When Humans Work Like Beavers: Riparian Restoration Enhances Invertebrate Gamma Diversity and Habitat Heterogeneity

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Abstract

Restoration has the potential to increase habitat heterogeneity through the creation of unique habitat patches that, in turn, increase regional species richness or gamma diversity. While biological diversity and habitat heterogeneity are important factors to consider under a shifting climate, restoration actions and outcomes rarely examine these components. In this study, we examined the effects of riparian beaver dam analog (BDA) restoration on aquatic invertebrate diversity and habitat heterogeneity. While the effects of BDAs on hydrology, geomorphology, and salmonid habitat have been explored, we are unaware of any studies assessing their effects on aquatic invertebrate diversity and the food web that supports them. We sampled aquatic

invertebrates, basal carbon resources, dissolved nutrients, turbidity, and water temperature in pre- and post-BDA pond, side channel, and mainstem habitat over a three-year period. The BDAs functioned similarly to natural beaver dams and created slow-water environments that accumulated fine particulate organic material (FPOM) and increased pelagic phytoplankton production. Nonmetric multidimensional scaling (nMDS), permutation multivariate analysis of variance (PERMANOVA), and Mantel's tests demonstrated that these changes led to the formation of a unique invertebrate community populated by lentic macroinvertebrates and zooplankton, which increased beta-diversity and gamma diversity. Further, BDAs in our study maintained high densities of invertebrates and buffered water temperatures in comparison to adjacent lotic habitats. These results support our hypothesis that BDAs can enhance invertebrate beta and gamma diversity through the creation and colonization of unique pond habitat and improve habitat and resource heterogeneity for native fishes under variable climate conditions.

Keywords: beaver dam analogs, beta diversity, climate change, gamma diversity, habitat heterogeneity, restoration.

Implications for Practice:

- Mimicking extirpated allogenic ecosystem engineers may provide habitat heterogeneity beneficial to native species.
- Increasing habitat heterogeneity through restoration actions can improve both beta and gamma diversity.

Introduction

Habitat homogenization is a major threat to global biodiversity (Alsterberg et al. 2017). Habitat loss can result in the proliferation of generalist taxa and declines of unique or specialist taxa, leading to strong decreases in regional species pools across landscapes (Hewitt et al. 2010). Furthermore, homogenization and degradation of freshwater habitats may exacerbate climate change impacts by creating barriers to migration, compounding the alteration of natural flow and thermal regimes, and increasing range expansion of invasive species (Mawdsley et al. 2009, Capon et al. 2013). More recently, the reintroduction of allogenic ecosystems engineers (e.g., beaver, *Castor canadensis*) to degraded habitats has been used to restore habitat heterogeneity and improve species richness (Law et al. 2017).

The extirpation of beavers and subsequent reduction in their pond and wetland habitat has led to significant losses in stream habitat heterogeneity throughout the western United States (Pollock et al. 2007). Historically, beaver dams created important habitat complexity in the form of diverse wetlands that recharged groundwater, supplemented stream flows during dry periods, and buffered against extreme water temperatures (Janzen & Westbrook 2011; Weber et al. 2017; Wade et al. 2020). Beaver dams also reverse and prevent channel incision by trapping sediment, which is associated with declines in stream velocity (Pollock et al. 2007). Such benefits have been shown to positively affect other species such as stream dwelling native fishes and riparian plants (Wright et al. 2002; Bouwes et al. 2016), particularly during dry periods and drought (White & Rahel 2008). Naturally occurring beaver dam wetland complexes are also known to increase gamma diversity by creating landscape-level habitat heterogeneity (Wright et al. 2002; Law et al. 2016; Washko et al. 2020). For example, Wright et al. (2002) found that beaver dams improved gamma diversity of riparian plants and Law et al. (2016) found similar results with aquatic invertebrates.

Although beavers are re-populating their historical range throughout the western United States, beaver dam analogs (BDAs) have more recently been used to restore stream habitat complexity and function, reverse channel incision, and create habitat for native species, such as salmonids (Bouwes et al. 2016; Weber et al. 2017). However, the effects of BDAs on stream invertebrate communities are relatively unknown, as most studies to date have focused on hydrologic and geomorphic change induced by BDA installations (Lautz et al. 2019; Nash et al. 2021). As BDAs become more common, information specific to their effect on biodiversity is necessary. Studies of naturally occurring beaver dams suggest that BDAs may improve regional species pools through the formation of slow-water habitat. Such habitats are relatively uncommon in numerous watersheds, particularly in steeper drainages or where beaver have been extirpated. As such, the use of BDAs to restore landscape-level habitat heterogeneity and species pools has received increasing attention in the literature (Bellard et al. 2012).

Here, we examine the effects of recently installed BDAs on aquatic invertebrate communities over a three-year period by comparing communities and habitat conditions pre- and post-restoration as well as to adjacent lotic environments. Our objectives were to test whether BDA restoration enhanced the regional species pool by increasing riparian habitat heterogeneity and if primary production, organic matter retention, and invertebrate abundance was greater in BDAs in comparison to pre-restoration conditions and nearby lotic habitats. Specifically, we predicted that BDA installation would create lentic habitat patches that would be colonized by unique taxa not present in nearby lotic habitats, thus increasing both beta diversity between habitats and regional gamma diversity. We also predicted that BDAs would increase pelagic chlorophyll a concentrations and organic matter retention, and that increases in these resources would lead to

the colonization of unique specialist taxa and increase zooplankton and macroinvertebrate densities in comparison to adjacent lotic habitat.

Methods

Study Site:

This study was conducted on French Creek, a third order tributary that flows to the Scott River, which is a major tributary to the Klamath River in Northern California (Fig. 1). The 8,330-hectare French Creek watershed flows north east from the Russian Mountains and is perennial in its lower reaches (Yokel et al. 2017). The French Creek watershed is underlain by granitic bedrock with low-gradient reaches composed of cobble, gravel, and sand alluvium (Yokel et al. 2017). Discharge in French Creek is driven by snowmelt in the higher reaches and rain in the lower reaches. High flow events typically occur during warm winter rains or rain-on-snow events between October and March (U.S. Geological Survey 2017). Additionally, high hydraulic conductivity of the valley sediments facilitates connections between stream surface flow and the underlying aquifer. Aquifer inputs are important during summer and fall low flow periods (Yokel et al. 2017).

Prior to the 1830's the Scott River Valley supported an abundant beaver population and was initially named Beaver Valley (Yokel et al. 2017). However, with the arrival of European trappers and settlers, beaver populations declined precipitously, as did the complex wetland habitat associated with their dams. Historically, these habitats were important for coho salmon and other native fishes, which used these habitats as high flow and thermal refugia (Pollock et al. 2004). Although much of the historical beaver wetland habitat has been lost, the Scott River and its tributaries still support a productive coho salmon population (National Marine Fisheries

Service 2014). One of the habitat types critical to coho salmon survival is slow-water habitat, used during juvenile over-wintering and -summering (National Marine Fisheries Service 2014).

Previous monitoring of French Creek found low coho salmon survival during high flow events, likely due to the lack of slow-water refuge habitats (Yokel et al. 2017). To restore such habitat features conducive to juvenile coho over-summering and over-wintering, four beaver dam analogs (BDAs) were installed within a side-channel of French Creek during June 2017 (Fig 1 & 2). The BDAs were created by driving 0.10-0.15-meter diameter wood poles approximately 0.46 m into the ground. Locally sourced willow branches were then woven into poles and covered in sediment on the upstream side, effectively creating a beaver dam analog. BDA sites were chosen based on channel morphology and expected pond inundation extent post-restoration.

Data Collection:

To characterize conditions prior to BDA restoration we sampled five side-channel sites and a mainstem French Creek site prior to BDA installation on 8 June 2017. The five side-channel sites consisted of four pre-BDA habitats and one site located upstream of these habitats as a control site. The control site was located outside the zone of influence of downstream BDAs. Post BDA installment, each habitat was sampled on 8 June 2018 and on 6-7 June 2019 (Fig. 1). At each site, we delineated a 50-meter sampling reach upstream of the BDA to collect environmental and invertebrate data on randomly placed transects within the reach. Random transects were selected using a random number table in the field and random numbers were drawn for each sampling reach.

Water Temperature & Chemistry

We collected water temperature data at fifteen-minute intervals using Onset HOBO Pro v2 water temperature data loggers placed within inundated areas of the BDAs, side-channel, and French Creek from 13 June 2017 through 6 June 2019. During each sampling event, we collected water grab samples located approximately at the center of each delineated reach and congruent with each invertebrate sampling period (June 2017, 2018, 2019). Water samples were analyzed for water chemistry (pH, turbidity [NTU], $NO_2^- + NO_3^-$ [NO_3-N], and soluble reactive PO_4^{3-} [SR-PO_4^{3-}]). We measured SR- PO_4^{3-} using ammonium molybdate spectrophotometric method (limit of detection [LOD approximately 0.0005 mg/L]) and NO_3-N using vanadium chloride spectrophotometric method (LOD = 0.01 mg/L) (Doane & Howarth 2003). Turbidity was determined using optical probes. We sampled suspended chlorophyll *a* by field filtering one liter of water through a pre-combusted glass-fiber filter (GF/F). Filters were then placed on dry ice in the field to slow biological processes and returned to the lab where they remained frozen until processed for Chlorophyll *a* and pheophytin *a* and *b*. Chlorophyll *a* and pheophytin *a* and *b* were measured using fluorometric methods.

Particulate Organic Matter and Epilithic Algae

We collected particulate organic matter (POM) by taking three kick samples at each site, from three randomly drawn transects that did not overlap with benthic invertebrate sampling locations. Random transects were selected using a random number table in the field. We froze POM samples immediately after collection in the field using dry ice. Samples were kept frozen until laboratory processing, where we thawed samples and separated them into two size fractions (fine particulate organic matter [FPOM] <1 mm; coarse particulate organic matter [CPOM] >1 mm) using a 1 mm mesh sieve. After separation, we dried each sample at 60 °C for 48 h and weighed the dried samples on an analytical balance (±0.01 g). We combusted the weighed dried samples

in a muffle furnace at 475 °C for 90 minutes or longer until the entire sample was reduced to ash. Combusted samples were reweighed to calculate ash-free dry mass (AFDM g) by subtracting the mass of the residual inorganic matter from the pre-combustion dry weight.

To quantify epilithic algae chlorophyll production, we collected three cobbles from three random transects at each study site in an area not previously disturbed by benthic macroinvertebrate or POM sampling. Random transects were selected using a random number table in the field. We scrubbed a 6.45 cm^2 area on each cobble using a fine bristled brush. Loosened biofilm was then rinsed into a tray and transferred into a sterile sample bag. Samples were then transferred into a dark bag and frozen using dry ice. Samples remained frozen until laboratory processing. In the laboratory, samples were thawed and filtered through pre-combusted GF/F. We recorded the volume of water to account for any dilution effects. Chlorophyll was measured by soaking filters in 90% ethanol for 24 hours prior to quantification by fluorometry and converted to pigment concentration (chlorophyll *a* [chl *a*] and pheophytin) (APHA 1998). Pigment concentrations are reported as benthic chl *a* μg $^-$L.

Benthic Macroinvertebrates

We collected stream benthic macroinvertebrates at each BDA replicate and side-channel at five randomly selected transects perpendicular to flow, along each 50-m reach. The five transect samples were then composited into one sample for a total area of 0.45 m^2 for each site at each BDA (n=4). In the pre-restoration BDAs and unaltered side-channel, we collected benthic macroinvertebrates by disturbing 0.09 m^2 of substratum to a depth of ~6 cm for one minute, while capturing entrained macroinvertebrates immediately downstream in a D-net (500-μm mesh). Some pre-restoration BDA sample sites lacked stream current during summer low flows and, thus, benthic macroinvertebrates were entrained by hand sweeping. Samples were taken

randomly along each transect. At French Creek, we collected benthic macroinvertebrates over three transects also using the D-net method. Each transect consisted of three subsamples (left, center, right) across the wetted width of the channel. Each transect was then composited to yield three independent samples (n = 3; sampled area = 0.27 m^2). Macroinvertebrates were sampled using the same methods for all three years of the study in French Creek and the side-channel site. However, during extreme low flows during 2018, the side-channel site was sampled without replication due to strong reductions in wetted area and limited habitat.

Post-restoration, BDAs experienced strong changes in hydrology, shifting the previously lotic habitat to lentic conditions. This facilitated the need for an amended sampling approach. Within BDA influenced habitat, a modified sweep technique was used to sample benthic macroinvertebrates. Similar to the previous technique, 0.09 m^2 of the substratum was disturbed to ~6 cm; however, due to the lack of current and increased depth, we swept the D-net over the area for one minute to capture entrained macroinvertebrates. Transects along each 50 meter reach were again selected randomly using a random number table.

All benthic macroinvertebrates were preserved in 95% ethanol in the field and transported to the laboratory where they were enumerated and identified. We subsampled each sample to a minimum count of 500 individual macroinvertebrates using a Folsom plankton splitter. Samples containing less than 500 individuals were completely enumerated and identified. Macroinvertebrates were identified to the lowest practical taxonomic level (usually genus or species) using keys published by Merritt et al. (2008), Wiggins (2018), and Thorp & Covich (2009), as well as various taxon-specific references. Worms were identified to the subclass Oligochaeta. Leeches and fingernail clams were identified to the families Glossiphoniidae and

Sphaeriidae, respectively. We assigned taxa to functional groups based on Merritt et al. (2008).

For data analysis, abundance data was standardized to square meter of benthic habitat sampled.

Zooplankton

We sampled zooplankton abundance at BDA, side-channel, and French Creek sites using

appropriate methods as necessitated by different habitat types (Corline et al. 2017). For BDA

sites, we threw a 15 cm diameter zooplankton net (153 µm mesh) the maximum length of the

habitat where depths were deep enough to accommodate the net and where there was no

noticeable flow (Corline et al. 2017). We retrieved the net several times and the length of the

rope for each retrieval was recorded. In French Creek, we collected zooplankton by holding a 30-

cm diameter zooplankton net equipped with a General Oceanics flow meter in the current for one

minute. Due to low water conditions, we sampled zooplankton at three locations at the side-

channel site in June of 2019 by filling a graduated cylinder and pouring 10 liters through the

zooplankton net for each sample. Zooplankton were preserved in 95% ethanol until laboratory

processing.

In the laboratory, each zooplankton sample was standardized to a volume of 100 mL for further

processing. Zooplankton samples were subsampled by removing and identifying individuals in

one mL aliquot increments until a count of 100 was reached for at least one zooplankton taxon.

For samples where a minimum count of 100 individuals was not attainable, all 100 mL of the

sample were processed. Zooplankton were identified to genus or species with keys from Thorp &

Covich (2009) and An Image-Based Key to the Zooplankton of North America (Hanley 2020).

To account for method variability between habitats, we standardized zooplankton abundance

(m^3) by dividing the total number of individuals (enumerated fraction X total fraction) by the

volume sampled (Corline et al. 2017). We estimated the volume sampled for the BDAs by the

rope length and net diameter (Eq. 1), while French Creek volume was estimated with a General Oceanics flowmeter (Miami, FL, USA) (Eq. 2).

$$Volume = \pi \times 0.075^2 \times Rope\ Length \times Num. Throws. \text{ (Eq. 1)}$$

$$Volume = \pi \times 15^2 \times Distance, \text{ where } Distance =$$

$$(Difference\ in\ Rotor\ Revolution\ (Final - Initial) \times 26,873)/999,999. \text{ (Eq. 2)}$$

Data Analysis

Alpha diversity was calculated using Shannon-Wiener diversity index and species richness. Species richness was calculated as the number of species within a replicate, habitat, or region. Differences in macroinvertebrate densities and diversity between years and BDA and French Creek habitats were tested using repeated measures ANOVAs (rmANOVA). Differences in zooplankton abundance and basal carbon resources between pre-BDA and BDA habitats were tested using rmANOVAs. Post-hoc Tukey HSD was used to determine statistical differences between habitats and years. Normality was determined using Shapiro-Wilkes tests. Data that did not meet normality assumptions were log transformed or inverse transformed for approximately normal distributions.

Multivariate analyses of beta diversity and environmental correlates included data from pre-BDAs, side-channel, BDAs, and French Creek. We log transformed macroinvertebrate densities prior to conversion to a Bray-Curtis dissimilarity matrix. Beta diversity or species turnover between habitats were visualized using Non-metric Multidimensional Scaling (nMDS) of Bray-Curtis dissimilarities. We used permutation multivariate analysis of variance (PERMANOVA) to test for significant groups within the dissimilarity data. Since PERMANOVA assumes that dispersion is equal between groups we performed tests for homogeneity. Pairwise tests for significance between groups was tested using pairwise.adonis function from the package

pairwise.adonis (Martinez Arbizu 2019). We assessed correlations between community and environmental dissimilarity with Mantel tests using Spearman's rank correlation. We used indicator species analysis to determine species contribution to group distinctiveness. Gamma diversity was calculated as the total taxa richness for all habitats sampled. Quantitative Venn diagram analysis was used to visualize shared and unique species between habitats and their contribution to gamma diversity (Chen & Boutros 2011). Side-channel and pre-BDA taxa were combined for 2017 as pre-BDA habitats were representative of the unmodified side-channel prior to BDA installation.

All community analyses were conducted in R 3.6.2 (R Core Team 2019) using *vegan* and *indicspecies* packages (De Cáceres 2013, Oksanen et al. 2013). Permutations were set to 999 iterations with a significance value 0.05. For data sorting and transformation of macroinvertebrate, zooplankton and water quality data, we used the packages *dplyr*, *reshape2*, and *tidyr* (Wickham 2012, Wickham et al. 2015, 2017, Wickham & Wickham 2016, Wickham & Bryan 2017). Visualizations were created using packages *ggplot2*, *ggforce, VennDiagram,* and *cowplot* (Chen and Boutros 2011, Wickham 2011, Pedersen 2019, Wilke et al. 2019).

Results

Temperature

Mean daily temperature varied seasonally across treatments (Fig. 3). The BDAs buffered temperatures in comparison to mainstem French Creek and side-channel habitat. Side-channel temperatures were most extreme, exhibiting higher highs and lower lows than both BDA and French Creek (Fig. 3). For example, summer side-channel mean maximum daily temperatures exceeded 20 $^{\circ}$C, while BDA exhibited maximums ranging between 15-20 $^{\circ}$C and French Creek

remained below 15 ℃. During winter, side-channel and French Creek habitats declined to mean minimum daily temperatures of -3 ℃ and 0 ℃ and below. Conversely, BDA minimum temperatures did not fall below 3 ℃.

Chlorophyll a, POM, and Zooplankton

There was no significant difference in suspended cholorophyll *a* between years (rmANOVA, df=2, F=5.14, P=0.05; Table 1). High chlorophyll *a* concentrations in the lentic pre-BDA habitat were likely a result of the entrainment of benthic chlorophyll *a* and may confound comparisons between habitats. Benthic chlorophyll *a* was significantly different between years (rmANOVA, df=2, F=6.32, P<0.05; Table 1). 2018 BDA habitats exhibited higher benthic chlorophyll *a* concentrations than both 2017 pre-BDA and 2019 BDA habitats, however, 2017 and 2019 BDA habitats were not significantly different from one another (TukeyHSD, α=0.05). FPOM was significantly different between years (rmANOVA, df=2, F=5.73, P<0.05; Table 1) with 2017 pre-BDA habitat exhibiting lower FPOM concentrations than 2018 and 2019 BDA habitats (TukeyHSD, α=0.05). There was no significant difference in FPOM concentrations between BDA habitats in 2018 and 2019 (TukeyHSD, α=0.05). Similarly, CPOM was significantly different between years (rmANOVA, df=2, F=6.491, P<0.05; Table 1), however, 2018 significantly differed from 2017 pre-BDA and 2019 BDA habitats. CPOM concentrations were not significantly different between 2017 and 2019 (TukeyHSD, α=0.05). Although zooplankton densities were higher in some BDA habitats, they were not significantly different between years (rmANOVA, df=2, F=0.33, P=0.604; Table 1).

Invertebrates

Macroinvertebrate density was significantly higher in pre-BDA and BDA habitats than French Creek (rmANOVA, df=1, F=16.557, P=0.0097; Table 1 & Fig. 4), but was not significantly different between years (rmANOVA, df=2, F=1.299, P=0.3150). Additionally, the interaction between year and habitat for macroinvertebrate density was not significantly different (rmANOVA, df=2, F=2.41, P=0.1402; Table 1 & Fig. 4). Shannon-Wiener macroinvertebrate diversity was significantly higher in French Creek than BDA habitats (rmANOVA, df=1, F=66.17, P<0.0001; Table 1 & Fig, 4). However, diversity was not significantly different between years (rmANOVA, df=2, F=11.78, P=0.2012), nor was the interaction between year and habitat (rmANOVA, df=2, F=0.014, P=0.9863). Taxa richness was significantly higher in French Creek than BDAs (rmANOVA, df=1, F=62.08, P<0.0001; Table 1 & Fig. 4) and was also significantly different between years (rmANOVA, df=2, F=6.60, P=0.009). The interaction between habitat and year was also significantly different (rmANOVA, df=2, F=3.97, P=0.041).

Beta diversity (species turnover between habitat types) increased after BDA restoration with the development of three distinct clusters (Fig. 5, stress = 0.12). Clusters were significantly separated by habitat type (PERMANOVA, df=2, R2=0.57, P<0.001, Perm=999). Post-hoc pairwise comparisons between groups demonstrated significant differences between all groups, except for pre-BDA and side-channel habitats (Table S1). Tests for heterogeneity of dispersion was insignificant ('betadisper', ANOVA, df=3, F=1.91, p=0.157) indicating that our clusters had similar dispersion and that the PERMANOVA results were valid. Mantel tests demonstrated that community dissimilarity was most strongly correlated with changes in FPOM, suspended chlorophyll *a*, turbidity (NTU), SRP, and nitrate concentrations (Table 2 & S2). All distances in water chemistry were significantly correlated with the macroinvertebrate community dissimilarity, except for benthic chlorophyll *a* and CPOM (α=0.05). Although all nutrients were

significantly correlated with community dissimilarity, differences between sites were small and likely did not have a biological effect on the invertebrate community.

We identified 38 unique indicator species during the study (Table S3). Pre-BDA habitat exhibited six predominantly lotic indicator species. Side-channel habitats exhibited four indicator species which were generally characterized as higher tolerance lotic species (Merritt et al. 2008). BDAs supported eight indicator species including lentic insects, zooplankton, ostracods, sphaeriid clams, and gastropods. Finally, French Creek had 20 indicator species, all of which were insect species, except water mites (trombidiformes).

BDAs enhanced gamma diversity of benthic invertebrates within the French Creek watershed (Fig. 6). Prior to BDA installation, side-channel and French Creek combined richness included 73 distinct taxa. Post BDA installation, gamma diversity increased to 86 and 98 species during 2018 and 2019, respectively. When BDA sites were removed from the 2018 and 2019 analysis, gamma diversity dropped to 73 and 72 species, respectively.

Discussion

Our study examined the effects of beaver dam analogs (BDAs) on the diversity, density, and community composition of benthic macroinvertebrates and zooplankton in a productive salmon stream. We found that our initial hypotheses were supported, as BDA restoration increased invertebrate beta and gamma diversity through the creation of unique and productive lentic habitats within the riparian zone that also enhanced invertebrate density when compared with adjacent lotic habitats. This is the first work, to our knowledge, that has demonstrated how BDA restoration affects landscape level processes including species diversity and habitat heterogeneity.

BDAs and Invertebrate Diversity

Restoration of riparian habitats using BDAs created unique habitat patches that substantially contributed to aquatic invertebrate gamma diversity. Previous studies of natural beaver-mediated habitats suggest that enhanced gamma diversity may be a function of increased habitat heterogeneity associated with beaver foraging activities and changes in hydrology (Hering et al. 2001; Wright et al. 2002; Smith & Mather 2013; Law et al. 2016; Stringer & Gaywood 2016). Similar to natural beaver dams, BDAs created patches of lentic habitat within predominantly lotic ecosystems, increasing habitat heterogeneity across the landscape (Hering et al. 2001; Bush & Wissinger 2016). Our data suggest that this lentic habitat allowed for the colonization of unique species not found in riparian side-channel or mainstem river habitat. For example, pond adapted *Siphlonurus sp.* and copepods were key indicators of BDA habitats. Further, approximately 50% of aquatic invertebrates associated with BDA habitat were unique (i.e., occurring only in BDA habitat). Studies on the direct influence of beaver ponds on gamma diversity are rare; however, Law et al. (2016) found that aquatic invertebrate gamma diversity increased by 28% with the presence of beavers. Similarly, here, we found that the presence of BDAs increased gamma diversity by 15-27%, depending on year. Interestingly, if BDAs were omitted from our analysis, gamma diversity remained relatively unchanged (γ=72-73 sp.) between years. Our findings strongly suggest that BDA restoration can enhance patch heterogeneity and species diversity, similar to processes documented in natural riparian areas (Sabo et al. 2005).

Consistent with our predictions, BDAs also enhanced beta diversity between riparian and mainstem river habitats, with community dissimilarity strongly associated with changes in basal carbon sources and turbidity. In natural beaver ponds, species turnover is associated with

changes in basal carbon resources, particularly the retention of FPOM (McDowell & Naiman 1986; Anderson & Rosemond 2007; Law et al. 2016). Similarly, FPOM and chlorophyll *a* concentrations were strongly associated with species turnover between pre-BDA, BDA, side-channel, and French Creek habitats. For instance, FPOM was, at times, 20 times greater in BDA habitats than adjacent habitats. Increased FPOM accumulation may have also strongly influenced the abundance of unique collector gatherer species, such as *Siphlonurus sp.* Nymphal *Siphlonurus sp.* are strongly adapted to pond and slow-water habitats that contain significant detrital accumulation (Kosnicki & Burian 2003). Chlorophyll *a* was also typically greater in BDAs than other habitats. High levels of suspended chlorophyll *a* concentrations associated with BDAs were likely due to the production of pelagic phytoplankton, whereas concentrations in lotic habitats likely reflected entrained benthic algae (McDowell & Naiman 1986). While macroinvertebrates in lentic environments typically do not benefit from high levels of pelagic productivity, such productivity is fundamental to the persistence of zooplankton (Thorp & Covich 2009), as was observed in BDA habitats.

Irrespective of year, alpha diversity in BDA habitats was lower than mainstem French Creek. In natural beaver ponds, lower alpha diversity is attributed to benthic homogenization associated with fine sediment accumulation and reductions in upstream velocities (Anderson & Rosemond 2007; Law et al. 2016; Washko et al. 2020). The BDA ponds in our study functioned similarly in this capacity, creating ponded regions upstream of BDAs, which facilitated sedimentation. Although inorganic sediment concentrations were not measured, FPOM was typically higher in BDAs when compared to mainstem French Creek. Presumably, increases in FPOM may encourage homogenization of benthic sediments by infilling interstitial spaces of benthos and

reducing habitat heterogeneity at BDA sites, while simultaneously increasing habitat heterogeneity at the landscape scale.

However, BDA alpha diversity increased during the second year of restoration, suggesting that invertebrate colonization dynamics and habitat maturation may also play a role in observed diversity. Restored habitats are seldom fully colonized within a year of installation, but typically accumulate species through time (Williams et al. 2007). This suggests that BDAs may not have attained maximum alpha diversity during the period of study and that dispersal limitation may be a governing factor in the colonization of these habitats. Active dispersers, such as aerial adult aquatic macroinvertebrates, can rapidly colonize new habitats while, passive dispersers or those lacking an adult aerial stage typically rely on stochastic events or assisted dispersal (Cáceres & Soluk 2002). As such, passive dispersers likely take longer to fully colonize newly restored habitats. This was consistent with our study, as passively dispersed *Daphnia* and *Bosmina spp.* were only found in BDAs during the second year of restoration.

Invertebrate Densities

In line with our initial predictions, BDA habitat supported higher densities of benthic macroinvertebrates and zooplankton than mainstem French Creek. Studies of natural beaver dams suggest that macroinvertebrate densities and biomass are typically higher in beaver ponds than nearby stream habitats due to increased retention of carbon resources, such as FPOM and CPOM (McDowell & Naiman 1986; Anderson & Rosemond 2007; Law et al. 2016). As previously discussed, BDAs in our study exhibited elevated levels of FPOM when compared with mainstem river conditions. Most macroinvertebrate genera found in BDAs, based on functional feeding guilds, utilize FPOM resources and likely benefited from enhanced food resources (Kosnicki & Burian 2003; Merritt et al. 2008). The BDA ponds also supported high

densities of zooplankton in comparison to adjacent lotic habitats. Lentic habitat created by BDAs likely promoted pelagic zooplankton colonization through decreased turbulence and increased chlorophyll *a* concentrations as found here (Pace et al. 1992). Turbulence is a key control on zooplankton community persistence, with high turbulence leading to decreased feeding and reproductive success (Sluss et al. 2008). High zooplankton densities have also been found in natural beaver ponds (Czerniawski et al. 2017).

Although our study did not test for differences in macroinvertebrate densities between side-channel and BDA habitats, a qualitative comparison demonstrates that BDA macroinvertebrate densities were more stable than those associated with side-channel habitats. This contrast in invertebrate population stability may be best explained by water year type. Dry years, such as those experienced in 2018, resulted in 88% reduction in macroinvertebrate density in side-channel habitats when compared with BDAs, possibly due to species competition, predation, thermal stress, or more generally, a lack of aquatic habitat (Dewson et al. 2007). At BDA sites, temperatures and wetted areas were not as strongly affected during dry years, likely enabling invertebrates to persist during otherwise stressful periods. The trend was also evident in zooplankton density between habitats. For instance, at times BDAs supported ~ 65 times greater zooplankton densities than the adjacent river habitat. While the primary focus of BDA restoration has emphasized flow and temperature refugia for native salmonids, consistent and calorically rich prey availability, such as zooplankton, within BDAs may be an important consideration with respect to fish habitat utilization and warrants further study (Lusardi et al. 2018, 2020).

Habitat Heterogeneity and Climate Change Implications

Our results suggest that BDAs have the potential to increase gamma diversity and slow species homogenization, while also potentially acting as important climate refuges. In the western United States, climate predictions suggest that aquatic systems will experience extreme droughts, unpredictable flow events, and increases in stream water temperature (Gershunov et al. 2013; Ficklin et al. 2013). These climate driven changes, compounded with habitat modifications such as channel incision, flow regulation, and water extraction, will disproportionally affect native species (Moyle et al. 2017) and could lead to homogenization of regional species pools by selecting for generalist taxa (Ledger et al. 2012). Studies in agricultural settings have found that increasing habitat heterogeneity improves beta diversity, reversing species homogenization patterns (Ponisio et al. 2016). This study is the one of the few to our knowledge to demonstrate this phenomenon in aquatic restoration, where both gamma and beta diversity was enhanced post BDA installation (but see Miller et al. 2010 for discussion of stream restoration and macroinvertebrate richness).

Similarly, we found that BDAs exhibited stable thermal regimes throughout the year when compared with side-channel and mainstem habitats. Temperature extremes have the potential to negatively affect juvenile salmonid rearing in numerous ways. For instance, extreme low temperatures can lead to direct mortality from freezing as well as decreased predator avoidance and growth (Metcalfe et al. 1999). Conversely, high temperatures can lead to fish mortality through indirect and direct mechanisms such as thermally induced starvation, reduced predator avoidance, and increased disease susceptibility (Marine & Cech 2004; Richter & Kolmes 2005). Such periods may be more frequent under future climate scenarios (Mantua et al. 2010). This study shows that BDA habitat buffered water temperature during summer and winter (Fig. 3) when compared with adjacent mainstem habitats.

The role of food in mitigating the effects of water temperature and loss of thermal habitat on native fishes is relatively understudied (Lusardi et al. 2020). BDAs provided stable and abundant food resources for foraging fishes that included high densities of macroinvertebrates and zooplankton. For instance, during the 2018 dry year, BDA habitat supported 31-times greater densities of aquatic macroinvertebrates than side-channel habitat and consistently provided greater zooplankton densities throughout the study period. The implications of this data are important. As water temperatures increase under a warming climate, coldwater fishes must either seek out coldwater refuge or balance the metabolic costs of increasing water temperature with prey resources. Habitats, such as BDAs, that buffer stream water temperatures and exhibit enhanced prey availability, may be uniquely suited to do this, offering a bioenergetic advantage under a shifting climate (Lusardi et al. 2016, 2020).

Acknowledgements

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Table 1. Basal carbon concentrations, zooplankton abundance, and macroinvertebrate metrics by habitat and year as mean (standard error). Values with NA standard error represents collections without replication and single values are reported. Zooplankton density was not measured in French Creek during 2018 due to low flows. *A significant difference between habitats; P<0.05. †A significant difference between years, P<0.05

	Pre-BDA	BDA Pond		French Creek		
	2017	2018	2019	2017	2018	2019
Basal Carbon Concentration						
	0.95	12.2	1.10	0.66	1.35	0.85
Suspended Chl. a (μg L^{-1})	(0.085)	(3.35)	(0.15)	(NA)	(NA)	(NA)
	1,205	4,203	1,196	157	6,764	4,463
Benthic Chl. a (μg m^{-2}) †	(650)	(358)	(114)	(NA)	(NA)	(826)
	13.92	271.29	38.82	46.56	3.73	74.88
CPOM (g m^{-2}) †	(3.84)	(50.54)	(7.13)	(NA)	(NA)	(3.55)
	1.08	8.67	6.31	1.22	0.43	1.18
FPOM (g m^{-2}) †	(0.26)	(1.04)	(1.01)	(NA)	(NA)	(0.14)
Zooplankton Abundance						

Density (ind. m^{-3})	504 (214)	6,915 (3,666)	1,699 (664)	4.49 (1.40)	(NA) (NA)	105
Macroinvertebrate Metrics						
Density (ind. m^{-2})*	8,295 (3,746)	4,278 (924)	7,343 (2,910)	1,091 (70.4)	2,118 (293)	3,710 (1,396)
Shannon-Wiener Diversity*	1.40 (0.67)	1.33 (0.15)	1.66 (0.13)	2.64 (0.02)	2.63 (0.13)	2.96 (0.08)
Taxa Richness*,[†]	26.5 (2.87)	13 (1.69)	25.2 (2.40)	36 (0.58)	38 (5.03)	44.3 (2.60)

Table 2. Summary of water quality and nutrient measurements by habitat and year. 'NA' = measurements were below the limit of detection.

	BDA			French Creek			Side-Channel		
	2018	2019		2017	2018	2019	2017	2018	2019
pH	7.32	7.7		7.05	7.4	7.47	7.35	7.26	7.6
Turbidity (NTU)	1.51	1.1		2.82	2.07	3.3	3.36	2.26	0.6
Total-P (ppm)	0.011	0.003		0.025	0.014	0.009	0.0174	0.02	0.006
SRP (ppm)	0.004	0.002		NA	0.003	NA	0.0042	0.014	0.003
Total-N (ppm)	0.101	0.158		0.504	0.094	0.307	0.6904	0.171	0.178
Nitrate (ppm)	0.005	0.002		0.003	0.001	0.002	0.0004	0.004	0.005

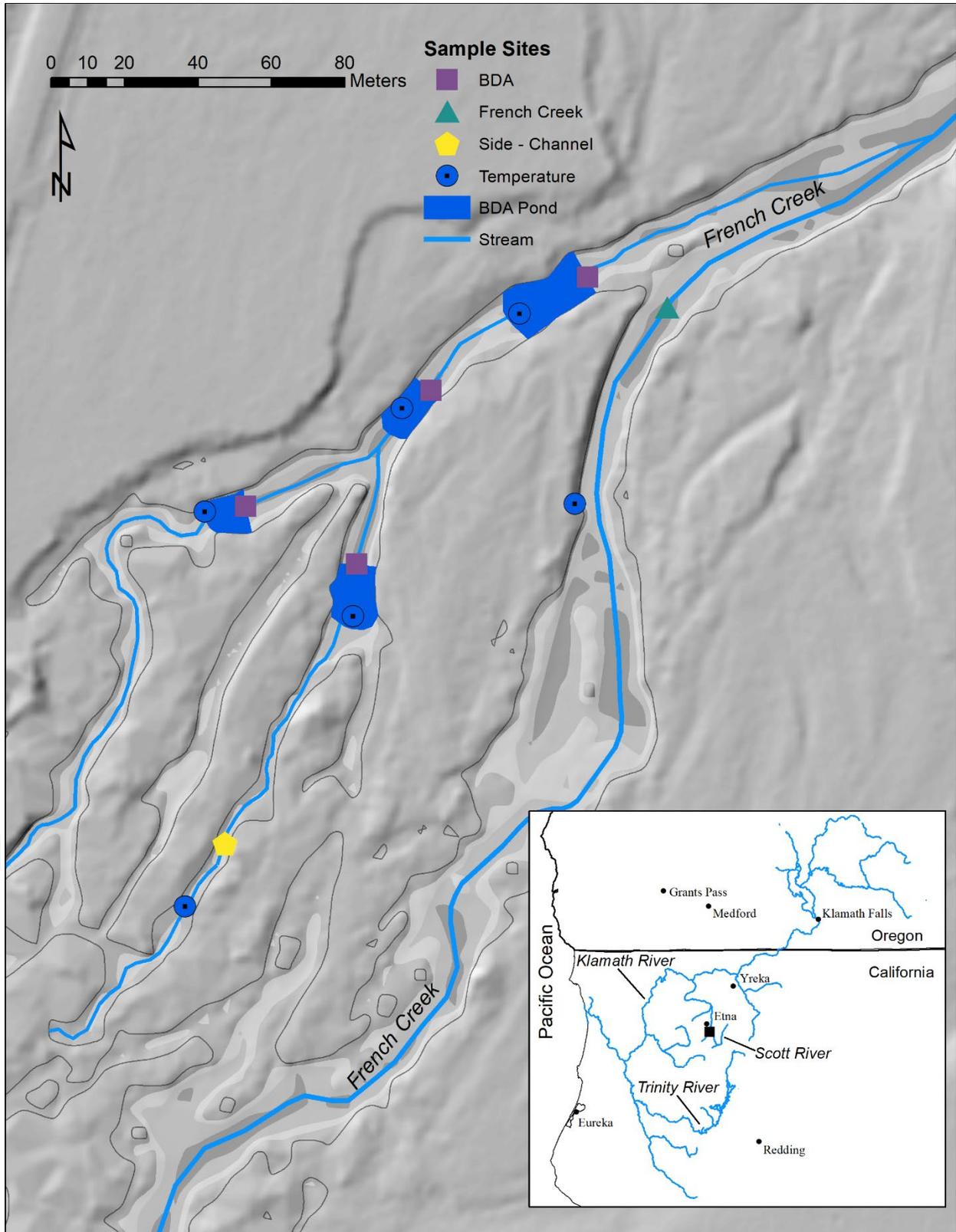|								
Ammonium (ppm)	0.015	0.004	0.004	0.033	0.224	0.0004	0.046	0.031
DOC (mg/L)	2.72	3.55	3.26	1.95	3.77	3.35	3.75	3.82

Figure 1. BDA (purple), side-channel (yellow), and French Creek (green) sampling sites from 2018-2019. Circles indicate temperature sensors sites. Note that samples were taken from BDA habitats prior to installation at BDA locations and were designated side-channel samples.

Figure 2. (A) Shallow and fast side-channel habitat on French Creek during high flows, prior to BDA installation. (B) Deep, slow-water habitat created upstream of a BDA one-year after installation. Prior to the installation of BDAs and the creation of pool habitat, slow-water overwintering habitat for juvenile coho salmon was rare in French Creek. Note rammed poles and interwoven willows of the BDA dam (B).
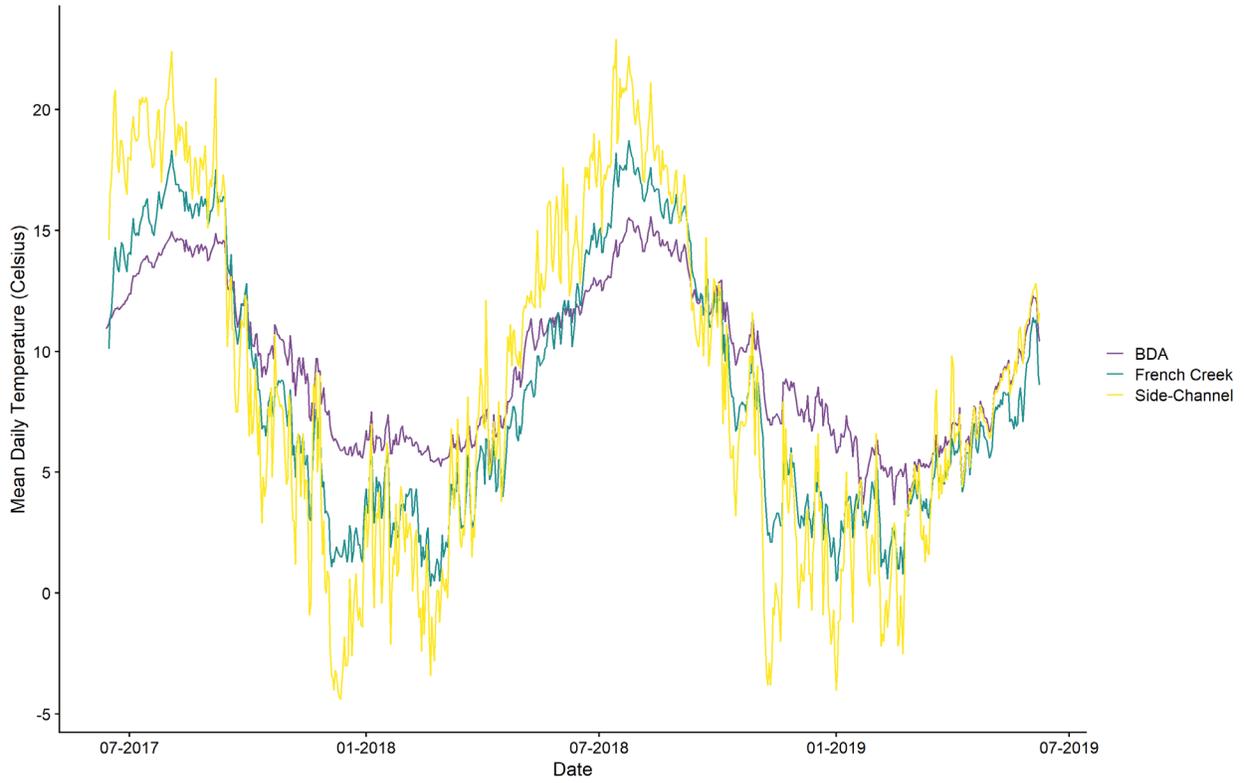
Figure 3. Mean daily temperature in BDA and daily temperature French Creek and side-channel habitat from 6/13/2017 to 6/8/2019.
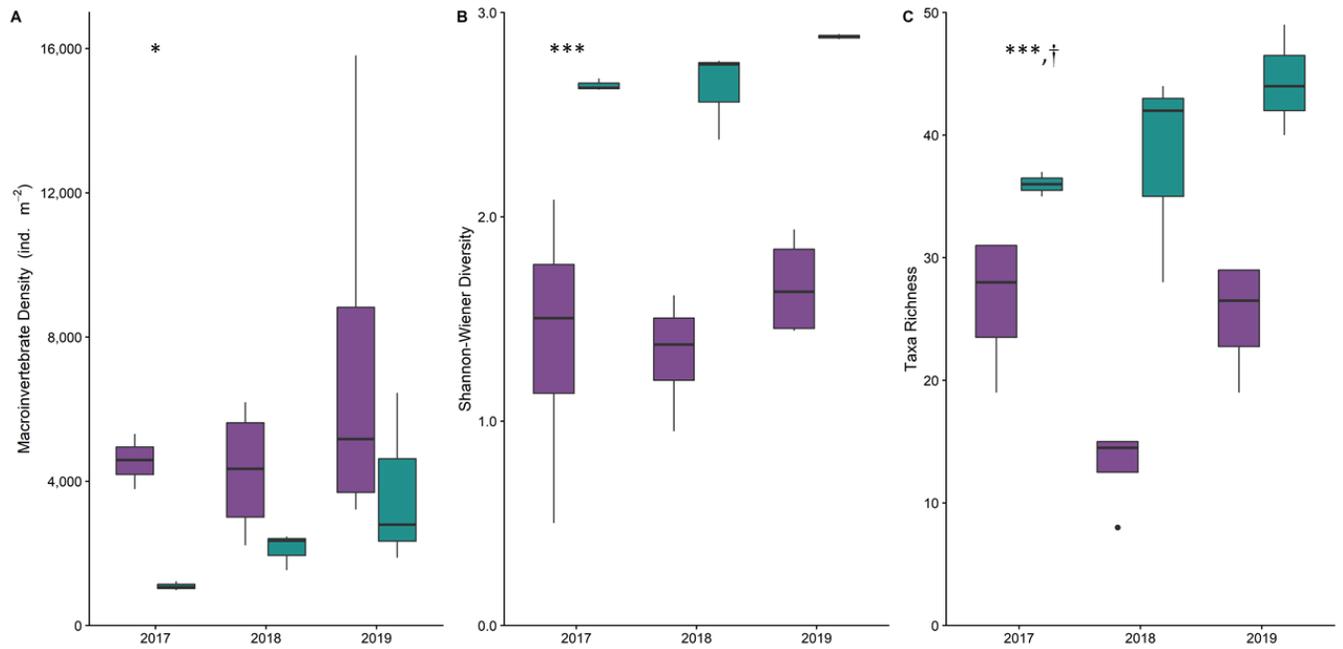
Figure 4. Boxplots of Macroinvertebrate density (A), Shannon-Wiener diversity (B), and taxa richness (C) for BDA (purple) and French Creek (green) habitats for years 2017, 2018, and 2019. Macroinvertebrate samples in 2017 were collected before BDA installation. * Demarks a significant difference between habitat (* P<0.01, *** P<0.0001) and † significant difference between years.
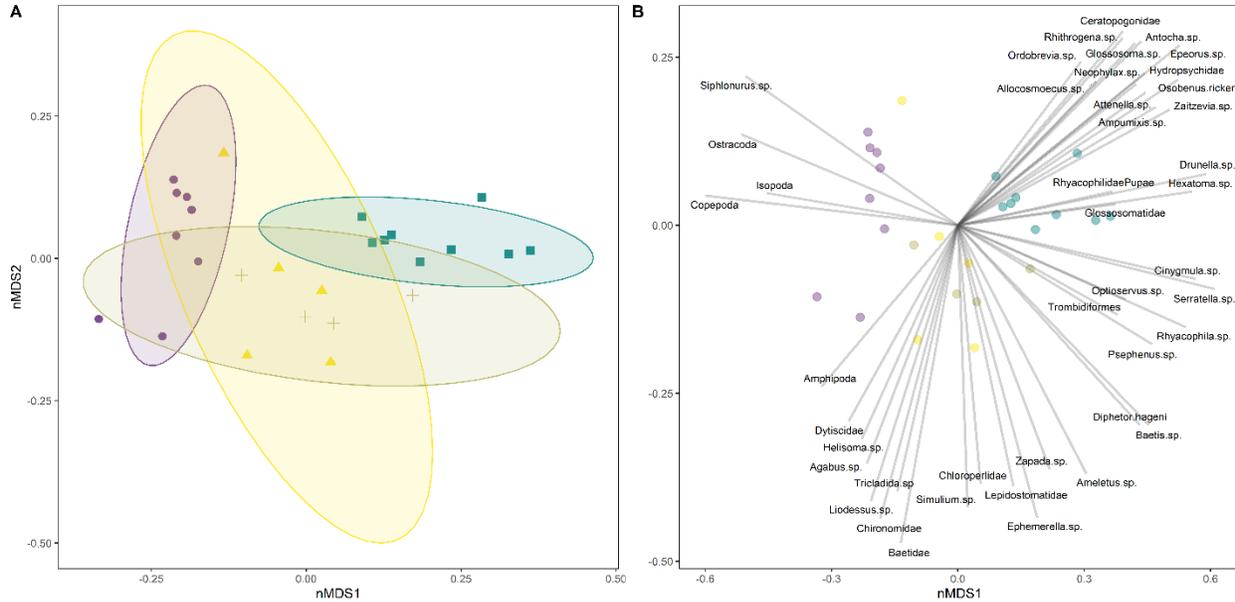
Figure 5. (A) Beta-diversity visualized using Non-metric Multidimensional Scaling (nMDS) of Bray-Curtis dissimilarity distances between pre-BDA, BDA, side-channel, and French Creek macroinvertebrate communities from 2017 to 2019 (stress 0.12). Distance between clusters indicate dissimilarity of aquatic invertebrate communities and beta-diversity between habitats. Habitat groups were significant different from each other (PERMANOVA, R^2=0.57, P<0.001), however, post-hoc analysis demonstrated that pre-BDA and side-channel communities were not significantly different. (B) vectors of species that were highly significant in driving beta-diversity between habitat patches (species vectors P≤0.001). Brown crosses = pre-BDA habitat, purple circles = BDAs, yellow triangles= side-channel, green squares = French Creek.
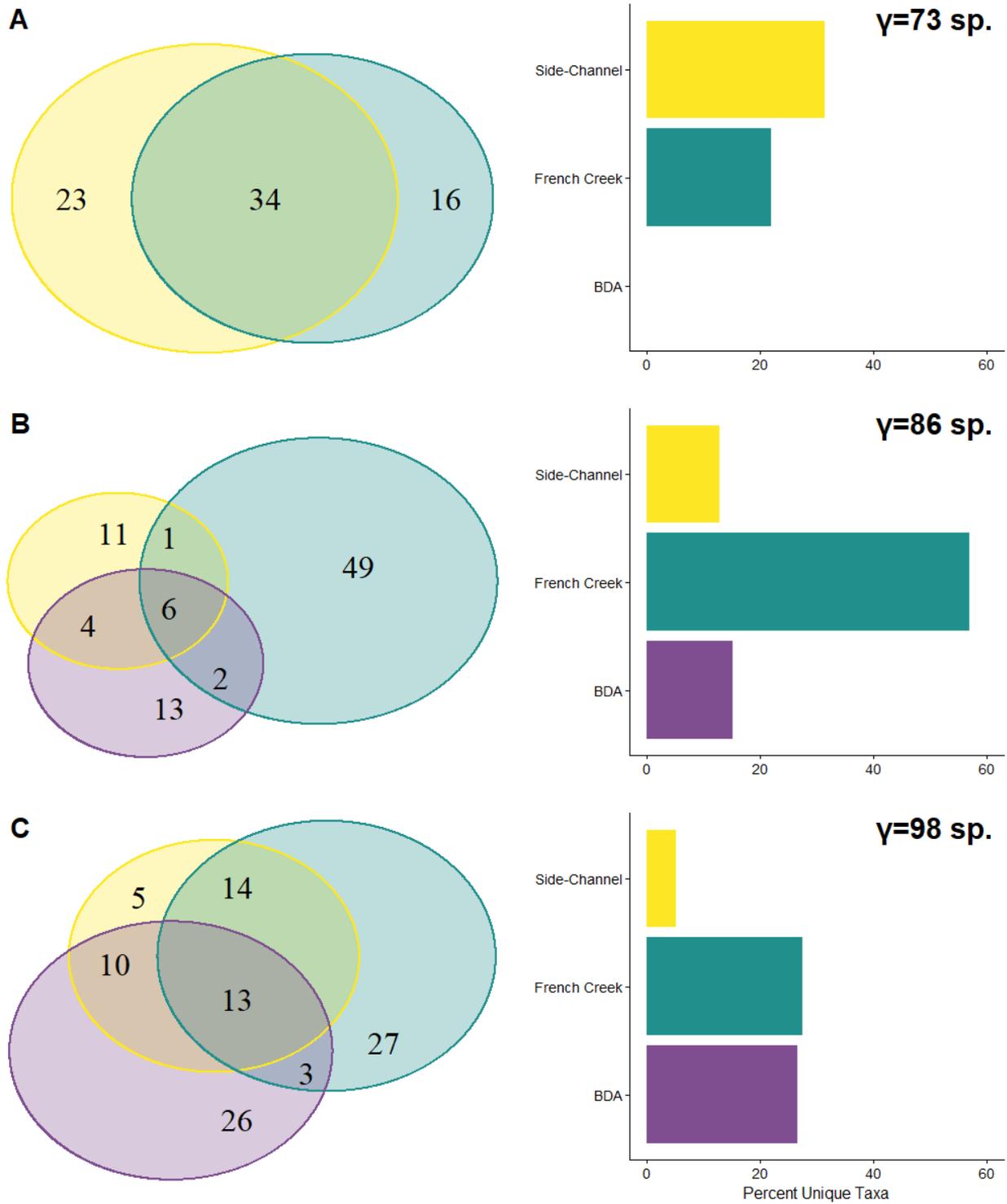
Figure 6. Quantitative Venn diagrams representing shared and unique species found in each habitat for 2017 (A), 2018 (B), and 2019 (C). Number of species found within each circle

represent alpha diversity of the habitat, differences in unique species between habitats represents beta-diversity across habitats, while the total number of species within all the circles represent landscape-level or gamma diversity. Bar plots of percent contribution of unique taxa to total gamma diversity (γ) due to change in landscape-level habitat heterogeneity from BDA restoration (side-channel[yellow], BDA [purple], and French Creek [green]). BDA habitats were not present in 2017.