0.1971$), while the beaver-augmented ponds and BDA ponds did not differ in maximum temperature. Similarly, stream pools had the lowest mean temperature by treatment (Pairwise Wilcox, $p < 0.001$), while the augmented BDA ponds had the highest mean temperature. Stream pools had the lowest minimum temperature (Pairwise Wilcox, $p < 0.001$), reaching lows overnight that the other treatment types are insulated from. Overall, from these graphs, we understand that the beaver-augmented ponds and BDA ponds have steadier temperatures, while stream pools are more variable. However, BDA ponds had the greatest temperature variance (Pairwise Wilcox, $p < 0.001$), followed by the beaver ponds (Pairwise Wilcox, $p < 0.001$), and stream pools had the smallest mean temperature variance (Pairwise Wilcox, $p < 0.001$).

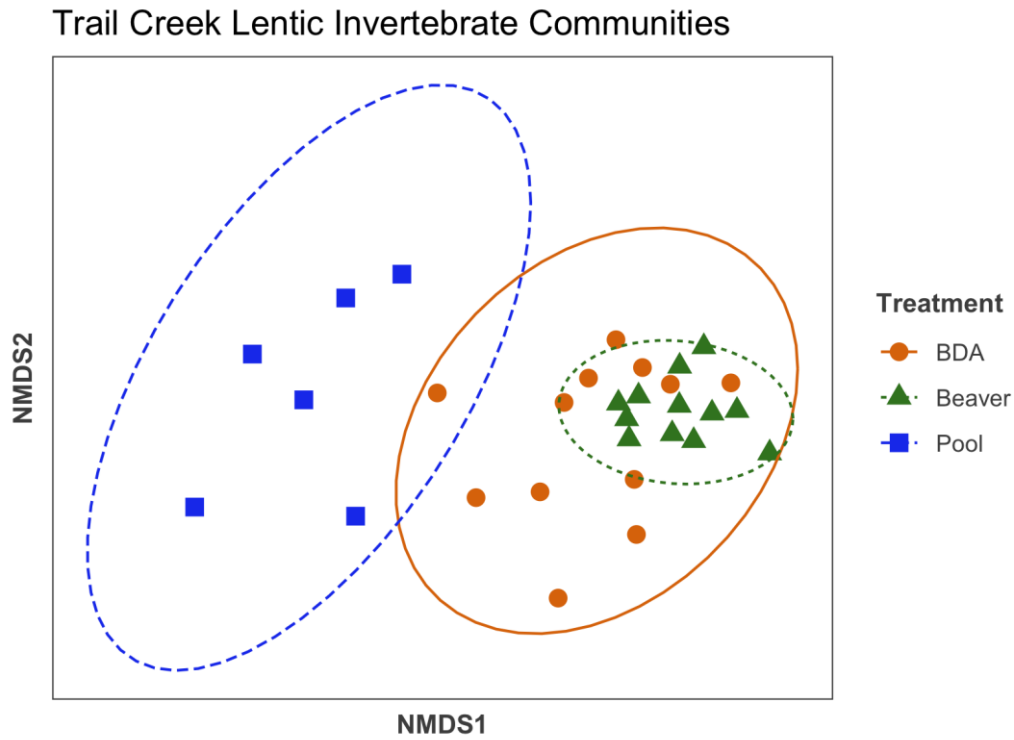


Figure 3. NMDS plot of data by treatment type.

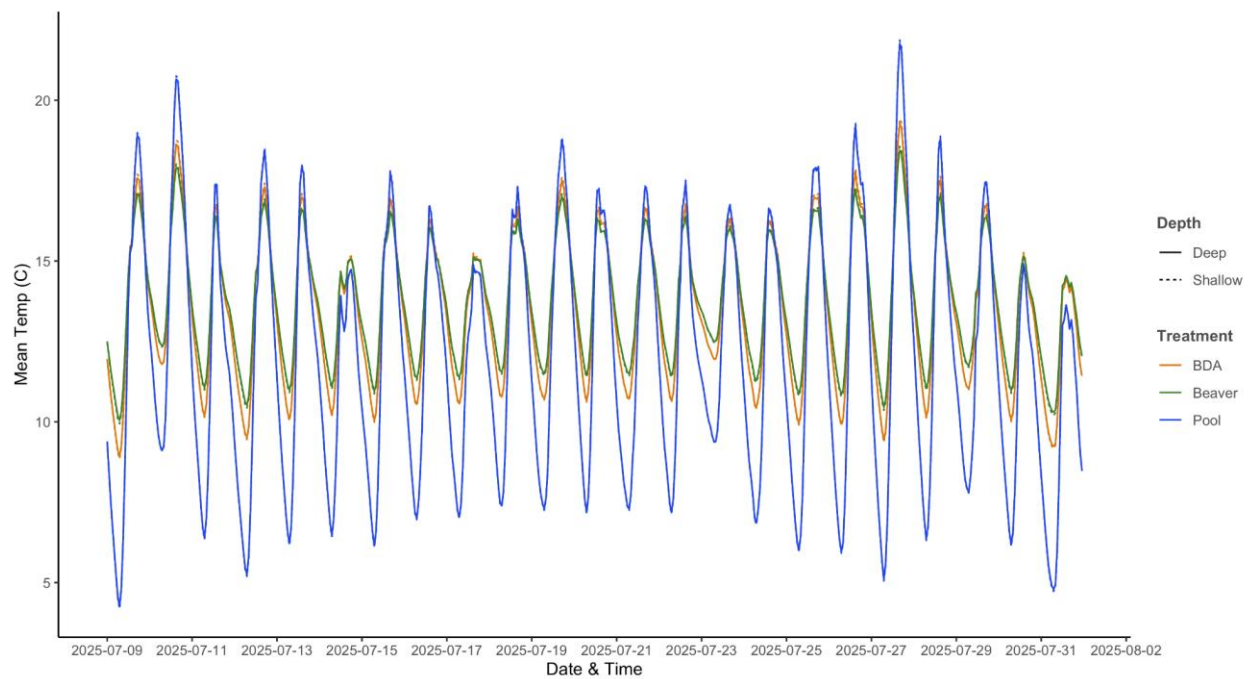


Figure 4. Mean temperature by date and time, across all three treatments.

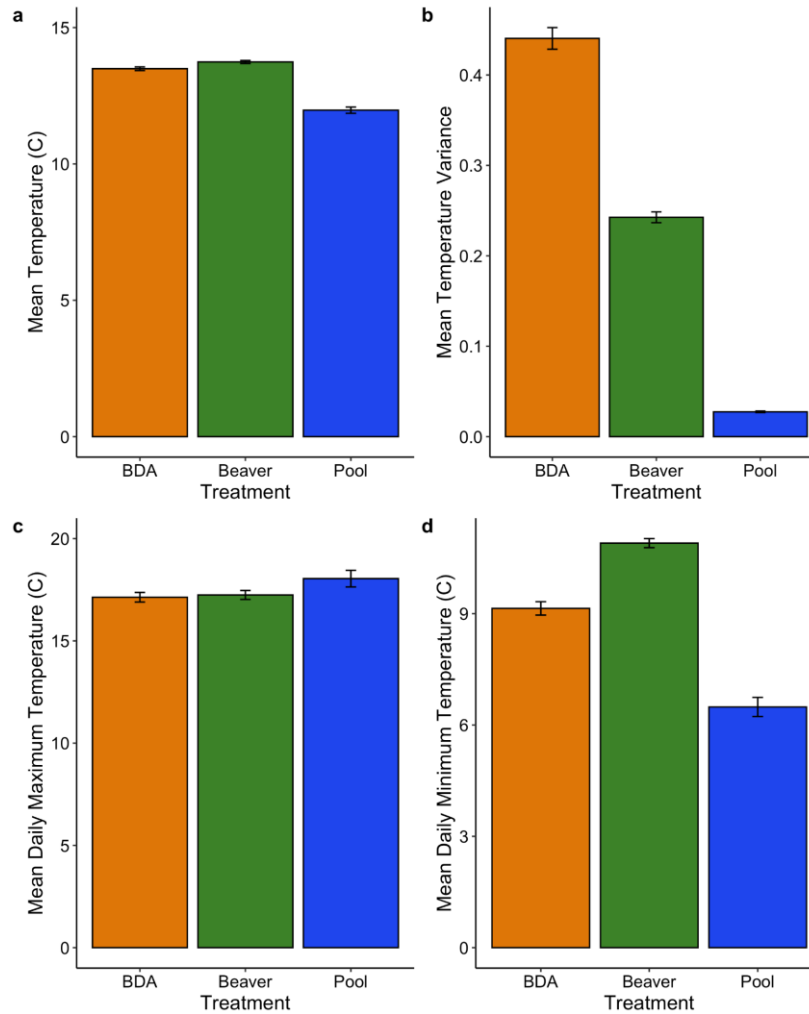


Figure 5. Temperature data, including the mean daily maximum temperature and minimum temperature, mean temperature variance, and mean temperature.

Discussion

Our results demonstrated significant differences in the macroinvertebrate communities within stream pools, augmented BDA ponds, and beaver ponds. Within the macroinvertebrate community surveys, we found that beaver pond communities fell within the augmented BDA pond communities (Figure 2). Conversely, other studies have found that beaver ponds have their own unique taxa makeup, showing that they are not a subset of other mature ponds but instead a diverse stage of wetland (Bush et al 2019). This result could be because the augmented BDA ponds support both lentic and lotic macroinvertebrates. This could also be explained by the fact that beaver-augmented BDA ponds have only recently been altered by beaver and are transitioning towards a wetland with their increased inundation and depth (Daniel & Washko 2025). We would expect to see a shift towards more wetland-associated taxa as the water becomes more lentic over time. Additionally, we only sampled the thawleg, and not the shallow, inundated sedge habitats around the border of the

ponds. We noted water striders, adult dragonflies, and *Limnephilus externus* in these areas, which are all wetland taxa common in regional beaver ponds (Rivera 2023).

In another study, it was demonstrated that age did not change the species composition in these beaver dams (Gonzalez Gutierrez & Washko 2024). However, a separate study found that in newly constructed beaver ponds, there was a higher species richness and abundance compared to older dams (Nummi et al 2021). Another study found that BDAs can instigate a significant shift in the trait composition and invertebrate communities found, even when species richness remains the same (Croll 2025). We found the same species richness, but a higher amount of lentic invertebrates in beaver augmented BDA ponds (augmented in the past year) compared to BDA ponds (installed in 2021). Another factor is that fish, specifically trout, were present in each of the treatment types. The predation pressure could make species richness more uniform (Nurminen et al 2018). This could also be attributed to the fact that no habitat is distinctly better, they just host different species.

For stream pools, Elmidae larvae, Ceratopogonidae, Tabanidae, Tipulidae, and *Brachycentrus* were significant. Elmidae larvae, Tabanidae, *Brachycentrus*, and Tipulidae all prefer the interstitial spaces and depend on these areas for feeding. Elmidae larvae are described as “clingers” and cling to substrate in fast-flowing water (Proctor et al 2015, Ch. 39). Tabanidae feed on their prey that hide in interstitial spaces. *Brachycentrus* live in both depositional and erosional zones in lotic habitats, and are known to be indicators of stream pools (Proctor et al 2015, Ch. 40). Tipulidae eat the detritus in the sheltered habitat beneath the rock, occupying and feeding in these spaces like the former invertebrates. Ceratopogonidae are generalists and prefer a range of habitats, and were found in all samples. One reason they could be significant in stream pools is that they are associated with finer sediment, which is typically in lentic areas (Washko 2020). In the BDA ponds, both Mites and Chironomidae were significant as indicator taxa, and both are generalists. Both species like the transitional areas between pond and stream (Proctor et al 2015, Ch. 25), which makes sense as the BDA ponds have conditions between lotic and lentic. As for the beaver augmented BDA ponds, Cladocera, Dytiscidae larvae, and Leptophlebiidae were all significant. Cladocera are water column swimmers and need slower water velocities (Proctor et al 2015, Ch. 28) matching the beaver pond habitat better as it was deeper and therefore likely slower. Dytiscidae larvae also are wetland-associated taxa and prefer slow-moving water (Washko et al 2022). Finally, for Leptophlebiidae, they are a swimming taxa that collects small particles of detritus (Proctor et al 2015, Ch. 34). Overall, we found that the traits of the macroinvertebrate communities matched the habitat characteristics, therefore the indicator taxa might be demonstrating that a wetland is evolving in the beaver augmented BDA ponds.

Future studies should consider measuring the aquatic communities over the years in the BDA ponds, to see if the invertebrates present remain lotic invertebrates, or if instead the macroinvertebrate communities begin to mirror natural beaver ponds. This could encompass a broader range of invertebrates and give a more holistic view of if invertebrates are more lentic or lotic in these various treatment types and where they might differ.

Temperature also differed by treatment. Pools have large temperature swings because the untreated reach of the creek is shallow and therefore susceptible to temperature change. This led to the stream pools having both the highest mean daily maximum temperature and

the lowest mean daily minimum temperature, and the overnight lows caused the stream pool average to be the lowest. BDA ponds had the highest mean temperature, which could be because the increased depth from the BDA structure causes insulation of temperature, but the water is not deep enough not to heat up during the day, thereby holding warmth overnight. The same seems to be true of the beaver-augmented BDA ponds, but they have a lower mean temperature than the BDAs. As aforementioned, other studies have found that beaver ponds are able to maintain cooler temperatures in the summer and warmer temperatures in the winter because of their volume (Weber et al 2017). Importantly, the beaver-augmented BDA ponds do not reach the high temperatures of the stream pools and are slightly cooler than the BDAs. The time of data collection, July 2015, was a drought year with lower than normal streamflow (Lawrence Berkeley Lab personal communication). Given these conditions, the beaver-augmented ponds may be cool refugia for thermally-sensitive montane stream organisms, especially given we did not measure at the deepest portion of the ponds (some of which were over 1m deep and had bank coverage). In other studies, it's noted that small scale thermal heterogeneity is an important facet of successful pond habitats (Majerova et al 2015). Beaver-augmented BDA ponds may contain cold refugia, and this is a path for future study. Since microhabitat complexity and heterogeneity that mirrors naturally-occurring habitat in nature is a large goal of restoration, our data shows that for temperature, BDAs may be a viable restoration method, especially if beavers do take over dam management.

Overall, when beaver assume management of BDAs, conditions of the resulting ponds change. Beavers increased temperature insulation by increasing depth, and invertebrate communities appear to be shifting as habitat becomes more wetland-like. Compared to the BDAs installed in 2021, the beaver augmented BDA pond communities are more lentic and we expect to see the ellipses shift to completely lentic once the wetland taxa begin moving in. Additionally, we would expect to see smaller temperature swings over time as the depth of the beaver pond regulates the temperature through the seasons. Beaver management of the habitat was a primary goal of restoration, and their presence is likely a main driver in the restoration reach moving towards the goal habitat of a montane wetland complex.

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