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RESEARCH ARTICLE

Effect of river and floodplain restoration and reconnection on aquatic macroinvertebrates: seasonal responses over time

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Innovative floodplain reconnection actions are being implemented in various river systems, with the goal of restoring natural processes that support dynamic floodplains, rivers, and aquatic ecosystems. But how effective are these restoration actions? Aquatic macroinvertebrates respond quickly to flow, substrate, and temperature changes. Therefore, we examined the response of benthic macroinvertebrate assemblages to an intensive river and floodplain restoration project in the South Fork McKenzie River of western Oregon (U.S.A.) for 3 years (spring and fall each year) following implementation. The restoration was expected to increase geomorphic heterogeneity and surface water inundation during low-flow conditions, thereby increasing biotic diversity. As predicted, the restored area had more surface water at base flow compared to pre-restoration conditions and, as such, supported two to four times greater macroinvertebrate biomass across the entire wetted area, whereas biomass on a per-square meter scale did not increase throughout the study. Restoration altered the physical conditions of riffle habitat types and macroinvertebrate community structure, reflecting slower-water traits. Although restoration did not appear to change habitat conditions in pools or glides, it did increase the number of these features across the active bottomland. Gamma diversity of macroinvertebrate taxa richness was higher in riffles post-restoration compared to pre-restoration and the control area. Alpha diversity of macroinvertebrate taxa richness did not increase following restoration, but Shannon diversity measures did increase for both riffles and pools, indicating a more even distribution of taxa biomass. These findings support the hypothesis that river and floodplain restoration can increase macroinvertebrate diversity and overall biomass.

Key words: community composition, disturbance, diversity, macroinvertebrate assemblages, process-based, stage 0 restoration

Implications for Practice

- Analysis of aquatic macroinvertebrate community structure, diversity-evenness metrics, and separation of geomorphic habitat types (e.g. pool vs. riffle) will help elucidate responses to river and floodplain restoration projects.
- Restoration effects on macroinvertebrate diversity and biomass were most pronounced in the second and third years following restoration, demonstrating the need for long-term monitoring to evaluate changes in the future.
- Restoration effects were observed in both spring and fall, even though macroinvertebrate taxonomic assemblages were quite different between seasons. However, non-regulated rivers with more extreme seasonal flow regimes may see different restoration effects between seasons.

Introduction

River valleys are inherently dynamic, reflecting patterns of seasonal floodplain inundation and drying. However, broad-scale modifications to river flow regimes (Poff et al. 1997) and direct changes to the geomorphology of rivers (Jones et al. 2001; Knox et al. 2022) have often resulted in simplified river networks with more limited seasonal habitats for native biota. For example, functioning floodplains that are either intact or restored facilitate laterally connected water during high- and low-flow periods (Tockner et al. 2000) and support complex ecosystems perpetuated through flood pulses (Junk et al. 1989). The temporal and spatial dynamic nature of connected floodplains supports diverse habitats that provide optimal places for juvenile salmon rearing under different flow conditions, leading to higher growth rates compared to less complex and less dynamic mainstem river channels (Jeffres et al. 2008).

Precipitous declines in freshwater biodiversity, as well as species-specific listing of aquatic biota under the U.S. Endangered Species Act, are motivating river restoration designed to restore eco-geophysical processes with the goal of enhancing ecosystem health (Tickner et al. 2020). Process-

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based restoration is intended to restore the capacity of systems to functionally process sediments, nutrients, and biota, creating self-sustaining and resilient ecosystems. Restoration efforts that target floodplain reconnection are often designed to restore natural processes (Beechie et al. 2010) with the goal of resetting river geomorphology and hydrologic interactions to facilitate ecological recovery (Cluer & Thorne 2014). Restoration to reset the base elevations of the valley bottom and to allow for a multichannel planform with hydrologic connectivity to the adjacent floodplain (e.g. restoration to stage 0 conditions) reflects a form of process-based restoration that is intended to confer biotic diversity and resilience in response to seasonal patterns of inundation and drying, as well as stochastic disturbances such as wildfire (Pugh et al. 2022). This type of valley reset restoration essentially makes the whole valley floor into active bottomland, even at lower flows.

Benthic macroinvertebrates, those living in and on the streambed, are often used for biomonitoring because they respond quickly to environmental changes, including stream restoration or disturbances that affect the channel substrate, morphology, or flow velocity (Townsend et al. 1997; Relyea et al. 2012; Hubler et al. 2024). Aquatic macroinvertebrates also possess genera-specific functional and habitat trait-based characteristics that can help elucidate changes in restored environments (Poff et al. 2006; Merritt et al. 2019). It is common for macroinvertebrate abundance and taxa richness to initially decline in response to pulse disturbances such as severe floods (Mundahl & Hunt 2011), debris flows (Cover et al. 2010; Foster et al. 2020), dam removal (Claeson & Coffin 2016; Carlson et al. 2018), or stream restoration involving channel morphology reconfiguration and sediment excavation or augmentation (Albertson et al. 2011; Jennings et al. 2023). These initial effects on assemblages are typically driven by substrate scouring, deposition, and instability but are usually short-lived. Longer-term effects are associated with changes to channel morphology, substrate size composition, and riparian vegetation that influence solar insolation, water temperatures, and nutrient dynamics (Cover et al. 2010; Claeson & Coffin 2016; Foster et al. 2020). Various macroinvertebrate taxa recover at different rates. Small-bodied Chironomidae midges and Baetidae mayflies (especially *Baetis* spp.) tend to recover very quickly, a result attributed to their high mobility in drift and as adults, fast growth, and multiple generations per year (Kiffney et al. 2004; Cover et al. 2010; Mundahl & Hunt 2011; Foster et al. 2020). Larger-bodied, slow-growing taxa with less dispersal capabilities (e.g. Ephemerellidae mayflies, Hydropsychidae caddisflies, and Perlidae or *Pteronarcys* stoneflies) may take longer to recover depending on the severity of disturbance and availability of nearby source populations (Cover et al. 2010; Mundahl & Hunt 2011; Foster et al. 2020). Intensive instream and floodplain restoration (e.g. restoration to stage 0 conditions) can cause an immediate pulse disturbance that results in a highly altered and evolving floodplain environment. While these types of restoration projects are becoming more common, comprehensive evaluations of the outcomes are less so (Flitcroft et al. 2022).

At the South Fork McKenzie River (SFMR) and Floodplain Enhancement Project in western Oregon, United States, restoration was implemented on 78.5 ha of the valley bottom along 2 km of the original channel (Fig. 1). The removal of artificial levees, regrading of channel and floodplain surfaces, and the addition of thousands of pieces of large wood led to the formation of an anastomosing (braided) channel planform. The combined effects have reduced longitudinal connectivity in the main channel, increased lateral connectivity, and likely increased vertical connectivity (Hinshaw et al. 2022). Geomorphic metrics of organic cover and substrate were also more spatially heterogeneous in the first 2 years following restoration (Hinshaw et al. 2022), providing greater local-scale habitat

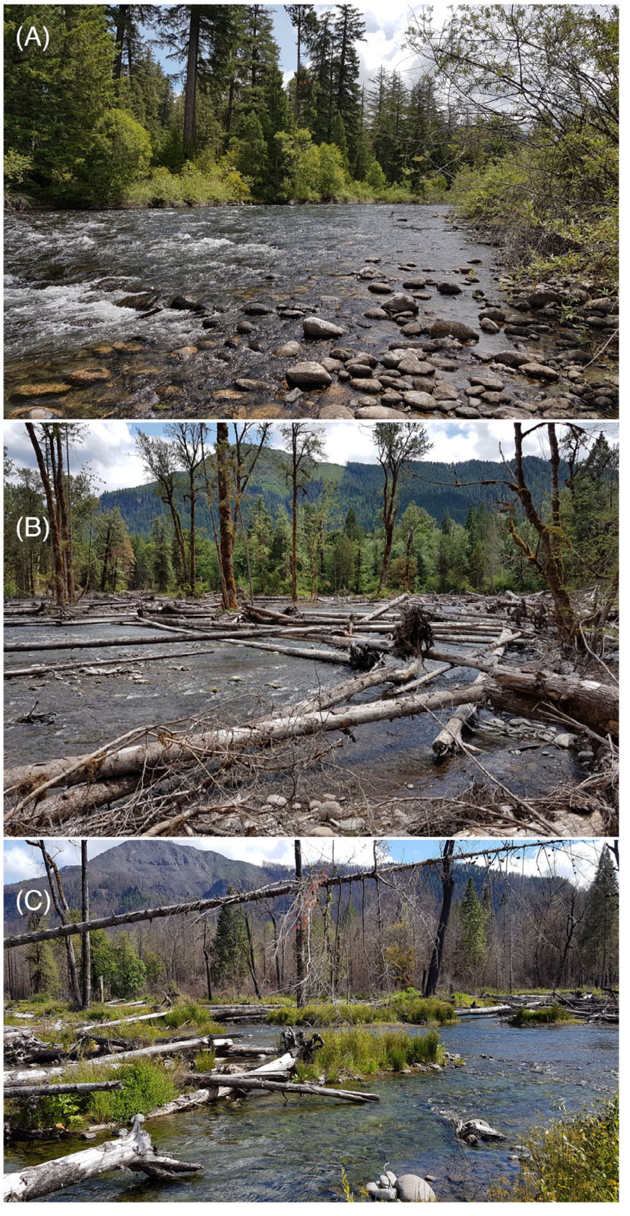

Figure 1. Photos of a (A) control riffle (unrestored; 20 June 2019), (B) treated riffle (1-year post-restoration; 20 June 2019), and (C) the same treated riffle (3 years post-restoration; 8 June 2021) in the lower South Fork McKenzie River, Oregon.

availability for organisms with multiple life cycle stages like aquatic macroinvertebrates. These changes in connectivity are predicted to support a more diverse mix of aquatic biota associated with lotic and lentic habitats, seasonal and perennial waters, and hyporheic upwelling.

This study provides a robust analysis of aquatic macroinvertebrate assemblages and biomass in response to large-scale river and floodplain restoration and reconnection in the SFMR by tracking macroinvertebrate assemblages across two seasons, late spring and fall, for 1 year pre-restoration and 3 years post-restoration, including post-restoration comparisons to an unrestored control reach. Our objectives were to evaluate if and how macroinvertebrate assemblages changed following restoration. We collected benthic macroinvertebrates from distinct waterbodies (pool, glide, or riffle sites) across longitudinal transects spanning the width of the bottomland to capture main and side channel wetted environments. The analysis does not follow a Before-After-Control-Impact (BACI) design because pre-restoration samples were not collected from the control area in the spring. Instead, we compare within-sample metrics (alpha diversity and mean biomass), as well as between-sample variability (beta diversity) and total sample variability (gamma diversity) and total biomass. We also compare macroinvertebrate community biomass structure between seasons, years, and restoration treatment. After restoration, we expected the river to spread out across the floodplain and that sites would reflect physical conditions and macroinvertebrate taxa associated with slower-water habitats that support greater invertebrate biomass. We hypothesized that the restored area would support greater macroinvertebrate diversity due to greater heterogeneity of geomorphic habitat types.

Methods

Study Area

The SFMR is located near Rainbow, Oregon, and drains approximately 560 km^2 (44.1605°N 122.2900°W; base elevation 340 m, Fig. 2). It is the largest tributary of the McKenzie River in the Western Cascade Range of Oregon. The region has a wet, temperate climate that promotes lush forests dominated by Douglas-fir (*Pseudotsuga menziesii*) and Western hemlock (*Tsuga heterophylla*) with Red alder (*Alnus rubra*) and Black cottonwood (*Populus trichocarpa*) adjacent to stream channels. The river provides habitat for spring Chinook salmon (*Oncorhynchus tshawytscha*), Bull trout (*Salvelinus confluentus*), and Pacific lamprey (*Entosphenus tridentatus*), among other species.

The SFMR restoration project area has an approximately 1% slope over a length of 3.1 km, and the valley bottom ranges in width from approximately 500–680 m. The project area lies 3.2 km downstream of Cougar Dam and Reservoir, built in 1963, which regulates discharge, water temperatures, sediment supply, wood, and nutrients to the lower river. The regulated discharge reduces the variability of high and low flows, but a seasonal flow regime is maintained to accommodate the life history of migrating salmonids (Fig. S1). Construction of Cougar Dam and other human modifications channelized the stream and severed river–floodplain connectivity. The resulting configuration was a single-thread, high-energy, transport-dominated channel, with few secondary channel areas that intermittently held water. Prior to restoration, the main channel was incised, armored with boulders, with little to no fines or gravel-sized substrate. The main channel and few side channels had limited pool habitat (12% area) and woody debris (3.8 pieces/km) (Bittner & Mattson 2006).

Restoration Implementation

River and floodplain restoration and reconnection along the SFMR had two main objectives: (1) increase geomorphic heterogeneity to create more habitat diversity for aquatic biota and (2) increase hydrologic connectivity and restore natural processes to recover a complex system that is resilient to disturbances. Unlike other river restoration projects that occur at the river scale only, this restoration project utilized the entire bottomland to disperse surface flow into multiple channels via an anastomosing planform following the stage 0 theoretical condition (Cluer & Thorne 2014) and implemented using the geomorphic gradeline approach (Powers et al. 2019).

The SFMR restoration, as of 2023, occurred in two phases over 2 years starting at the confluence of the South Fork with the McKenzie River mainstem and moving upstream (Fig. 2). Phases 1 and 2 were implemented in the summers of 2018 (59.5 ha) and 2019 (19 ha), respectively, across the full extent of the bottomland. During project construction, some flow was held back at the upstream dam, and the rest of the flow was redirected down a relic side channel to allow access by bulldozers and large cranes to the restoration area. Generally, the channel and floodplain were graded to the average slope of the valley (i.e. the geomorphic gradeline). Native alluvium was redistributed from leveed banks and higher portions of the floodplain to incised channels and other lower portions of the floodplain (higher or lower portions were determined relative to the geomorphic gradeline). A few deeper pools and higher elevation vegetated islands were left to enhance habitat complexity. Many unanchored large wood pieces, greater than 20.3 cm in diameter, were added across the newly connected bottomland (Fig. 1). Phase 1 placed 2675 wood pieces, and phase 2 placed 1264 wood pieces. Wood was distributed in a lattice configuration fairly evenly across the bottomland. This allowed the water to move the substrate and wood after restoration in accordance with natural channel evolution and essentially made the entire valley floor into bottomland. The regulated flow of the SFMR is such that even at low summer flows, the reconnected floodplain channels were mostly inundated and perennial.

Inundated Area

We estimated the inundated area at base flow across the project area from multi-spectral orthoimagery maps developed pre- and post-restoration. Pre-restoration data was collected in summer 2016 (discharge 8.78 m^3/s) by the Oregon State Imagery Program. Post-restoration data was acquired in summer 2020 (discharge 14.22 m^3/s) by drone. Imagery was analyzed in ArcGIS Pro (ver. 2.4), estimating inundated area using the supervised

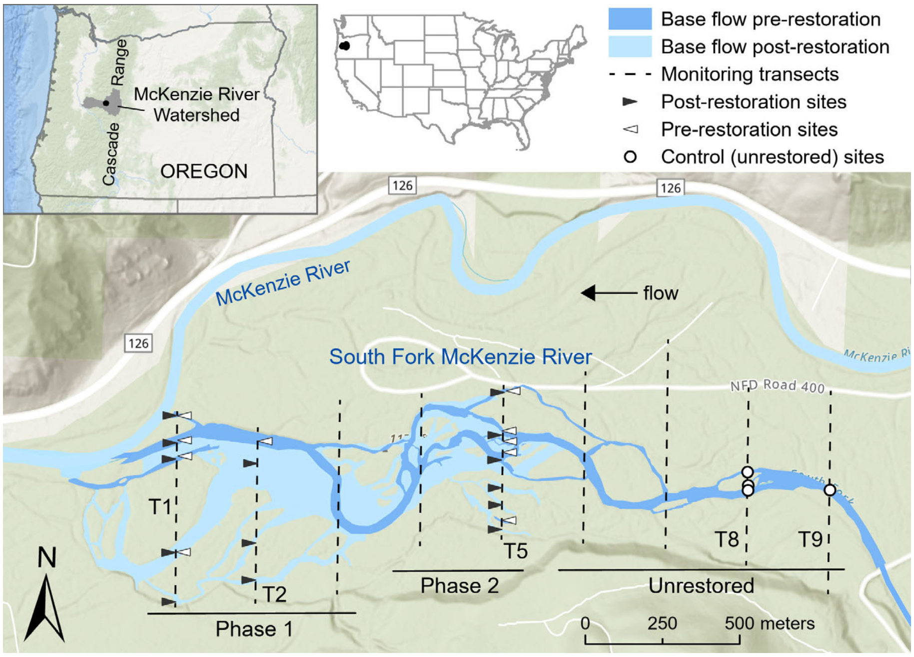

Figure 2. S.F. McKenzie River restoration area (downstream transects 1–5) and control/unrestored area (upstream transects 6–9) with base flow inundated areas from pre- and post-restoration phases. Phase 1 was restored summer 2018 and phase 2 was restored summer 2019. macroinvertebrate samples were collected at all separate waterbodies (sites) crossing transects 1, 2, 5, 8, and 9.

classification tool and a normalized difference vegetation index derived from the imagery for each year (Flitcroft et al. 2022). Although the area of inundation post-restoration was observed to change slightly from year to year and between late spring and fall (authors personal observation from field visits, Shannon M. Claeson, 2020-2021, USFS), the change was minor compared to the change due to the restoration.

Sampling

The large extent and geomorphic complexity of the restored areas led to difficulties with traditional channel-scale reaches for macroinvertebrate sampling, partly because we did not know where water would be present after restoration. As part of a larger monitoring effort, longitudinal transects spanning the width of the bottomland were established prior to restoration within the project and control areas (Fig. 2). This cross-valley transect-based approach allowed for the sampling of different waterbodies as they developed over time. For macroinvertebrate sampling, we selected a few transects predicted to be associated with Earth movement and levee deconstruction that would also contain both mainstem and floodplain habitats, and control transects upstream of the restoration area. Uniformity of habitats and channel bedforms in the unrestored control area allowed the selection of two transects (T8 and T9) to capture available conditions. Due to the extensive modification and complexity of the restored areas, three transects (T1, T2, and T5) were surveyed to capture habitat and biological variability. Macroinvertebrate sample collection began in early fall 2017 and continued in the late spring (May/June) and early fall (September/October) through 2021; except no control samples were collected in spring 2018 and no pre-restoration or control samples in fall 2018 (Table 1).

We collected macroinvertebrate samples at all distinct (physically separated by land) waterbodies (i.e. sites) along the selected cross-valley transects. To be sampled, each site had to have surface water at least 10 cm deep and an area of at least 10 m^2. Samples were collected with a kick-net (500-µm mesh size, 0.093-m^2 collection area) against the streambed and hand-scrubbing the substrate to a depth of approximately

Table 1. Number of macroinvertebrate samples collected from separate waterbodies (sites), categorized by habitat type, in the restoration and control areas of the lower S.F. McKenzie River (total $n = 107$). Spring samples were collected in June and fall samples were collected in September–October of each year. No control samples were collected spring 2018. No fall samples were collected in 2018. *Post-wildfire samples (Holiday Farm Fire, September 2020).

				Restore	*Restore*	*Control*
Season	*Year*	*Time*	*Total*	*Pool–glides*	*Riffles*	*Riffles*
Spring	2018	Pre	10	3	7	0
	2019	Post	12	3	5	4
	2020	Post	17	6	7	4
	2021	Post*	15	3	9	3
Spring	Total		54			
Fall	2017	Pre	13	2	7	4
	2019	Post	12	3	5	4
	2020	Post*	12	3	5	4
	2021	Post*	16	4	9	3
Fall	Total		53			

10 cm for 1 minute. In low-flow areas, the substrate was alternately disturbed and waved by hand into the sampling net or swept up with the net. At each site, 10 subsamples were spatially distributed across the site and within 10 m upstream and 10 m downstream of the transect, combined in the field (1 sample/site/date) and preserved in 80% ethyl alcohol for lab identification and enumeration. For each sample, we recorded simple environmental conditions: (1) site wetted width and length (if not continuous, e.g. pond); (2) maximum depth and subsample depths; (3) overall site geomorphic habitat type (riffle, glide, or pool); (4) canopy cover (visually estimated %); and (5) subsample substrate % size category (fines, gravel, cobble, boulder, and bedrock) which were combined for a site total % per substrate categories.

In the lab, composited macroinvertebrate samples were subsampled for a minimum of 600 individuals. Most macroinvertebrates were identified to genus or species (Merritt et al. 2019), except for some non-insects that were assigned higher taxonomic levels (Acari [superorder], Ostracoda [class], Nematoda [phylum], Oligochaeta [subclass]). To estimate biomass (dry mass, mg/m^2), the body length of each individual was measured to the nearest 0.5 mm in length, sorted by size class, counted, and converted to biomass with family-specific length to dry mass regressions (Benke et al. 1999). We divided subsample results by the fraction subsampled to obtain full-sample estimates standardized to 1 m^2. We classified aquatic invertebrates into six trait categories (Poff et al. 2006; Merritt et al. 2019) related to life history, thermal or flow regime, or food resources: (1) generations per year (multivoltine [MV], univoltine [UV], and semivoltine [SV]); (2) mature body length (small <9 mm, medium 9–16 mm, and large >16 mm); (3) thermal preference (cold stenothermal, cool–warm eurythermal, and warm eurythermal); (4) habitat affinity (lentic, lotic, lentic, and lotic); (5) habit (burrow, climb, sprawl, cling, and swim); and (6) functional feeding groups of collector–gatherer (CG), collector–filterer (CF), scraper (SC), shredder (SH), and predator (PR). Taxa in the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) were used to calculate EPT taxa richness and biomass.

Wildfire

A wildfire in early September 2020 burned across the lower S.F. McKenzie River and floodplains (Holiday Farm Fire, 70,170 ha). The entire restored and control area of the SFMR burned, with most of the project area experiencing 51–75% vegetation basal area mortality (MTBS 2024). Unfortunately, there were no river or floodplain sections that did not burn to compare against fire-affected sites. For most analyses, we present results over a temporal scale by season and year. If there was a fire effect, we would expect to see a clear change or shift in the temporal pattern after the fire (samples collected fall 2020 and spring/fall 2021), although we would still not be able to definitively determine if the change was due to the fire or continued changes to the system post-restoration over time. Because of these limitations, we do not perform any statistical tests to measure fire effects.

Data Analysis

This study is a comparison of restoration to control (unrestored) samples for 3 years post-restoration, with 1 year pre-restoration samples from the restored area. Samples were usually collected in late spring and early fall. However, pre-restoration samples were not collected from the control area in the spring, thus the analysis does not follow a BACI design. Sample size was also uneven between the restoration and control areas (Table 1) due to unequal sampling effort among years: (1) control transects were not sampled in spring 2018, (2) no samples were collected in fall 2018 due to restoration implementation taking longer than anticipated, and (3) restored transect 5 was not sampled in 2019. Sample size also varied over time because of the variability of waterbodies present in the restoration area at different flows, especially post-restoration as more water was spread across the floodplain.

Due to these sampling design complications, we utilize the following simple statistical and graphical methods to illustrate differences between the restoration and control samples, pre- and post-restoration:

(1) Alpha, beta, and gamma diversity estimates,
(2) Plots of diversity and biomass ranges,
(3) Non-metric multidimensional scaling (NMDS) of macroinvertebrate community biomass with joint plots to display correlated taxa traits and environmental conditions,
(4) Indicator species analysis to highlight taxa driving variation in the community structure.
(5) Multi-response permutation procedure to test for differences in community structure.

Macroinvertebrate alpha, beta, and gamma diversity was assessed using species presence/absence data (taxa richness), except for the Shannon diversity index, which was assessed using species biomass (mg/m^2). Within-sample variation, alpha diversity, as represented by taxa richness, was the number of taxonomically unique species present per sample. Alpha diversity, as represented by the Shannon diversity index which compares the proportional biomass of species, was calculated using the function “diversity” (vegan package, v2.6.6.1) of R Statistical Software (v4.4.0, R Core Team 2024). Taxa variation among samples, beta diversity, as represented by Jaccard’s dissimilarity index (range 0–1, with 1 indicating completely different taxa), was calculated with the R function “vegdist” (vegan package, v2.6.6.1). Total diversity, gamma diversity, was the total number of taxonomically unique species present in a group of samples. Because gamma diversity is extremely sensitive to sample size and sizes differed considerably among restoration treatment groups, we used rarefaction to calculate 95% confidence intervals for richness counts at the smallest group sample size with the R function “estimateD” (iNEXT package, v3.0.1). Rarefaction uses random resampling techniques to estimate taxa counts at reduced sample sizes. Diversity metrics were tabulated by restoration treatment (control vs. restore), time (pre- vs. post-restoration), and habitat type (riffle vs. pool–glide). Season is not included as a grouping variable because of the resulting small sample size of some groups by habitat type that would limit analysis, and the overall results are the same as when seasons are combined.

While the macroinvertebrate biomass per square meter of benthos can be helpful to compare biomass density, we also estimate the total biomass across the entire inundated area for the restored and control areas, for each year pre- and post-restoration, and for each season. We calculated the mean macroinvertebrate biomass (mg/m^2) from samples collected per restoration Phase per year and season (phase 1: mean of T1 and T2 samples, phase 2: mean of T5 samples). We then multiplied each phase's mean biomass by each phase's wetted area (m^2) at base flow pre-restoration and post-restoration (see Section 2.3) per year and season. We recognize that this estimate is coarse and makes some assumptions: (1) macroinvertebrate sample biomass is averaged together regardless of habitat type because wetted area was not measured for each habitat type, and (2) pre- and post-restoration wetted area was only measured once (2016 and 2020, respectively) and in the summer, even though macroinvertebrate biomass was measured annually and seasonally.

We used NMDS with Sorensen distance to explore differences in macroinvertebrate community structure among restoration treatments, habitat types, and season. Ordinations were performed on macroinvertebrate biomass (mg/m^2) that was log-transformed to preserve zeros $\log_{10}(x + 1)$. Taxa with low sample frequency (54 taxa present in one or two samples only) were not included in the analyses. Three different NMDS ordinations were performed: (1) complete dataset of 107 samples and 212 taxa, (2) riffle dataset of 80 samples and 182 taxa, and (3) pool–glide dataset of 27 samples and 112 taxa. Correlated environmental or taxa trait variables (Pearson correlation, $r \geq |0.45|$) are displayed as joint-plot vectors on the ordination plots. Vector direction indicates positive association, and length indicates correlation strength.

To test differences in macroinvertebrate biomass community structure among treatment groups by season and habitat type, we used non-parametric multi-response permutation procedures (MRPP; McCune & Grace 2002) which provide a likelihood p value and an effect size (A) that measures the chance-corrected, within-group homogeneity ($A > 0$ indicate stronger differences in assemblages and $A \leq 0$ indicate no difference between groups). We combined the riffle fall control pre- and post-restoration samples into one control group because there were not enough control pre-restoration samples to use as its own group in a meaningful test, and the NMDS plot of riffle samples showed overlapping pre-and post-restoration control samples.

Indicator species analysis (ISA; Dufrêne & Legendre 1997) was performed on the riffle dataset of macroinvertebrate biomass to identify key taxa influencing community structure differences by restoration treatment. The significance of each taxon's indicator value (IV) was evaluated using Monte Carlo tests with 1000 permutations. Only taxa with IVs greater than 25 and p value less than 0.05 are reported. The NMDS, MRPP, and ISA analyses were performed using PC-ORD v.7 (MjM Software, Gleneden Beach, OR, U.S.A.).

Results

Physical Conditions

Prior to the restoration in SFMR, and in the upstream control reach, much of the water was constrained to a single-thread, high-energy, transport-dominated system with little wood and coarse substrates. After restoration, even at low flow, the water spread out across the floodplain and flowed through multiple, often wide, anastomosing channels. The addition of nearly 4000 pieces of large wood greatly increased the amount of large wood throughout the floodplain and wetted channels compared with pre-restoration and control reaches.

Geomorphic habitat types after restoration included more pool or glide waterbodies (i.e. sites) compared with pre-restoration and control reaches (Table 1). The control reach contained no pools or glides, only riffles. Along transects T1, T2, and T5 pre-restoration, only three pool–glide waterbodies existed. Two of these sites had enough water for macroinvertebrate sampling in fall 2017, and all three sites were sampled in spring 2018, for a total of five pre-restoration pool–glide samples. In comparison, eight pool–glide waterbodies existed post-restoration: three were present before and after restoration, three were created post-restoration (new channels or old side channels that gained water post-restoration), and two were riffles pre-restoration that became glides post-restoration. These post-restoration pool–glide sites were only semi-connected to the main channels but were mostly perennial.

Substrate size compositions of riffles, on average, shifted from mostly cobble (56%) and boulder (23%) in the pre-restoration and control samples to fines (silt and sand, 23%) and gravel (55%) post-restoration (Fig. S2). Pools remained primarily composed of fines pre- to post-restoration (mean 97–88%) but shifted slightly post-restoration to include some gravel (11%). Glides shifted from fines (55%), gravel (30%), and cobble (10%) pre-restoration to more fines (67%) and cobble (17%) and less gravel (10%) post-restoration.

Inundated Area

An important goal of river and floodplain reconnection is to increase the distribution of water across the valley bottom at base flow (Fig. 2). At SFMR, restoration phases 1 and 2 combined, the post-restoration inundated area at base flow was nearly 3× larger than pre-treatment. Phase 1 post-restoration wetted area was 3.5× larger than pre-treatment (pre 4.5 ha to post 15.4 ha), and phase 2 post-restoration wetted area was 2.2× larger than pre-treatment (pre 3.8 ha to post 8.4 ha). Inundation at the upstream control area (5.1 ha) remained the same during the study.

Macroinvertebrates Overall

We identified 266 aquatic macroinvertebrate taxa collected throughout the study, of which 114 were EPT, 67 were Chironomidae, and 26 were non-insects (including 10 snails). Many of these species were infrequently observed (e.g. 20% were found in only one or two samples). Of the 107 macroinvertebrate samples collected, most samples were from the restored floodplain due to more water inundation creating more distinct waterbodies (i.e. sites) along the longitudinal transects, as opposed to the control area.

Macroinvertebrate biomass per square meter of streambed from restoration and control samples tracked similarly over time, before and after restoration, except in 2019 when biomass per square meter is greater from control samples than from restored samples (Fig. 3A). However, after restoration, more floodplain area was inundated with water, providing more habitat for aquatic macroinvertebrates. When total macroinvertebrate biomass was estimated across the entire wetted area of the restoration and control areas per year, we found large differences between these areas. Total macroinvertebrate biomass was relatively low and similar between restoration and control areas during pre-restoration and in 2019, but in 2020 and 2021, restored biomass increased 2-4-fold compared to control biomass (Fig. 3B).

The macroinvertebrate community structure of all 107 samples was primarily organized by habitat type (pool, glide, or riffle) and season of collection (spring or fall). The all-sample NMDS produced a two-dimensional solution with moderately low stress (0.15) and explained 88% of the variation in assemblages (Fig. 4). Axis 1 explained 76% of the variation and was driven by a gradient of pool–glide–riffle habitat types and lentic taxa associated with slower currents and fine substrate (Dytiscidae $r = -0.77$, *Callibaetis* $r = -0.73$, *Dixella* $r = -0.66$, Culicidae $r = -0.57$, and *Phaenopsectra* $r = -0.55$) to lotic taxa associated with riffles and coarse substrate (*Hydropsyche* $r = 0.74$, *Rhyacophila brunnea/vemna* group $r = 0.72$, *Ampumixis dispar* $r = 0.68$, *Micrasema dimicki* $r = 0.67$, and *Hesperoperla pacifica* $r = 0.64$). Axis 2 explains 12% of the variation and is split between fall samples with greater predator biomass (*Zapada cinctipes* $r = -0.67$, *Rhithrogena* $r = -0.61$, Capniidae $r = -0.59$, *Lepidostoma*

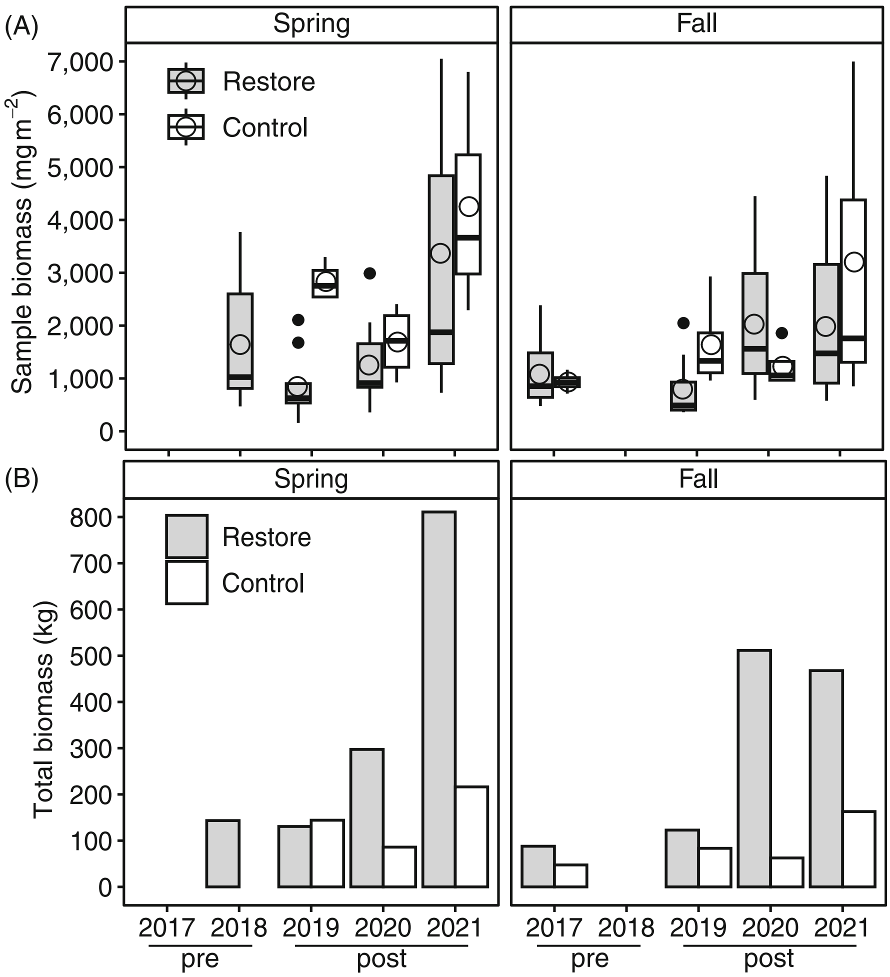

Figure 3. Macroinvertebrate biomass by (A) sample, per square meter of streambed (log10-transformed, mg/m^2), and (B) total, across the entire wetted area of the restoration and control areas per year (kg), grouped by restoration treatment (restore vs. control). Pre-restoration samples were collected in fall 2017 and spring 2018, and post-restoration samples were collected in 2019–2021. Boxplots show the median (dark bar), mean (hollow circle), first and third quartiles (box), lower and upper whiskers, which extend to 1.5 times the inter-quartile range (vertical lines), and outlying points (solid dots). See Figure 1 for wetted areas pre- and post-restoration.

$r = -0.50$, *Skwala* $r = -0.47$) versus spring samples with greater scraper biomass (*Drunella coloradensis/flavilinea* $r = 0.71$, *Matriella teresa* $r = 0.68$, *Cinygmula* $r = 0.60$, *Epeorus albertae* group $r = 0.59$, *Baetis alius* $r = 0.57$, and *Diphetor hageni* $r = 0.52$). Macroinvertebrate assemblages will differ by season due to taxon-specific life history, yet the seasonal difference observed here explained very little of the variation in the ordination compared to the variation explained by habitat type. Therefore, the following analyses focus on differences within habitat types, while still showing seasonal responses when appropriate.

Macroinvertebrates in Riffles

Restored riffle samples supported a greater number of macroinvertebrate taxa overall (gamma diversity) compared to control and pre-restoration samples, even after gamma diversity estimates were rarified to the lowest sample size of four samples (Table 2). Mean sample richness (alpha diversity) was not different between restored and control riffle samples (Table 2), yet there was an increase in mean Shannon diversity of taxa biomass from the restored samples, which was most pronounced in the latter 2 years of the study (Fig. 5A). Jaccard dissimilarity among riffle samples (beta diversity) was similar between restored pre- and post-restoration samples but higher than control samples (Table 2).

The restoration had the strongest effect on macroinvertebrate community structure in riffles for both spring and fall (Fig. 6A). The NMDS of riffle samples produced a three-dimensional solution with moderately low stress (0.14) and explained 84% of the variation in the data, with 21% explained by axis 1 (restoration), 48% by axis 2 (season), and 15% by axis 3 (not shown). As with the NMDS ordination of all samples, there were clear differences in the riffle community structure by season (axis 2). Spring samples were associated with proportionately more biomass comprised of scraper and cold thermal preference individuals. Fall samples were associated with proportionately more biomass comprised of predator and cool–warm thermal preference individuals.

Even though the macroinvertebrate community structure of spring and fall riffle samples was different, both seasons show a similar shift in community structure post-restoration (axis 1) and were correlated with many of the same taxa traits and environmental conditions. Riffle specific MRPP comparisons indicated stronger group differences between the post-restoration samples compared to the pre-restoration or control groups ($A > 0.08$, $p \leq 0.0001$), and weaker group differences between pre-restoration and control ($A = 0.03$, $p > 0.001$), for both spring and fall (Table S1). The post-restoration riffle samples had taxa associated with higher Shannon diversity, more total and lentic taxa, and proportionately more biomass comprised of lentic and burrowing individuals. Restored riffle samples also had environmental conditions associated with more silt/sand, gravel, large wood, and emergent vegetation. These taxa and environmental traits are attributes of slow water habitats. In contrast, the unrestored samples (control and pre-restoration) were associated with proportionately more biomass comprised of clinger and collector-filtering individuals, and more cobble and boulder—attributes of faster flow with coarse, stable substrate.

Results from the ISA found 28 indicator taxa for restored riffle samples and 19 indicator taxa for unrestored riffle samples, control and pre-restoration combined (Table S2). Indicator species for restored samples were comprised of more lentic taxa (11% lentic, 21% lotic) compared to indicator species for unrestored samples (0% lentic, 47% lotic). Lentic taxa biomass also generally increased over time post-restoration, primarily in the second and third years after restoration (Fig. 5B). Lentic mean % biomass prior to restoration and in control reaches was usually much less than 1% per season per year and in the first year after restoration was still less than 2% per season but increased to 3–7% in the second and third years after restoration. Regarding taxa life history, restored samples had fewer SV (less than

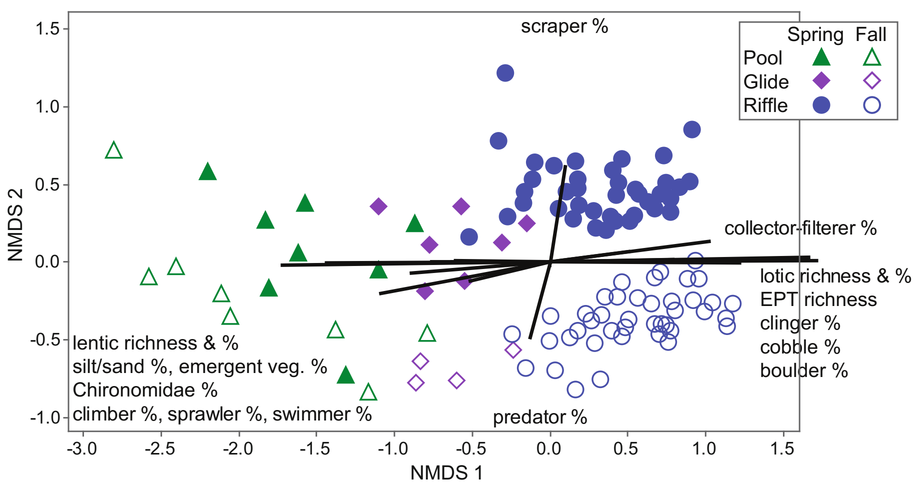

Figure 4. Ordination plot of all macroinvertebrate assemblage samples collected in the spring and fall from pools, glides, and riffles ($n = 107$). Samples are distributed by habitat type (NMDS 1) and season (NMDS 2). Joint-plot vectors show the direction and magnitude of taxa trait or environmental variables correlated with the NMDS ordination axes ($r \geq |0.45|$). Taxa trait % variables are biomass proportions and richness variables are taxa counts.

Table 2. Macroinvertebrate alpha, beta, and gamma diversity metrics by habitat type and restoration treatment group. Alpha and beta metrics are sample means with 95% confidence intervals (CI: lower-upper). Gamma metrics are the observed number of taxa followed by rarefaction estimates with 95% CI calculated at the lowest sample size (*n*) within each habitat type. Letters denote mean metric rankings and overlapping CI.

Habitat	*Riffle*	*Riffle*	*Riffle*	*Riffle*	*Pool–glide*	*Pool–glide*
Treatment	*Control*	*Control*	*Restore*	*Restore*	*Restore*	*Restore*
Time	*Pre*	*Post*	*Pre*	*Post*	*Pre*	*Post*
n	4	22	14	40	5	22
Alpha diversity (taxa richness)						
Mean	53.0	53.8	52.2	59.5	42.4	41.6
95% CI	43.3–62.7	49.7–58.0	47.0–57.4	56.4–62.5	33.8–51.0	37.5–45.7
Ranking	abc	ab	ab	a	bc	c
Alpha diversity (Shannon diversity of taxa biomass)						
Mean	2.23	2.30	2.10	2.75	1.66	2.28
95% CI	1.83–2.62	2.13–2.46	1.89–2.31	2.63–2.88	1.31–2.02	2.11–2.45
Ranking	bc	b	bc	a	c	b
Beta diversity (Jaccard dissimilarity of taxa richness)						
Mean	0.56	0.62	0.65	0.66	0.75	0.73
95% CI	0.49–0.63	0.61–0.63	0.64–0.66	0.65–0.66	0.69–0.80	0.72–0.74
Ranking	c	c	b	b	a	a
Gamma diversity (taxa richness)						
Total	95	172	154	211	110	178
Rarify *n*	4	4	4	4	5	5
Rarify est.	95	105.4	104.4	120.5	110	105.3
95% CI	88.2–101.8	101.5–109.4	99.4–109.5	117.7–123.2	103.1–116.9	100.5–110.1
Ranking	b	b	b	a	b	b

one generation per year) indicator species but more UV (one generation per year) indicator species (11% SV, 46% UV) compared to unrestored samples (42% SV, 21% UV), whereas the % MV (more than one generation per year) is similar (43 and 37%, respectively). *Juga plicifera* snails had the highest observed IV for unrestored samples. *J. plicifera* are long-lived (generally live for 5–7 years and reach reproductive maturity after 3 years) and, because of their large size, can comprise a major portion of the standing biomass (Furnish 1989). We observed decreased Juga biomass post-restoration with some signs of recovery 2–3 years after restoration, especially in the fall (Fig. 5C). Prior to restoration and in the control reaches, Juga mean % biomass ranged from 17 to 56% per season per year, while post-restoration mean biomass ranged from 0.5 to 10%.

Macroinvertebrates in Pools and Glides

Although the restoration did increase the number of mostly perennial pool–glide waterbodies along the sampling transects (from three to eight distinct sites, pre- to post-restoration), there is no apparent effect of the restoration on the pool–glide macroinvertebrate community structure (Fig. 6B). The NMDS of pool–glide samples produced a two-dimensional solution with moderately low stress (0.15) and explained 86% of the variation in the data, with 77% explained by axis 1 (approximately pools vs. glides) and 9% by axis 2 (approximately seasonal difference). Pool–glide specific MRPP comparisons failed to find group differences between the pre- and post-restoration samples for either spring ($A = 0.01$, $p = 0.57$) or fall ($A = 0.04$, $p = 0.14$) (Table S1).

Within the pool–glide samples, we did not see an increase in taxa richness (alpha or gamma) from pre- to post-restoration, nor an increase in sample heterogeneity (beta diversity) (Table 2). However, as with riffle samples, there was an increase in mean Shannon diversity for all post years in the spring and a slight increase in the fall (Fig. 7A), indicating a more even distribution of taxa biomass after restoration. There was also a noticeable increase in the biomass of certain Baetidae mayflies, specifically *Anafroptilum*, *B. alius*, *Callibaetis*, and *D. hageni* in the spring and *Callibaetis* in the fall (Fig. 7B). None of these taxa were new to the lower SFMR; they were all collected before and after restoration, but they showed a consistent increase in biomass over the time frame of this study.

Wildfire

One of the main objectives for river and floodplain restoration in the SFMR was to create a system that is resilient to disturbances. During post-restoration monitoring, a large and intense wildfire burned through the restored and unrestored river and floodplain. As a result, the samples collected in fall 2020 and 2021, and spring 2021, were both post-restoration and post-fire. While we were unable to test for an impact from the wildfire explicitly, because the entire area burned, we did not see a clear change or temporal deviation in macroinvertebrate community structure or metrics after the fire. Any temporal changes observed appear to follow the post-restoration trend and were not specific to the time frame of the wildfire. Regardless of

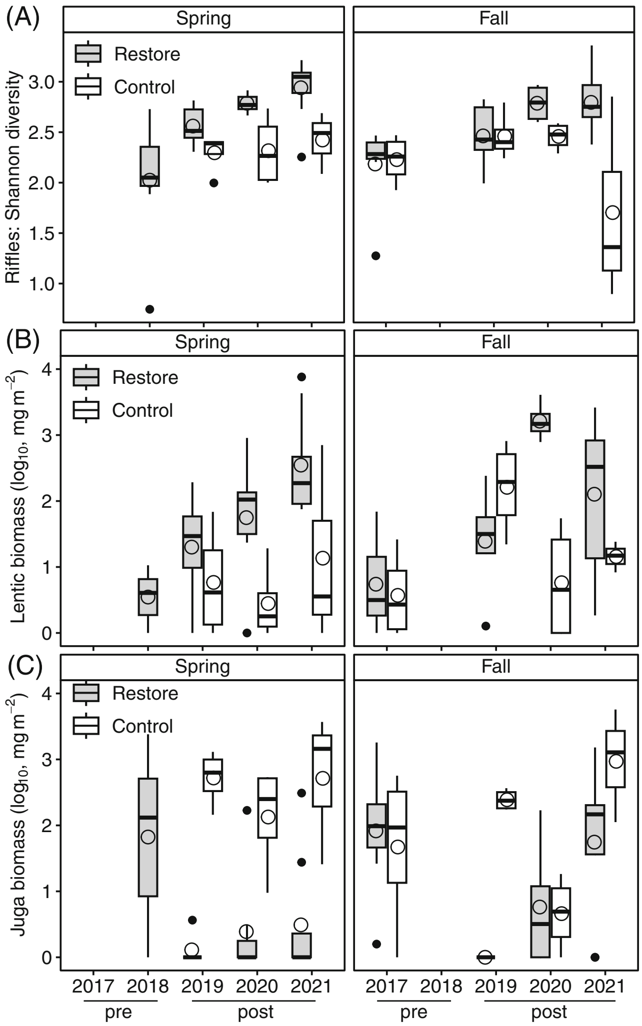

Figure 5. Riffle macroinvertebrate (A) Shannon diversity, (B) lentic biomass, and (C) Juga biomass grouped by restoration treatment (restore vs. control). Biomass in plots B and C was $\log_{10}$-transformed. Pre-restoration samples were collected in fall 2017 and spring 2018, and post-restoration samples were collected in 2019–2021.

the restoration, the lower SFMR will likely not experience typical watershed-scale fire effects such as fine sediment deposition, flooding, or warmer water due to loss of canopy cover. This reflects the location of the restoration area downstream of a high-head dam that regulates flow, thermal conditions, and sediment transport.

Discussion

River and floodplain restoration designed with the goal of enhancing aquatic ecosystem function by resetting base elevations of the valley bottom (as suggested by Powers et al. 2019) should be followed by multiple years of monitoring to evaluate biological responses. By monitoring aquatic macroinvertebrate communities for 3 years and in two seasons at the SFMR, we found strong connections between inundated area as well as habitat-specific responses linked to post-restoration physical conditions. Key findings of this work demonstrate the need for differentiation between slow-and fast-water biological sampling, the importance of pre-restoration data collection, and the need to look beyond taxa richness to other biological metrics such as the Shannon diversity index and community composition to capture the nuanced response of the biological community to river and floodplain restoration.

Floodplain Inundation

A primary objective of restoration to a stage 0 condition is to increase hydrologic connectivity across the bottomland at base flow and during high-flow events. In the SFMR, discharge is regulated by an upstream dam which reduces the variability of high and low flows, but a seasonal flow regime is maintained to accommodate the life history of migrating salmonids. After restoration, more surface water at summer base flow was observed owing to an increase in lateral connectivity across the floodplain, reconnection of relic side-channels, and more vertical connectivity to the water table (Flitcroft et al. 2022). Greater macroinvertebrate biomass (two to four times) at the scale of the restored bottomland, in the second and third years after restoration, was primarily due to increased wetted area and not fine-scale assessments of macroinvertebrate biomass at the per-m^2 scale. These results are consistent with other studies that noted the importance of including the larger inundated floodplain area in observing increased macroinvertebrate biomass (Braccia et al. 2023) and productivity (Jennings et al. 2023) for floodplain reconnection projects. Increased overall biomass has the potential to increase available food resources for aquatic and terrestrial fauna, thus enhancing connections across trophic levels in the aquatic-riparian ecosystem. Other forms of restoration, such as large wood addition, may affect change to the in-stream portion of the river only and not increase overall biomass. Floodplain restoration projects, like this one that engage both the river and disconnected floodplains, facilitate the distribution of water across the bottomland at base flow.

Restoration Effects by Habitat Type

Another objective of river and floodplain restoration is to increase biotic diversity through geomorphic heterogeneity. Diversity can be quantified in different ways (e.g. taxa richness or diversity indices) and at various scales (e.g. alpha, beta, or gamma). While we did not find an increase in mean taxa richness at the sample scale (alpha diversity) after restoration, we did see increased Shannon diversity measures in both riffle and pool–glide habitats, indicating a more even distribution of taxa biomass after restoration. Shannon diversity increases in the SFMR followed a similar response timing as a small stream in California following channel restoration by natural flows, which reported higher macroinvertebrate Shannon diversity after 1.5 years in pools and after 2.5 years in runs/riffles (Chin et al. 2021). Because riffles are subject to a wider variety of flow velocities and moving sediment or wood compared to pools, complex macroinvertebrate communities may take longer to

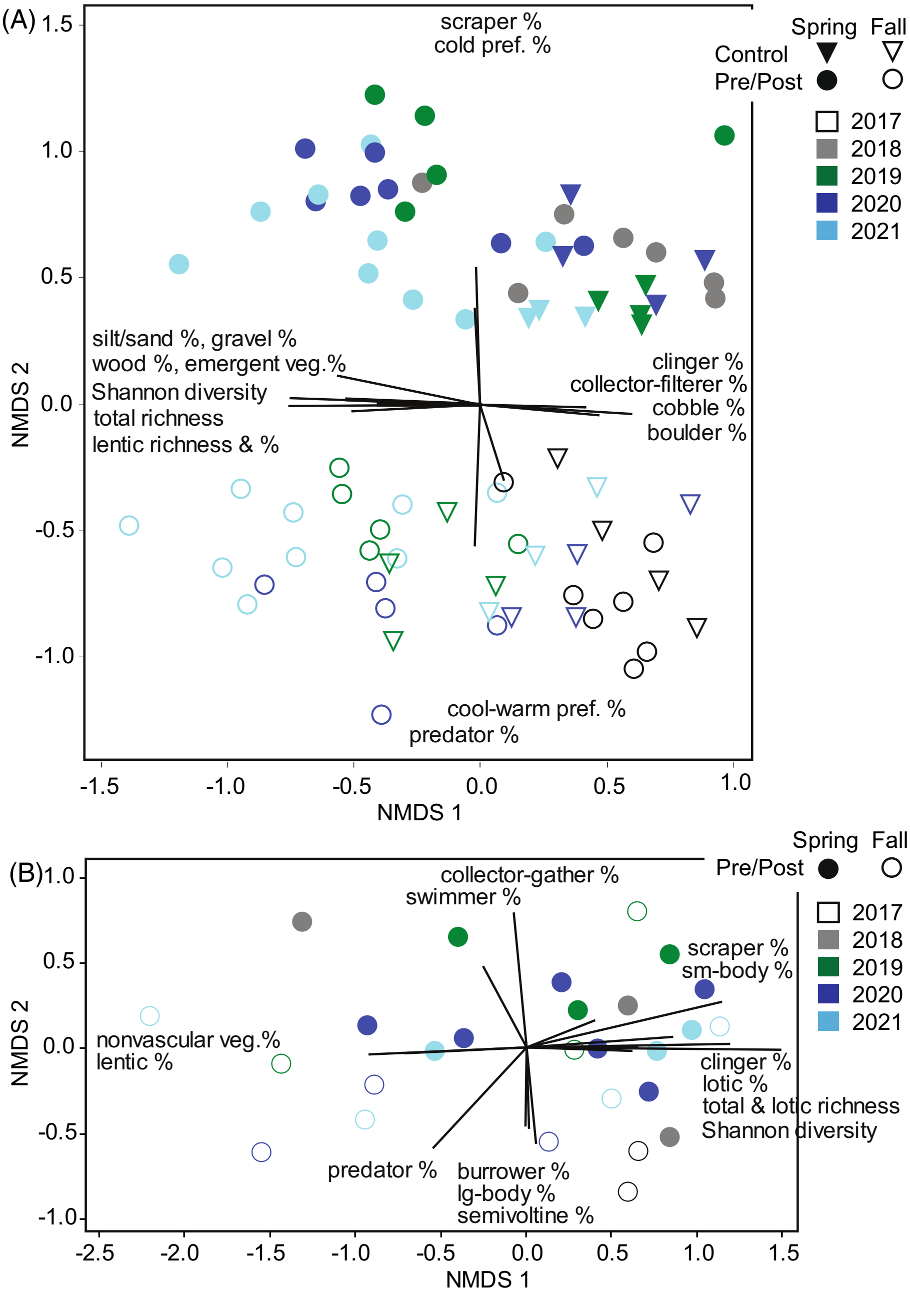

Figure 6. Ordination plots of macroinvertebrate taxa by biomass from (A) riffle samples ($n = 80$) and (B) pool–glide samples ($n = 27$). Samples are categorized by season, treatment type, and year collected. The pool–glide samples are all pre- or post-restoration as there were no pool–glide sites in the control area. Pre-restoration samples were collected in fall 2017 and spring 2018. Post-restoration samples were collected in 2019–2021. Joint-plot vectors show the direction and magnitude of taxa trait or environmental variables correlated with the NMDS ordination axes ($r \geq |0.45|$). Taxa trait % variables are biomass proportions and richness variables are taxa counts.

develop. In the SFMR, we also observed greater macroinvertebrate gamma diversity in post-restoration riffles compared to pre-restoration or control riffles, and beta diversity varied by habitat type. After restoration in the SFMR, Jennings et al. (2023) noted that an increase in habitat heterogeneity (main channel, side channel, and wetted forest habitats) supported greater beta diversity of macroinvertebrate communities. In a stream in the more arid environment of eastern Oregon, Noone et al. (2024) attributed a greater diversity of macroinvertebrates in floodplain restored reaches to the creation of off-channel habitats. These findings support the hypothesis that floodplains with complex habitat mosaics offer a variety of conditions necessary to support diverse species assemblages. This diversity has the potential to support broader metapopulations of

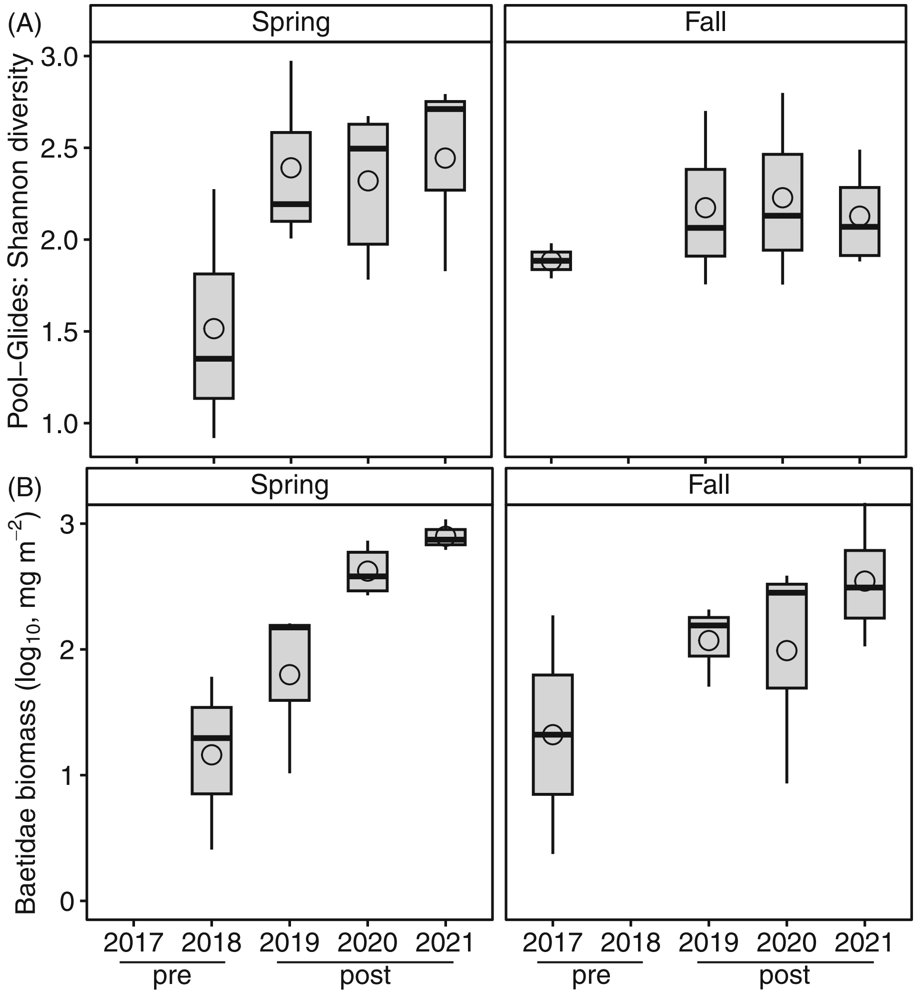

Figure 7. Pool–glide macroinvertebrate (A) Shannon diversity and (B) mayfly Baetidae biomass (log_{10}-transformed) from the restored area only (no pools or glides in the control area). Pre-restoration samples were collected in fall 2017 and spring 2018, and post-restoration samples were collected in 2019–2021. Boxplots show the median (dark bar), mean (hollow circle), and first and third quartiles (box).

macroinvertebrates through the presence of patches of floodplain habitat throughout the river system (Stanford et al. 2005; Stouffer & Bascompte 2011; Bellmore et al. 2015; Uno & Pneh 2020).

River and floodplain restoration in the SFMR appears to have altered the physical conditions of riffle habitats and, in response, the macroinvertebrate community structure reflecting slower-water environmental and taxa traits. Riffles changed from primarily fast and deep flow with cobble and boulder substrate before restoration to variably wide and shallow flow with gravel and fine substrate and even some emergent vegetation (rooted vegetation, often sedges) after restoration. These changes are most evident in the increase in the number of lentic macroinvertebrate taxa and their biomass (e.g. *Anafroptilum*, *Lepidostoma*, *Hydatophylax hesperus*, and *Sialis*) and the decrease in *Juga* biomass observed post-restoration. *Juga plicifera* snails are especially telling because they are typically abundant in western Oregon in clear, fast-flowing forested streams with coarse, stable substrates (Furnish 1989). These snails are also long-lived and able to exert a "pervasive influence on the availability of food resources, habitat patches and stream community structure" through exploitative competition of both autochthonous and allochthonous food sources (Furnish 1989). The fact that their biomass was severely diminished 1 year after restoration in both spring and fall suggests, at least, a shift toward smaller, less stable substrate and corresponds with our measurements of substrate size composition. Their biomass remained low for the next 2 years in the spring, but began to rebound in the fall, possibly due to more stable flow and substrate conditions in the fall compared to spring.

Unlike riffles that were abundant in the SFMR, it may be difficult to see a restoration effect on macroinvertebrate assemblages from pool–glide habitat types because there were very few sites present pre-restoration and none in the control area. This sampling design conundrum is part of the reason for the restoration, to increase geomorphic diversity. Prior to the restoration, only three pool–glide waterbodies (i.e. sites) existed along the sampling transects. After restoration, eight distinct pool–glide waterbodies were present at different times. It should also be noted that pools in the SFMR were seasonally connected pool–glide complexes (disconnected at low flows). Glides were perennially connected but could mimic pool conditions at low flows. These pool–glide habitats supported lentic macroinvertebrate communities. Lentic habitats may be relatively taxa-poor (low alpha diversity), but they support some taxa not found in lotic habitats and therefore contribute to higher beta and gamma diversity (Hood & Larson 2013; Epele et al. 2019).

While we did not see a clear increase in EPT or Chironomidae biomass over time in the pool–glide habitat types, we did observe an increase in Baetidae mayfly biomass throughout the length of the study. Baetid nymphs are small-bodied, MV, collector-gatherers, and swimmers—common generalist taxa post-disturbance (Anderson 1992; Foster et al. 2020). These findings are consistent with two other studies following floodplain and channel restoration. Baetidae abundance was higher in pools in a California stream over a year after restoration (Chin et al. 2021). In a small, forested stream in Kentucky, mayfly abundance and biomass were consistently higher in restored pools, but not riffles, up to 5 years after restoration (Braccia et al. 2023). There, mayfly abundance was driven by *Ephemera*, *Caenis*, and *Stenacron*, a mix of MV and SV taxa. Longer-term monitoring may reveal a transition from generalist taxa to a more lentic-specific community.

Sampling Diverse Habitat Types

Comparing macroinvertebrate assemblages by habitat type was important in this study to discern restoration effects. Classic reach-scale macroinvertebrate sampling methodologies, such as Rapid Bioassessment Protocols (Barbour et al. 1999) or the Environmental Monitoring and Assessment Program multi-habitat protocol (Kaufmann et al. 1999), that lump samples from different habitat types may not prove as useful for restoration assessments compared to habitat-specific methodologies. Braccia et al. (2023) also found the separation of pools and riffles to be a key factor in the detection of restoration effects on macroinvertebrates, with effects most notable in pools, while we found effects most notable in riffles. Chin et al. (2021) found that differentiation in macroinvertebrate community structure based on habitat type became more pronounced over time as a restored stream channel developed discrete step-pool morphology. These studies provide evidence for the benefit of separating habitat types during macroinvertebrate sample collection and analysis.

Seasonal Differences

Even though macroinvertebrate assemblages in the SFMR were clearly different between late spring and early fall sampling, restoration effects were mostly similar between these seasons, although some effects appeared stronger in the spring possibly due to more water coverage prior to low summer flows. Another study in the SFMR also observed seasonal shifts in macroinvertebrate composition over the course of 1 year and no consistent differences in restoration effects on seasonal biomass patterns (Jennings et al. 2023). Thus, it appears that the restoration affected macroinvertebrate populations across multiple seasons; however, the SFMR is regulated by an upstream dam which dampens seasonal flow variability. Other streams with more extreme seasonal flow regimes may see different effects between seasons.

Pre-Restoration Sampling

Having pre-restoration samples can be both informative and complicate analyses. Most river and floodplain restoration efficacy studies do not include pre-restoration samples (e.g. Braccia et al. 2023; Jennings et al. 2023; Noone et al. 2024). Yet, being able to compare the same area before and after restoration, in addition to a control area, allows for a more robust comparison of restoration effects. Many studies assume that a control area in the same stream as the restored area has equivalent physical and biological conditions prior to restoration. In the SFMR, for example, had we not collected samples prior to restoration from main channel and off-channel waterbodies, we would have assumed that the restoration created all new pools and glides (when in reality a few existed pre-restoration, contributing to pre-restoration diversity). By making that assumption, we would have incorrectly credited the restoration with a much stronger effect on geomorphic diversity and macroinvertebrate assemblages, including many new taxa found only in the pool–glide habitats.

In this study, we demonstrate the importance of pre- and post-restoration data collection and the important role of control sites in accounting for interannual variability. Following restoration in the SFMR, we observed greater taxonomic diversity and a shift in macroinvertebrate community structure in riffles, likely responding to a variety of physical changes (e.g. flow, substrate, wood, etc.). Continued monitoring is needed to evaluate long-term biological responses (e.g. 5- and 10-years post-restoration), allowing for a richer understanding of the effects of river and floodplain reconnection projects.

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LITERATURE CITED

Albertson LK, Cardinale BJ, Zeug SC, Harrison LR, Lenihan HS, Wydzga MA (2011) Impacts of channel reconstruction on invertebrate assemblages in a restored river. Restoration Ecology 19:627–638. https://doi.org/10.1111/j.1526-100X.2010.00672.x

Anderson NH (1992) Influence of disturbance on insect communities in Pacific northwest streams. Hydrobiologia 248:79–92. https://doi.org/10.1007/BF00008887

Barbour MT, Gerritsen J, Snyder BD, Stribling JB (1999) Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, second edition. EPA 841-B-99-002. United States Environmental Protection Agency, Washington, D.C.

Beechie TJ, Sear DA, Olden JD, Pess GR, Buffington JM, Moir H, Roni P, Pollock MM (2010) Process-based principles for restoring river ecosystems. Bioscience 60:209–222. https://doi.org/10.1525/bio.2010.60.3.7

Bellmore JR, Baxter CV, Connolly PJ (2015) Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. Ecology 96:274–283. https://doi.org/10.1890/14-0733.1

Benke AC, Huryn AD, Smock LA, Wallace JB (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308–343. https://doi.org/10.2307/1468447

Bittner B, Mattson K (2006) Level II stream survey report South Fork McKenzie River 2005. McKenzie River Ranger District, McKenzie Bridge, Oregon

Braccia A, Lau J, Robinson J, Croasdaile M, Park J, Parola A (2023) Macroinvertebrate assemblages from a stream-wetland complex: a case study with implications for assessing restored hydrologic functions. Environmental Monitoring and Assessment 195:394. https://doi.org/10.1007/s10661-023-10983-7

Carlson PE, Donadi S, Sandin L (2018) Responses of macroinvertebrate communities to small dam removals: implications for bioassessment and restoration. Journal of Applied Ecology 55:1896–1907. https://doi.org/10.1111/1365-2664.13102

Chin A, O'Dowd AP, Mendez P, Velasco K, Florsheim JL, Laurencio LR, Deventhal RD (2021) Toward natural approaches in restoration: experiments of co-evolving physical and biological structures in a self-organizing step-pool channel. River Research and Applications 37:1480–1493. https://doi.org/10.1002/rra.3851

Claeson SM, Coffin B (2016) Physical and biological responses to an alternative removal strategy of a moderate-sized dam in Washington, U.S.A. River Research and Applications 32:1143–1152. https://doi.org/10.1002/rra.2935

Cluer B, Thorne C (2014) A stream evolution model integrating habitat and ecosystem benefits. River Research and Applications 30:135–154. https://doi.org/10.1002/rra.2631

Cover MR, de la Fuente JA, Resh VH (2010) Catastrophic disturbances in headwater streams: the long-term ecological effects of debris flows and debris floods in the Klamath Mountains, northern California. Canadian Journal of Fisheries and Aquatic Sciences 67:1596–1610. https://doi.org/10.1139/F10-079

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345–366. https://doi.org/10.2307/2963459

Epele LB, Brand C, Miserendino ML (2019) Ecological drivers of alpha and beta diversity of freshwater invertebrates in arid and semiarid Patagonia (Argentina). Science of the Total Environment 678:62–73. https://doi.org/10.1016/j.scitotenv.2019.04.392

Flitcroft RL, Brignon WR, Staab B, Bellmore JR, Burnett J, Burnett P, et al. (2022) Rehabilitating valley floors to a stage 0 condition: a synthesis of opening outcomes. Frontiers in Environmental Science 10:892268. https://doi.org/10.3389/fenvs.2022.892268

Foster AD, Claeson SM, Bisson PA, Heimburg J (2020) Aquatic and riparian ecosystem recovery from debris flows in two western Washington streams, U.S.A. Ecology and Evolution 10:2749–2777. https://doi.org/10.1002/ece3.5919

Furnish JL (1989) Factors affecting the growth, production and distribution of the stream snail Juga silicula (Gould). PhD dissertation. Department of Entomology, Oregon State University, Corvallis.

Hinshaw S, Wohl E, Burnett JD, Wondzell S (2022) Development of a geomorphic monitoring strategy for stage 0 restoration in the South Fork McKenzie River, Oregon, U.S.A. Earth Surface Processes and Landforms 47:1937–1951. https://doi.org/10.1002/esp.5356

Hood GA, Larson DG (2013) Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal Canada. Wetlands 34:19–29. https://doi.org/10.1007/s13157-013-0476-z

Hubler S, Stamp J, Sullivan SP, Fernandez M, Larson C, Macneale K, Wisseman RW, Plotnikoff R, Bierwagen B (2024) Improved thermal preferences and a stressor index derived from modeled stream temperatures and regional taxonomic standards for freshwater macroinvertebrates of the Pacific Northwest, U.S.A. Ecological Indicators 160:111869. https://doi.org/10.1016/j.ecolind.2024.111869

Jeffres CA, Opperman JJ, Moyle PB (2008) Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California River. Environmental Biology of Fishes 83:449–458. https://doi.org/10.1007/s10641-008-9367-1

Jennings JC, Bellmore JR, Armstrong JB, Wisseman RW (2023) Effects of process-based floodplain restoration on aquatic macroinvertebrate production and community structure. River Research and Applications 39:1709–1723. https://doi.org/10.1002/rra.4174

Jones JA, Swanson FJ, Wemple BC, Snyder KU (2001) Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conservation Biology 14:76–85. https://doi.org/10.1046/j.1523-1739.2000.99083.x

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river floodplain systems. Pages 110–127. In: Dodge DP (ed) Proceedings of the International Large River Symposium (LARS). Vol 106. Canadian Special Publication of Fisheries and Aquatic Science, NRC research press, Ottawa, Canada.

Kaufmann PR, Levine P, Robison EG, Seeliger C, Peck DV (1999) Quantifying physical habitat in wadeable streams. EPA/620/R-99/003. United States Environmental Protection Agency, Washington, D.C.

Kiffney PM, Volk CJ, Beechie TJ, Murray GL, Pess GR, Edmonds RL (2004) A high-severity disturbance event alters community and ecosystem properties in West Twin Creek, Olympic National Park, Washington, U.S.A. American Midland Naturalist 152:286–303. https://doi.org/10.1674/0003-0031(2004)152[0286:AHDEAC]2.0.CO;2

Knox RL, Wohl EE, Morrison RR (2022) Levees don't protect, they disconnect: a critical review of how artificial levees impact floodplain functions. Science of the Total Environment 837:155773. https://doi.org/10.1016/j.scitotenv.2022.155773

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon

Merritt RW, Cummins KW, Berg MB (eds) (2019) An introduction to the aquatic insects of North America. 4th ed. Kendall Hunt Publishing, Dubuque, Iowa

MTBS (Monitoring Trends in Burn Severity) Data Explorer (2024) USDA Holiday Farm Fire. https://apps.fs.usda.gov/lcms-viewer/mtbs.html (accessed 12 Feb 2024)

Mundahl ND, Hunt AM (2011) Recovery of stream invertebrates after catastrophic flooding in southeastern Minnesota, U.S.A. Journal of Freshwater Ecology 26:445–457. https://doi.org/10.1080/02705060.2011.596657

Noone WN, Edwards PM, Pan Y, Thorne C (2024) Floodplain restoration and its effects on summer water temperature and macroinvertebrates in Whychus Creek, Oregon (U.S.A.). River Research and Applications 2024:1–19. https://doi.org/10.1002/rra.4383

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime. Bioscience 47:769–784. https://doi.org/10.2307/1313099

Poff NL, Olden JD, Vieira NKM, Finn DS, Simmons MP, Kondratieff BC (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. Freshwater Science 25:730–755. https://doi.org/10.1899/0887-3593(2006)025[0730:FTNONA]2.0.CO;2

Powers PD, Helstab M, Niezgoda SL (2019) A process-based approach to restoring depositional river valleys to stage 0, an anastomosing channel network. River Research and Applications 35:3–13. https://doi.org/10.1002/rra.3378

Pugh BE, Colley M, Dugdale SJ, Edwards P, Flitcroft R, Holz A, et al. (2022) A possible role for river restoration enhancing biodiversity through interaction with wildfire. Global Ecology and Biogeography 31:1990–2004. https://doi.org/10.1111/geb.13555

R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Relyea CD, Minshall GW, Danehy RJ (2012) Development and validation of an aquatic fine sediment biotic index. Environmental Management 49:242–252. https://doi.org/10.1007/s00267-011-9784-3

Stanford JA, Lorang MS, Hauer FR (2005) The shifting habitat mosaic of river ecosystems. Internationale Vereinigung für Theoretische Und Angewandte Limnologie: Verhandlungen 29:123–136. https://doi.org/10.1080/03680770.2005.11901979

Stouffer DB, Bascompte J (2011) Compartmentalization increases food-web persistence. Proceedings of the National Academy of Sciences U.S.A. 108:3648–3652. https://doi.org/10.1073/pnas.1014353108

Tickner D, Opperman JJ, Abell R, Acreman M, Arthington AH, Bunn SE, et al. (2020) Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. Bioscience 70:330–342. https://doi.org/10.1093/biosci/biaa002

Tockner K, Malard F, Ward JV (2000) An extension of the flood pulse concept. Hydrological Processes 14:2861–2883. https://doi.org/10.1002/1099-1085(200011/12)14:16/17<2861::AID-HYP124>3.0.CO;2-F

Townsend CR, Scarsbrook MR, Dolédec S (1997) Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. Journal of the North American Benthological Society 16:531–544. https://doi.org/10.2307/1468142

Uno H, Pneh S (2020) Effect of source habitat spatial heterogeneity and species diversity on the temporal stability of aquatic-to-terrestrial subsidy by emerging aquatic insects. Ecological Research 35:474–481. https://doi.org/10.1111/1440-1703.12125

Supporting Information

The following information may be found in the online version of this article:

Table S1. Non-parametric MRPP pairwise tests of macroinvertebrate assemblages among restoration treatment groups by habitat type and season.

Table S2. Macroinvertebrate significant ($p < 0.05$) indicator species (ISA) collected from riffle restored samples or riffle unrestored samples.

Figure S1. SF McKenzie River discharge (cm, daily mean) at Cougar Dam, approximately 4 km upstream of the restored reaches.

Figure S2. Substrate size composition (mean %) from macroinvertebrate samples grouped by restoration treatment and habitat type.

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