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Floodplain Restoration and Its Effects on Summer Water Temperature and Macroinvertebrates in Whychus Creek, Oregon (USA)

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ABSTRACT

Stream restoration is a proposed climate adaptation tool; however, outcomes of floodplain restoration on stream temperature have been debated. Despite a growing number of studies that investigated water temperature in restored streams, few have quantified temperature variations in new habitat types created by restored hydrogeomorphic processes to explore the effects on aquatic macroinvertebrates. We evaluated the hypotheses: (1) restoration increases habitat diversity, (2) habitat diversity increases water temperature variability, and (3) restoration increases the diversity of macroinvertebrate assemblage and temperature associations. In August 2021, we collected environmental data to describe the aquatic habitats, water temperature and quality (continuous and discrete), and macroinvertebrates in 40 riffle, pool, and off-channel sites in a stream being restored, Whychus Creek, Oregon, USA. Our study is a site comparison of three reaches—one restored in 2012, another restored in 2016, and an unrestored (control) that will soon undergo restoration. Evaluations of the hypotheses show: (1) Habitat diversity in restored reaches is effectively three types of aquatic habitats versus only one in the control (riffles), (2) water temperature variability in habitats created by restoration (off-channel) is high and low, and suggest a range of hyporheic connectivity and flow paths are present, and (3) restoration created a different macroinvertebrate assemblage, with 16 additional taxa in off-channel habitats, and the range in macroinvertebrate thermal optima is approximately doubled when off-channel macroinvertebrate thermal optima are accounted for. Our results support the idea that floodplain restoration creates more diverse thermal conditions and different macroinvertebrate communities in restored stream reaches.

1 | Introduction

Among contributing factors that degrade habitats for aquatic macroinvertebrates, and lead to the demise of their diversity, distribution, and abundance (Sánchez-Bayo and Wyckhuys 2019) are alterations to the natural thermal regime that regulate the timing of emergence for adult aquatic insects, their size, and survival (Allan and Castillo 2007). The thermal regime describes the spatial and temporal variations in water temperature. Four categories are used to group the factors that influence the thermal regime of rivers: topography (including vegetation), atmospheric conditions, stream flow, and streambed (including hyporheic exchange and groundwater inputs) (Caissie 2006). Habitat alteration, for example, damming or

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channelization reduces habitat complexity and aquatic insect diversity (Allan and Castillo 2007; Kennedy and Turner 2011) through changes in the topography, stream discharge, and streambed, which reduce daily, seasonal, and annual variation in flow and temperature, resulting in changes to temperature minima and maxima. It is no surprise that when the more natural thermal regime minima and maxima are re-established, then aquatic insect diversity increases (Rader, Voelz, and Ward 2007; Voelz and Ward 1991). Due to this recognition, calls have been made to incorporate thermal regimes into environmental flow assessments to benefit extirpated assemblages of native organisms (Olden and Naiman 2010). Process-based restoration approaches in general (Beechie et al. 2010) and, more specifically, floodplain restorations of the type we focus on in this study (Powers, Helstab, and Niezgoda 2019), show promise in their ability to restore complexity to both the habitats and thermal regimes of rivers (Weber et al. 2017; Flitcroft et al. 2022).

In alluvial watersheds, the Stream Evolution Model proposed by Cluer and Thorne (2014) describes the potential benefit to biota and ecosystem function as a stream progresses from a channelized, or incised, Stages 2 or 3 channel that is disconnected from its floodplain to an anastomosing or anabranching planform that is fully-connected (Stages 0 or Stage 8). Such floodplain reconnections were originally proposed by a French team: under the concept of river freedom of space (espace de liberté des rivières) (Biron et al. 2014). In recent decades, practitioners of stream restoration have used Stage 0 or 8 conditions as novel, process-based restoration targets for degraded rivers that emphasize dynamic and diverse stream conditions (Bouwes et al. 2016; Powers, Helstab, and Niezgoda 2019). Cluer and Thorne (2014), used a qualitative appraisal of Stage 0 and 8 conditions to reason that ecosystem benefits may include: high biodiversity; flood and drought refugia for aquatic species; high resistance to disturbance by floods, droughts, and wildfires; reliable baseflow; abundant vegetation growth, and amelioration of water temperatures. A key component of restoration to Stage 0 or 8 is to reconnect the river's hydro-system in the vertical, lateral, and long-stream directions at base flow. This supports complex interactions between surface and sub-surface water bodies based on exchanges between channel flows and those in the hyporheic zone; water in the alluvial aquifer beneath the floodplain and perirheic water in the regional groundwater (Hauer et al. 2016), and seasonal replenishment and drainage of water in the floodplain "sponge" (Wheaton et al. 2019).

Monitoring of Stage 0/8 projects in the Pacific Northwest of the USA, has demonstrated that at least some of the ecosystem benefits foreseen by Cluer and Thorne (2014) may be realized in practice (e.g., Powers, Helstab, and Niezgoda 2019; Braccia et al. 2023, and for a comprehensive review see, Flitcroft et al. 2022). Scott (2024), for example, reported on pool scour (and pool habitat formation) in a Stage 0 valley bottom restoration with widespread wood placement. However, in reviewing the literature we have found no studies that quantify diel water temperature variations in the complex morphologies created by full floodplain reconnection (a.k.a. restoration to Stage 0/8), and descriptions of the linkages between these water temperature variations and patterns in the restored aquatic macroinvertebrate assemblage.

Aquatic macroinvertebrates have long been used in bioassessment for their utility as an indicator of changes in environmental conditions such as habitat degradation, sedimentation, and changes in water quality including water temperature (Barbour et al. 1999; Waite, Pan, and Edwards 2020). Reviews of restoration outcomes on macroinvertebrates report increases in taxa richness and diversity and several functional indicators of change (density, functional feeding group, and Ephemeroptera–Plecoptera–Trichoptera EPT diversity) (Al-Zankana et al. 2020); however, these metrics are rarely assessed (England et al. 2021), and in any case, declines in aquatic biota may continue following restoration due to factors operating at scales larger than those that can be addressed in a reach-scale project (Bernhardt and Palmer 2011). A secondary limitation in the ability of post-restoration appraisals to detect changes in macroinvertebrates is that post-treatment monitoring only continues for short durations. For example, Smith et al. (2020) used a before-after-control-impact approach to evaluate macroinvertebrates in a recreated wet meadow (from an incised channel) and reported no benefit at all with 3 years of post-treatment data.

To accurately characterize restoration successes, calls have been made for more quantitative and intensive sampling efforts in appraisal methods (England et al. 2021), and qualitative measures. In this context, Nash et al. (2021) proposed a useful approach to monitoring restoration effectiveness, based on identifying the relevant hydrologic processes and using qualitative and quantitative data to document whether projects either do or do not evolve along the pathways anticipated. Several monitoring programs have been implemented in this way, including tracking: changes in groundwater levels and longitudinal stream warming (Flitcroft et al. 2022); responses to fauna (Bouwes et al. 2016; Edwards et al. 2020), and floral succession (Orr et al. 2020). Given the authors' background in using bioindicators to track trajectories of stream restorations, we selected macroinvertebrates to evaluate the performance of process-based, floodplain reconnection projects. Specifically, we use patterns in macroinvertebrate taxa and community traits and their associations with selected environmental variables (McCune, Grace, and Urban 2002) to identify and explore causal links defined in our conceptual model Data (S1).

This study was designed to measure environmental conditions in the aquatic habitats of restored reaches in Whychus Creek, OR, USA, responsible for spatial patterns in macroinvertebrate diversity and assemblage. This watercourse is suited to our needs because it features reaches that were fully reconnected to their floodplains in 2012 and 2016, as well as an unrestored reach in which restoration will take place later (planned for 2024). In our study, we evaluated the hypotheses that restoration of channelized stream reaches into Stage 0/8 fully reconnected floodplains: (1) increases the geomorphic habitat diversity, (2) increases the spatial temperature variations, and (3) results in a different macroinvertebrate community with different temperature associations. We evaluated habitat diversity using an existing geomorphic habitat dataset from the three reaches and the environmental data from our sample sites collected during our field study to describe the habitat quality, measured the water temperatures and quantified variability in different habitats, and interpreted patterns in the macroinvertebrate community by comparing macroinvertebrate assemblages, their traits, and environmental variables between the three reaches.

2 | Methodology

2.1 | Study Area and Restoration Approach

Whychus Creek (Figure 1) is a predominantly glacial-fed stream flowing through woodlands of ponderosa pine and bitterbrush (Table 1) that historically supported habitat for coldwater fish like steelhead (*Oncorhynchus mykiss*) and Chinook salmon (*Oncorhynchus tshawytscha*). Modern-day settlement in the area (circa 1900) led to severe degradation of the stream (Mork and Houston 2016). Channel manipulation, damming, and water extraction effectively disconnected the stream from the floodplain and shifted flows from perennial to intermittent. Efforts to restore salmon and steelhead populations in Whychus Creek began in the early 2000s through the removal of engineered infrastructure, acquisition of instream water rights, and seeding the river with hatchery-origin juvenile fish. Concurrent with these efforts have been land acquisition and floodplain restoration by the watershed council and partners to recreate a perennial riparian ecosystem that provides ecosystem services to support resilient and robust populations of aquatic biota.

Upstream and downstream boundaries of restored and control reaches are shown in Figure 1 (same reaches used by Edwards et al. 2020). For the purposes of this study, we refer to Camp Polk Meadow, Whychus Canyon (Reach 4), and the unrestored reach (Canyon Reach 3) as restored 2012, restored 2016, and control, respectively (reach descriptions in Data S1). The location of the control reach was advantageous because it was approximately 7 km downstream from the restored 2012 reach, and directly upstream from the restored 2016 reach that, because of the proximity of the control and Restored 2016 reaches, we assumed any differences between those two reaches were due to restoration effect (rather than position in the watershed), and the control would not be affected by any changes caused by the restoration projects. Data collection, in mid-August 2021, was timed to characterize aquatic habitats and water temperatures during the hottest time of year, when we expected environmental gradients and spatial variability in water temperatures would be maximized.

2.2 | Sampling Design and Site Selection

The study reaches were sampled for macroinvertebrates (method described in the next section), and environmental data were recorded in pool, riffle, and off-channel habitat types. The sampling design was balanced so that five samples from each habitat type in each reach were collected. Sample sites for each habitat type in each reach were established at the location of the target habitat type with an emphasis put on locations where we anticipated that hyporheic upwelling would be greatest. For example, hyporheic upwelling is known to occur at the downstream portion of riffles (Tonina and Buffington 2007). In addition, the presence of bubbling or clear water, relative to the milky-colored stream water caused by glacial flour present in this system during the study, was a further indication of upwelling hyporheic flow in those sites Data (S1). Sites ($n = 40$) were grouped into eight a priori sample groups (i.e., restored 2012 riffle, restored 2012 pool, restored 2012 off-channel, restored

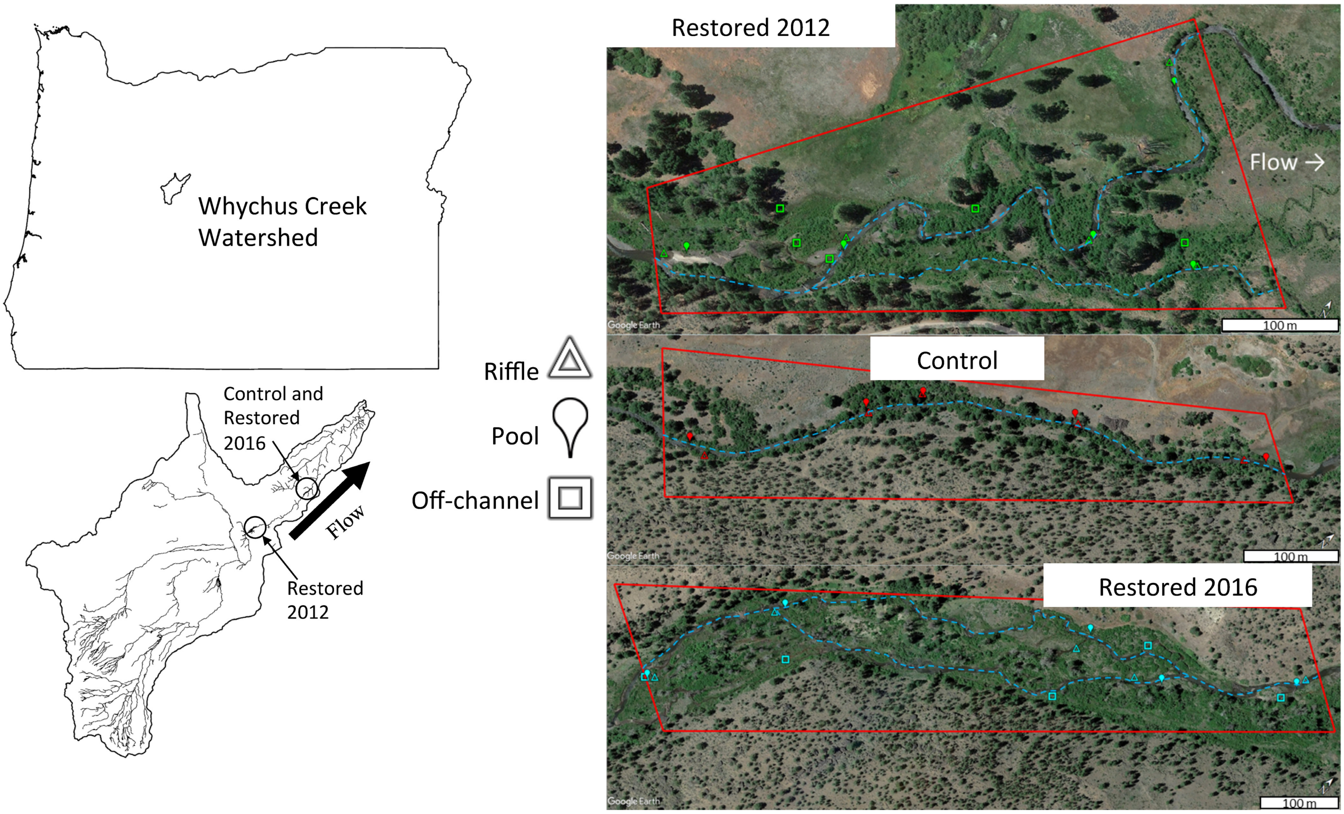

FIGURE 1 | State of Oregon showing the Whychus Creek watershed and the locations of the three study reaches circled. Satellite imagery of the three study reaches (boundaries in red) and the sampling locations are shown. Primary stream channels are shown with dashed blue lines. [Color figure can be viewed at wileyonlinelibrary.com]

2016 riffle, restored 2016 pool, restored 2016 off-channel, control riffle, and control pool). The control reach did not contain off-channel habitats.

A team of three scientists trained to assess geomorphic habitats conducted the sampling and data collection (Table 2). We had no preconceptions regarding the distributions of geomorphic habitat types but selected sample sites (Figure 1) based on systematically walking/wading the long-stream and lateral extents of the study reaches and visually identifying and characterizing geomorphic habitat types beginning at the downstream reach boundary and proceeding upstream. Photo reconnaissance (with GPS points used for georeferencing) of targeted habitat types was used to mark the sites selected for sampling.

2.3 | Field and Lab Protocol

Macroinvertebrate sampling used a semi-quantitative collection method (controlled fixed area). The steps were as follows: (1) define a sub-sample area on stream substrate (an open-bottom 5-gal bucket with circumferential area = 0.0026 m^2), (2) disturb substrate by hand while pumping a bilge pump 20 times (19.0 L of water and macroinvertebrates) into a 500 μm D-frame net to complete one sub-sample, (3) move immediately left or right in the same habitat unit (but not overlapping) and collect the second sub-sample using the bilge pump procedure, (4) composite subsamples into a plastic container, and (5) label with unit ID, habitat, date, time, reach, and sample notes. Sample collection began at the downstream limit of each study reach and proceeded upstream, except for the control reach, which was sampled from upstream to downstream (due to time constraints). Descriptions of the macroinvertebrate sample preservation, identification procedure, and taxonomy determinations are found in the Appendices. Macroinvertebrate taxonomy was resolved to Northwest Standard Taxonomic Effort Level 1 (PNAMP 2015), typically genus or family, with exceptions noted in the identification procedure (Appendix A).

To record water temperature, we used (1) a field meter (with verified accuracy against a NIST traceable thermometer) for discrete measurements at the maximum depth of the unit, and (2) temperature loggers for continuous measurements secured near the streambed or maximum depth of the unit (30 min intervals for a 48 h period) (Table 2). The accuracy of the continuous loggers was verified within 1.5°C of the field meter with two field audits during their deployment (with exceptions noted in Data S1). Calibration of the field meter, and collection of other parameters, were done with methods described by Wagner et al. (2006). Quality assurance procedures for the water temperature data are described in Appendix B. Percent canopy cover, velocity, depth, and average substrate size were recorded at each site (Table 2).

2.4 | Macroinvertebrate Attribute Scores

Trait scores for thermal preference were assigned to each taxon using Poff et al. (2006). Trait states for thermal preference included three categories: cold stenothermal or cool eurythermal, cool/warm eurythermal, and warm eurythermal (Table 3). Thermal preference is a qualitative measure of temperature

TABLE 1 | Watershed metrics for Whychus Creek. Base flow reported in Powers, Helstab, and Niezgoda (2019).

Watershed name	Annual rainfall (mm)	Drainage area (km^2)	Base flow (m^3/s)	Stream length (km)	Forest land (%)	Agricultural (%)	Rangeland (%)	Mineral (%)	CIR[a] (%)	OSC[b] (%)
Whychus Creek	500 mm	652.7	0.7	48	68	16	7	5	5	2

Note: Land use data from Aylward and O'Connor (2017).
[a] Commercial/industrial and residential.
[b] Open space/conservation.

TABLE 2 | List of data collected, measurement unit, and method for environmental data in Whychus Creek.

Parameter	Unit	Methods
Water temperature	Degrees celsius (°C)	1 Continuous thermistor[a] (ODEQ 2013) 2 Field audits (Instantaneous measurements with handheld meter[b]) (ODEQ 2013)
Specific conductivity	Microsiemens per centimeter (µS/cm) at 25°C (µS/cm @ 25°C)	Instantaneous measurement with handheld meter[b] (Wagner et al. 2006)
Dissolved oxygen	Percent dissolved oxygen (%)	Instantaneous measurement with handheld meter[b] (Wagner et al. 2006)
Cover	Percent (%)	Densiometer (Lemmon 1956)
Velocity	Meters per second (m/s)	Electromagnetic (Marsh-McBirney Inc. 1990)
Depth	Centimeter (cm)	Described in Appendix A
Average substrate size	Centimeter (cm)	Described in Appendix A

[a] Pendant, onset HOBO brand (Reported accuracy ± 0.53°C; Onset 2014).
[b] Model: 600 OMS V2, YSI brand (Reported accuracy ± 0.15°C; YSI 2012) and EcoSense EC300A, YSI brand (Reported accuracy ± 0.2°C; YSI 2017).

preference and a labile trait that shows a strong response to changes in environmental gradients (Poff et al. 2006). Due to limitations that arise from regional differences in trait scores (taxa phenotype), those from Poff et al. (2006) were modified accordingly. A dataset of trait states for thermal preference was available for a subset of the Whychus macroinvertebrate taxa from local environmental consultants Cole Ecological Inc. (courtesy of Upper Deschutes Watershed Council) based on prior macroinvertebrate surveys conducted in the study reaches (Oregon Department of Environmental Quality ecological and tolerance attributes coding, unpublished information).

Thermal optima, a quantitative measure of temperature, was assigned to each taxon based on information in Huff et al. (2008) and Oregon Department of Environmental Quality ecological and tolerance attributes coding when available (unpublished information). The thermal optima of taxa represents the weighted mean value for all sites where the taxa are present (Huff et al. 2008). When attributes were listed at the taxonomic resolution of genus or species, prior macroinvertebrate surveys (courtesy of Upper Deschutes Watershed Council) from the three reaches were used to determine the most likely genus or species in the respective reaches. For the taxa Chironomidae, we used the thermal optima for the genus *Tanytarsus* as they are the dominant taxa of this family found in the reaches. Final determinations of thermal optima are provided in Table 3.

2.5 | Calculation of Diversity Metrics

Calculations and analyses described in the following sections were performed in R v4.1.2 (R Core Team 2018). Diversity metrics were calculated for estimates of geomorphic habitat diversity and macroinvertebrate taxa diversity. First, an existing habitat dataset was used (data source Oregon Department of Fish and Wildlife Aquatic Inventories Program) with four habitat groups described by Edwards et al. (2020) pools, riffles, the off-channel, and other types. We calculated a diversity index with the Shannon-Wiener index using the diversity function (vegan package v2.6-2; Oksanen et al. 2024). The minimum value of the Shannon-Wiener index is zero, for example, when only one habitat type or taxa is present. Furthermore, the index was used to calculate the true diversity (Jost 2006) for reach level comparisons of habitat diversity. The calculation used for true diversity was Euler's number (e) raised to the diversity index value and rounded to the nearest whole number.

Second, we evaluated macroinvertebrate diversity. For the assessment of the macroinvertebrate community, taxa richness was estimated using a rarefaction method described by Gotelli and Ellison (2012) and a source code for rarefying species data (link in citation). Target counts for individual macroinvertebrates are typically between 300 and 500; however, because our control reach samples contained counts fewer than or equal to 195 (individuals), we set the rarefaction threshold at 195. Therefore, 50% of samples from the restored reaches (10 from restored 2012, and 5 from restored 2016) were randomly subsampled to 195 individuals. This accounting of differences in the number of taxa identified reduced the dependence of taxa richness on sample abundance (Hill 1973). Taxa richness estimates were calculated by summing the total number of unique taxa per sample using the Reyni function (vegan) with scales set to zero for richness and one for true diversity (Hill 1973; Jost 2006). True diversity was plotted for comparisons of diversity between the reaches using the ggplot function (tidyverse package; Wickham et al. 2019). Only samples from riffle habitats were compared and plotted to control for differences in the sampled area between the reaches (because restored reaches had off-channel habitat), standardize the comparison (abundance in pool samples was generally low), and because abundance and diversity are usually highest in riffle habitats (Barbour et al. 1999).

2.6 | Temperature Time-Series and Coefficient of Variation

Time-series water temperature data were summarized with the coefficient of variation and descriptive metrics: minimum, mean, and maximum water temperature in Excel.

TABLE 3 | Whychus Creek taxa list with trait state for thermal preference and thermal optima.

Taxa	Thermal preference[a]	Thermal optima (°C)[b]
Acentrella	2	19.5
Aeshnidae	2	20.7
Agapetus	1	18.6
Agraylea	2	17.4
Amphizoidae	1	NA
Ampumixis	2	15.8
Anagapetus	1	NA
Ancyronyx	2	NA
Atherix	2	22.1
Attenella	2	17.0
Baetidae	2	NA
Baetis	2	16.6
Brachycentrus	2	16.6
Brachycera	2	16.5
Caenidae	3	NA
Caudatella	1	13.6
Ceratopogonidae	2	17.0
Chironomidae	2	16.8
Cinygma	1	15.6
Cinygmula	1	15.5
Cleptelmis	2	18.5
Corduliidae	2	20.7
Culicidae	2	NA
Decapoda	2	NA
Dicosmoecus	1	20.6
Dryopidae	2	NA
Dytiscidae	2	18.2
Empididae	2	16.5
Epeorus	1	19.6
Ephemerella	2	14.4
Ephydridae	2	20.0
Glossosoma	2	16.6
Haliplidae	1	19.2
Haliplus	1	19.2
Hemiptera	2	19.6
Heptageniidae	1	NA
Heterlimnius	2	15.8
Hydroporinae	2	18.2
Hydropsyche	2	18.5
Hydroptila	2	21.5
Isoperla	2	15.9
Laccophilus	2	NA
Lara	2	15.8
Micrasema	1	15.6
Mystacides	2	17.2
Narpus	2	17.5
Nematocera	2	16.8
Neoclypeodytes	2	18.2
Ochrotrichia	2	19.7
Odonata	2	20.7
Optioservus	2	19.6
Oreodytes	2	18.2
Paraleptophlebia	2	16.4
Petrophila	2	NA
Philopotamidae	2	17.4
Polycentropodidae	2	16.1
Psychoglypha	1	16.1
Pteronarcys	1	15.2
Rhithrogena	1	16.1
Rhyacophila	2	15.5
Serratella	2	16.1
Sialis	2	17.1
Sigara	2	19.6
Simuliidae	2	17.4
Siphlonurus	2	NA
Skwala	1	18.6
Suwallia	2	16.5
Sweltsa	2	15.9
Thamaleidae	2	NA
Tipulidae	2	17.2
Trombidiformes	1	NA
Tropisternus	2	16.3
Yphria_californica	2	NA

(Continues)

TABLE 3 | (Continued)

Taxa	Thermal preference[a]	Thermal optima (°C)[b]
Zaitzevia	2	19.0
Zapada	1	17.2

[a] 1 = Cold stenothermal or cool eurythermal, 2 = Cool/warm eurythermal, 3 = Warm eurythermal. Data source: Poff et al. (2006) and Oregon Department of Environmental Quality ecological and tolerance attributes coding (unpublished information).

[b] Data source: Huff et al. (2008) and Oregon Department of Environmental Quality ecological and tolerance attributes coding (unpublished information).

The coefficient of variation is used as a measure of spread, and an independent measure from the mean (Gotelli and Ellison 2012). Because the coefficient of variation is independent of the mean, it was a useful metric to assess the variability of water temperatures between different stream reaches and habitats while removing the influence of higher or lower means caused by spatial and temporal variability in the stream. Expressed as a percentage, between 0 and 100, the coefficient of variation increases as the magnitude between min and max increases. For five sites that did not have time-series data, two field measurements (audits) were used to calculate the coefficient of variation. Time-series data were plotted to show the range of water temperatures in the reaches and habitats using the ggplot function (tidyverse). Statistical tests to measure differences between water temperature metrics in the three reaches were not conducted. This was not the aim of our study, and there were limitations in the study design (i.e., a short period of data collection) to test the differences.

2.7 | Data Analysis

Data analyses were performed with the metaMDS function in the vegan package only on the macroinvertebrate dataset. To test for differences among the assemblages in the three reaches we used the pairwise.adonis2 function (Martinez Arbizu 2020). The pairwise.adonis2 is a nonparametric statistical test based on permutational multivariate analysis of variance (i.e., PERMANOVA, Anderson 2001) performing a multilevel pairwise comparison that allows strata to be defined to constrain permutations (999 permutations were used). The strata were used (strata = habitat type) because the study design was nested (habitat types nested within reaches). A subset of data was used for the test, with only pool and riffle samples to control for differences in the off-channel taxa and greater sampling effort (more samples) in restored reaches. We tested dispersions of the samples in each reach using the betadisper and permutest functions (vegan). We chose not to analyze other data statistically due to a small sample size of the habitat data, differences in the total area surveyed between reaches, and lack of spatial independence in our site selection (i.e., reaches were physically segregated Hurlbert 1984).

Nonmetric multidimensional scaling (NMDS) was chosen as an ordination technique to visualize the macroinvertebrate community. Macroinvertebrate counts were relativized using a square root transformation to reduce the influence of dominant taxa on the assemblage composition. The data matrix expressed each taxon contained in a sample as a relative proportion of the taxa in that sample. Sample points in the ordination plot can be interpreted as more similar in assemblage if they occur close to one another in the ordination space. For this study, we used the Bray-Curtis distance measure. NMDS stress is a measure of the representation of the data produced in the two-dimensional NMDS plot. Stress of 0.15, falls within the range of fair-poor, generally considered satisfactory for the data provided, whereas stress of <0.10 provides an excellent representation of the data in ordination space (McCune, Grace, and Urban 2002).

To explore differences in community structure between reaches and habitats we ordinated all macroinvertebrate samples in NMDS space. The ordination matrix contained 40 samples × 75 taxa. Intrinsic taxa were added to show the common taxa driving the separation of samples in the ordination using the envfit function (vegan). The NMDS axes were interpreted to describe patterns between the reaches and habitats.

An additional ordination was performed for the off-channel macroinvertebrate samples. We chose to analyze the data this way because (1) of obvious differences in the off-channel macroinvertebrate community, (2) it reduced longitudinal patterns that arise in NMDS, (3) environmental drivers in this habitat could be observed, and (4) there were no off-channel samples from the control site. Environmental variables were plotted on the ordinations using the envfit function to assess the relationships between patterns of macroinvertebrate assemblage and environmental variables. Environmental variables with low correlations ($r^2 < 0.3$) and those with limited interpretive value were omitted. For example, velocity in off-channel habitats was zero and percent dissolved oxygen varies based on the time of day measured so those parameters were not used to interpret the data.

The time of year that macroinvertebrate samples are collected creates high spatial and temporal variability when analyzing taxonomic composition, specifically because of the emergence timing of macroinvertebrates. Therefore, functional aspects of the macroinvertebrate community, like traits, can complement taxonomic approaches. Trait scores (derived from Poff et al. 2006) were assigned to each taxon using the match function and were expressed as a relativized proportion of the trait state within each sample. We evaluated differences in a group of cold stenothermal or cool eurythermal taxa (Temperature trait state 1; Table 3) using bubble plots to visualize the relative differences in ordination space. Thermal optima were calculated for each sample using the functcomp function (FD package; Laliberté, Legendre, and Shipley 2009). The functcomp function takes (1) a matrix of taxa composition by sites and (2) a matrix of one or several taxa attributes for each taxa, and calculates the weighted mean of taxa attributes, weighted by the abundance of each taxa. Differences in thermal optima for each of the three reaches were shown with boxplots (ggplot function). However, two samples were omitted due to low total abundance (fewer than 50 individuals), which skewed the weighted average. We plotted the thermal optima for samples in the off-channel ordination using the ordisurf function (vegan) to visualize the relationships between thermal optima and environmental variables. This analysis was also done on riffle and pool samples Data (S1).

Common summary metrics for the macroinvertebrate samples were used to aid in interpreting the results and were calculated in Excel. Composition measures were calculated from nontransformed abundance data to summarize the macroinvertebrate samples in each reach. Metrics included percent Ephemeroptera, Plecoptera, Trichoptera (%E, %P, %T, and %EPT), percent Chironomidae, percent Elmidae taxa, and percent Rhithrogena taxa.

3 | Results

3.1 | Stream Habitat Diversity

Values of the Shannon index of diversity, a diversity measure for geomorphic habitat (from existing habitat data), were 1.06, 0.94, and 0.27 for the restored 2012, restored 2016, and control reaches (Table 4). The true diversity was effectively three habitats for the restored 2012 and restored 2016 reaches (pools, riffles, and other habitat types), and one for the control reach (riffles). Off-channel and other habitat types comprised a small percentage of the habitat area in the restored 2012 and restored 2016 reaches (2%–15%) but were absent in the control reach. Riffles had the highest measured velocities, followed by pools, and velocity in the off-channel was zero (Table 4).

We observed several differences in the habitats between the reaches shown in Table 4. Depths were generally deeper in the restored 2012 off-channel, compared to the restored 2016 off-channel. The control reach had the highest median percent canopy cover for riffles and pools compared to the two restored reaches. Generally, canopy cover was lowest in the restored 2016 reach. Percent dissolved oxygen was similar (~100%) among pools and riffles in all three reaches, however, off-channel habitats in both the restored 2012 and restored 2016 reaches ranged from anoxic to supersaturated (measurements were taken between 900 and 1700 h). Conductivity generally decreased from the upstream restored 2012 reach, proceeding downstream to the control reach, and most downstream restored 2016 reach. The highest recorded conductivity was in off-channel habitats.

3.2 | Temperature Time-Series and Variability

The time-series water temperature data for pools (min: 9.7°C, max: 19.2°C) and riffles (min: 9.8°C, max: 20.6°C) within each reach were comparable, but this was not the case for off-channel habitats (min: 9.7°C, max: 28.9°C) (Figure 2). Time-series water temperature for the off-channel habitat type included sites that exhibited water temperature variations that were either cooled, buffered, lagged, or some combination of these. Also, the highest water temperatures measured (27.6–28.9°C) were recorded in three off-channel sites. We acknowledge the uncertainty associated with these measurements, particularly the uncertainty associated with the measurements due to the lack of a calibration procedure on the data loggers. While unfortunate, our justification is that we (1) were under time constraints due to recent wildfire in the area, and (2) used a thermistor (with an accuracy of ±0.2°C verified against a NIST meter) for field comparisons with the data loggers. Of 35 temperature loggers, 13 compared within ±0.5°C of two field meter audits, 11 compared within ±1°C of two field meter audits, and the remaining 11 compared within ±1.5°C of at least one field audit. Due to the data collection interval of the loggers (30 min), and the timing of the comparison readings with the field meter not matching exactly, we believe these comparisons were adequate for this study.

Calculated coefficients of variation ranged between 5% and 30%, demonstrating there was low to moderate variability in the water temperature among the sampling sites (Table 4). Coefficients of variation for riffles and pools in the control reach ranged between 13% and 16%; a smaller range than those observed in pools and riffles in the restored 2012 (16% and 20%) and restored 2016 (12% and 20%) reaches. Generally, coefficients of variation were higher in the off-channel habitats in the restored 2012 and restored 2016 reaches, the exceptions being two sites with coefficients of variation of only 5%.

3.3 | Macroinvertebrate Assemblage Structure and Temperature Associations

A total of 9504 benthic macroinvertebrates from 75 macroinvertebrate taxa (Appendix C) were identified in the samples ($n = 40$). The total number of taxa identified per reach is 67, 51, and 35 for the restored 2012, restored 2016, and control reaches, respectively. Macroinvertebrates from the families Elmidae and Chironomidae account for 27% and 23% of the total abundance, respectively, and EPT individuals comprised 41% of the total abundance (primarily Ephemerpotera). The remainder 9% include taxa from the orders Diptera, Coleoptera, Trombidiformes, Odonata, Lepidoptera, Hemiptera, Megaloptera, and Decapoda. The total numbers of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa for each reach are 33, 23, and 17 for the restored 2012, restored 2016, and control reaches, respectively.

Rarefied taxa richness for all samples ranges from 4 to 30 taxa per sample and the median is 16. The median taxa richness in riffles is 20 (range 19–25), 17 (range 13–20), and 16 (range 15–25) for the restored 2012, restored 2016, and control reaches. Effective numbers of taxa in riffles showed small differences between the restored and control reaches (Figure 3).

Ordination shows similarities in the macroinvertebrate assemblages within each a priori group (Figure 4). Within-reach variability (represented by NMDS 1, x-axis) is greater than that between reaches (represented by NMDS 2, y-axis). Generally, ordination establishes that differences within pool and riffle sample groups are smaller than differences in the off-channel sample groups. Macroinvertebrate samples from the off-channel differ from riffle and pool samples by Ephemeroptera taxa Baetidae, Caenidae, Heptageniidae, and *Siphlonurus*, Trichopteran taxa *Mystacides* and *Psychoglypha*, Odonata (dragonflies and damselflies), Coleoptera (Dytiscidae, Haliplidae, Hydrophilidae), a Hemiptera taxon *Sigara*, Culicidae (mosquito), *Sialis* (alderfly), and Decapoda (crayfish).

Pool and riffle samples generally cluster on the right side of the ordination because they share many of the same taxa including: Ephemeroptera taxa *Baetis* spp., Ephemerellidae, Heptageniidae, and Leptophlebiidae; Plecoptera taxa Chloroperlidae, Nemouridae, Perlodidae, and Pteronarcyidae

TABLE 4 | Habitat metrics and environmental data for the three reaches of the study in Whychus Creek.

Reach habitat metrics				Environmental variables[b]			Water quality and temperature[b]		
Reach	Habitats	Habitat area (%)	Shannon diversity	Velocity (m/s)	Depth (cm)	Canopy cover (%)	Dissolved oxygen (%)	Conductivity (µS/cm @ 25°C)	CV (%)
Restored 2012	Off-channel	2	1.06[a]	0 (0, 0)	38 (17, 50)	25 (4, 83)	95 (15, 160)	85 (49, 85)	14 (5, 26)
	Riffle	30		1.1 (0.3, 1.8)	15 (12, 26)	9 (0, 42)	101 (98, 102)	51 (49, 53)	19 (17, 20)
	Pool	53		0.8 (0.2, 2.2)	46 (34, 49)	12 (3, 95)	101 (98, 103)	52 (48, 54)	17 (16, 17)
	Other	15							
Restored 2016	Off-channel	3	0.94[a]	0 (0, 0)	15 (8, 26)	11 (3, 40)	95 (8, 118)	55 (42,128)	16 (5, 30)
	Riffle	60		1.6 (0.8, 2.4)	13 (12, 22)	4 (3, 22)	104 (102, 104)	44 (42, 44)	14 (12, 15)
	Pool	31		0.2 (0.0, 2.0)	47 (30, 56)	13 (2, 30)	103 (101, 104)	43 (43, 44)	14 (14, 20)
	Other	6							
Control	Riffle	92	0.27[a]	1.7 (1.4, 1.9)	22 (14, 29)	43 (21, 93)	100 (99, 100)	45 (45, 47)	15 (15, 16)
	Pool	8		1.1 (0.8, 1.4)	42 (33, 59)	61 (32, 97)	100 (99, 100)	46 (45, 46)	15 (13, 15)

Abbreviation: CV = Coefficient of variation for water temperature data.

[a] Reach-level metric.

[b] Reported as median (minimum, maximum) values of the five sites for each habitat type within the reach.

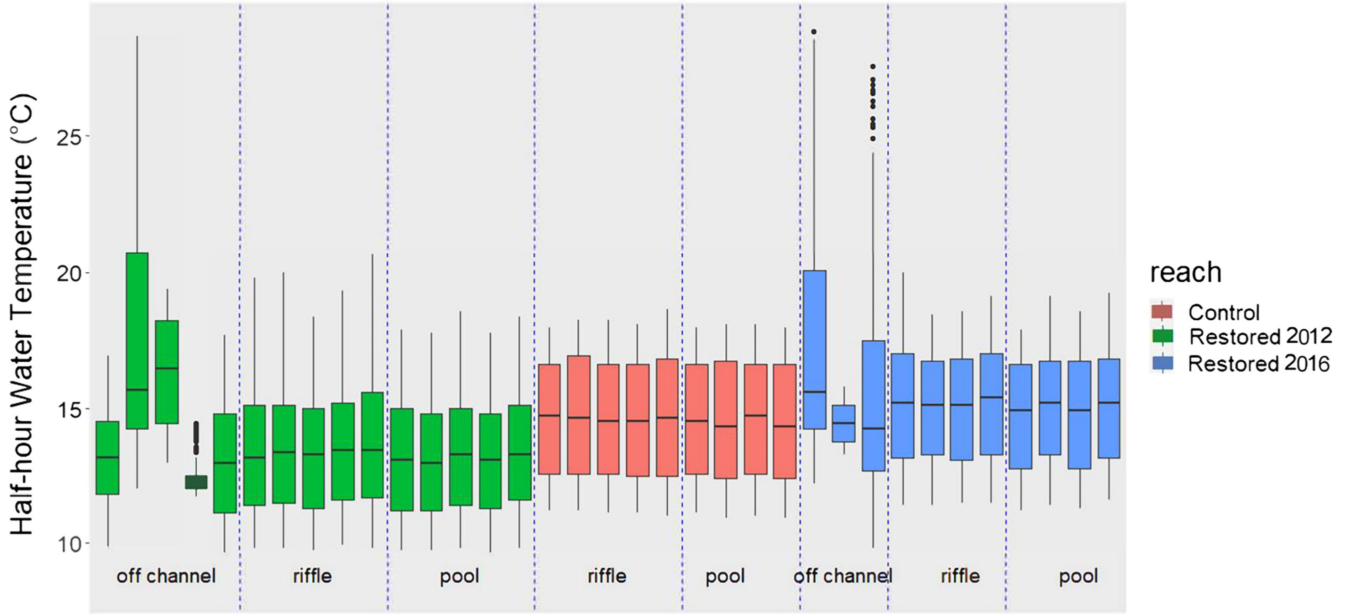

FIGURE 2 | Water temperature for each sampling site was plotted with boxplots. The colored region shows the upper and lower quartiles, the dark bar shows the median, and the lines extend to the upper and lower deciles. Points represent potential outliers. [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 | Boxplots showing distributions for the effective numbers of taxa per sample in riffles. The colored region shows the upper and lower quartiles, the dark bar shows the median, and the lines extend to the upper and lower deciles. Points represent potential outliers. [Color figure can be viewed at wileyonlinelibrary.com]

(Giant Stonefly, except none found in the restored 2012 reach); Trichoptera taxa Brachycentridae, Glossosomatidae, Hydropsycheidae, Limnephilidae (October Caddisfly, except none found in restored 2016 reach), and Rhyacophilidae; Diptera (*Atherix* and Simuliidae); Coleoptera family Elmidae; Trombidiformes; Pyralidae; and Hemiptera. Notably, there is a more diverse assemblage of EPT taxa in the restored 2012 reach pools and riffles that leads to a distinct grouping of those sample points in the ordination. Several Trichoptera taxa found only in the restored 2012 reach include Hydroptilidae, Leptoceridae, Limnephilidae (Northern caddisfly), Philopotamidae, Phryganeidae, and Polycentropodidae. The differences between reaches in macroinvertebrate assemblage, using only a subset of the data (pool and riffle samples), are significant (Restored 2012 vs. control $F=7.356$, $p=0.001$; Restored 2012 vs. restored 2016 $F=5.270$, $p=0.001$; Restored 2016 vs. control $F=1.534$, $p=0.043$: Table 5). There is no evidence that the dispersions of the samples in each reach differed ($F=2.523$, $p=0.108$).

Ordination of the off-channel macroinvertebrate samples (Figure 5) reveals associations between the environmental variables, the macroinvertebrate assemblages, and the thermal optima for the community. The off-channel ordination was rotated to align the horizontal axis along the vector for the water temperature coefficient of variation. Water temperature coefficients of variation, maximum water temperatures, and mean water temperatures correlate positively with NMDS axis 1 ($r^2=0.53$, 0.50, and 0.30, respectively) while depths correlate negatively with NMDS axis 1 ($r^2=0.45$). The vector for mean water temperatures is strongest in the direction of three restored 2016 off-channel samples. A group of four restored 2012 and two restored 2016 off-channel samples represent assemblages dominant with Chironomidae (>50% of the total abundance per sample). Additionally, the samples in this group contain copepods Data (S1). One sample does not group near any other samples in the ordination space. That sample contains no Chironomidae taxa and Elmidae taxa account for 63% of its total abundance. The remainder of the assemblage for the outlying sample is made up of the Ephemeroptera taxa *Paraleptophlebia* and *Siphlonurus*, Diptera, Odonata, *Sialis*, and Hydroporniae taxa. The ordination represents a nonlinear gradient in thermal optima. The same analyses on riffle and pool samples represent linear gradients in thermal optima and show there was more variation in temperature optima within reaches versus between reaches Data (S1).

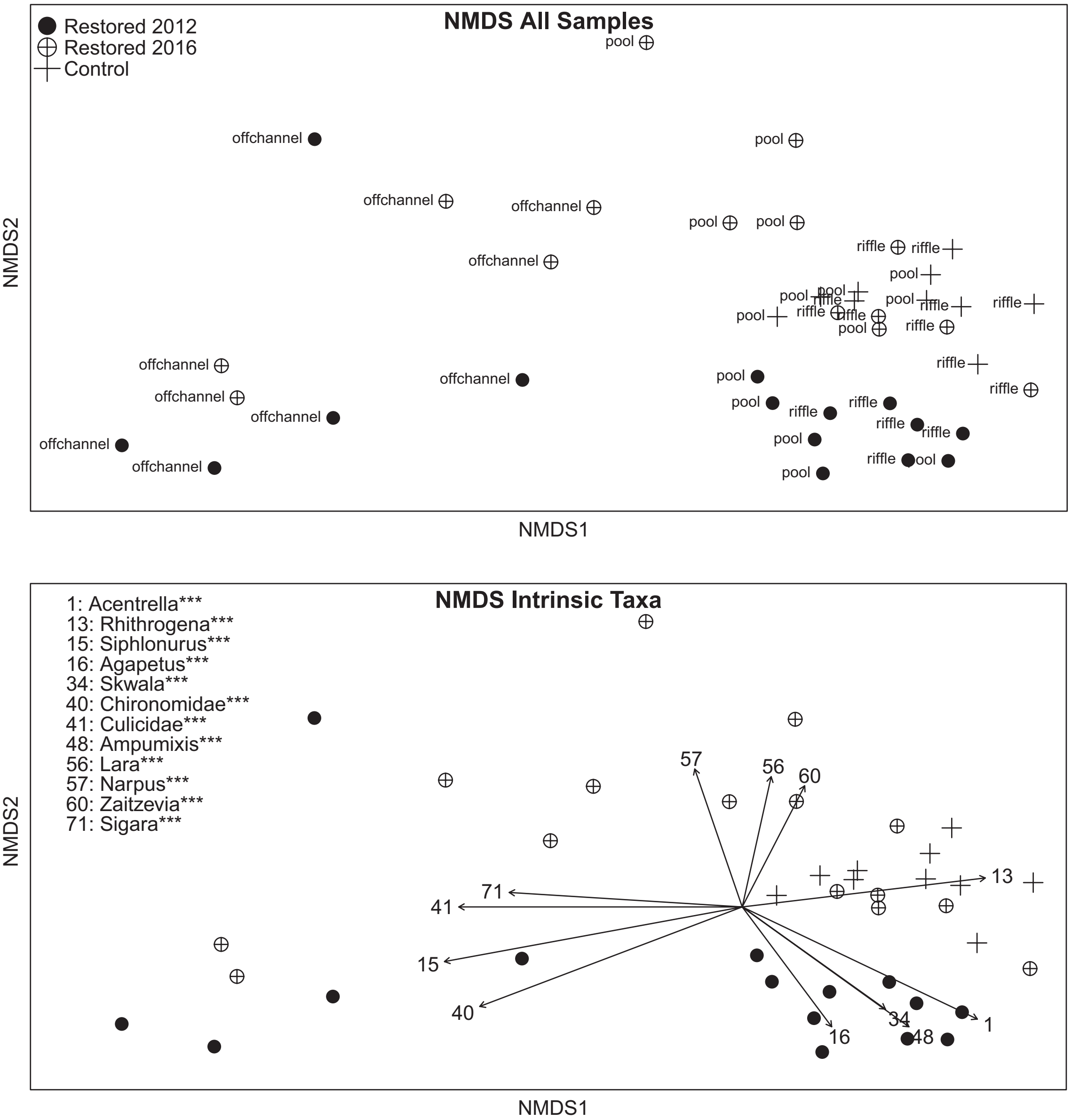

FIGURE 4 | Nonmetric Multidimensional Scaling (NMDS) ordination of macroinvertebrate assemblage for each sample collected in the three reaches and three habitat types (upper) (stress = 0.153). Variation in NMDS1 (*x*-axis) represents within-reach variability in community assemblage. Both the transition and restored reaches show similar variability along nmds1. Variation in NMDS2 (*y*-axis) represents between-reach variability in community assemblage. Significantly correlated intrinsic taxa ($p < 0.001$) are overlaid (lower) showing which taxa are driving the site distribution. The direction of the vector corresponds with the direction of increasing value. The length of the vector signifies the correlation.

TABLE 5 | Nonparametric PERMANOVA pairwise tests among macroinvertebrate assemblages in pool and riffle samples from three reaches in Whychus Creek.

Comparison	*F*-statistic	*p*
Restored 2012 versus control	7.356	0.001
Restored 2012 versus restored 2016	5.270	0.001
Restored 2016 versus control	1.534	0.043

Bubble plots for macroinvertebrate traits show the relative differences in the proportion of coldwater stenothermic taxa in the reaches (Figure 6). Coldwater stenothermic taxa include *Agapetus*, Amphizoidae, *Anagapetus*, *Caudatella*, *Cinygma*, *Cinygumula*, *Dicosmoecus*, *Epeorus*, Haliplidae, *Haliplus*, Heptageniidae, *Micrasema*, *Psychoglypha*, *Pteronarcys*, *Rhithrogena*, *Skwala*, *Zapada*, and Trombidiformes. Generally, pool and riffle samples contain the highest proportions of coldwater taxa and range from 0.08 to 0.30 and 0.20 to 0.36, respectively. The off-channel samples range from relative proportions of 0 to 0.14 coldwater taxa.

Weighted average thermal optima show the median thermal optima is 17.9°C (range: 16.8–18.3°C), 17.7°C (range: 17.0–19.0°C), and 17.3°C (range: 17.0–18.0°C) in the restored 2012, restored 2016, and control reaches (Figure 7). Overall, variation in thermal optima is lowest in control reach riffles (range = 0.4°C), highest in restored 2016 pools (range = 2.7°C), and intermediate in off-channel (range = 2.1°C).

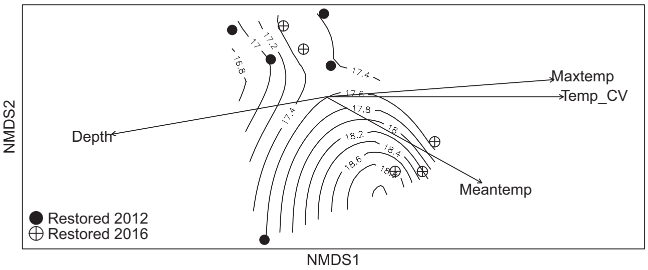

FIGURE 5 | Nonmetric Multidimensional Scaling (NMDS) ordination (stress = 0.082) of macroinvertebrate assemblage for each sample collected in the off-channel habitat type with environmental variables overlaid for interpretation of the relationship between macroinvertebrate community and environmental gradients. Environmental variables include Maxtemp-maximum water temperature; Meantemp-mean water temperature; Temp_CV-temperature coefficient of variation; and depth (sample unit depth). The direction of the vector corresponds with the direction of increasing value. The length of the vector signifies the correlation. Contour lines show the community weighted mean thermal optima (°C) for each sample in ordination space.

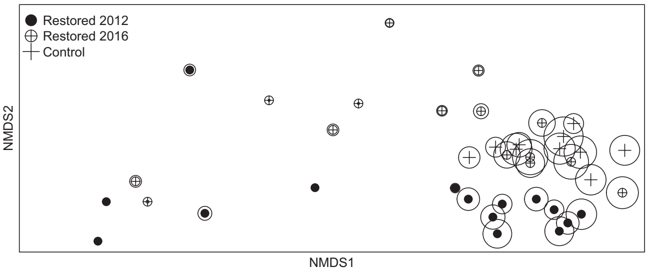

FIGURE 6 | Bubble plot shows the relative proportions of coldwater stenothermic macroinvertebrates in NMDS ordination space (stress = 0.153) for the three reaches.

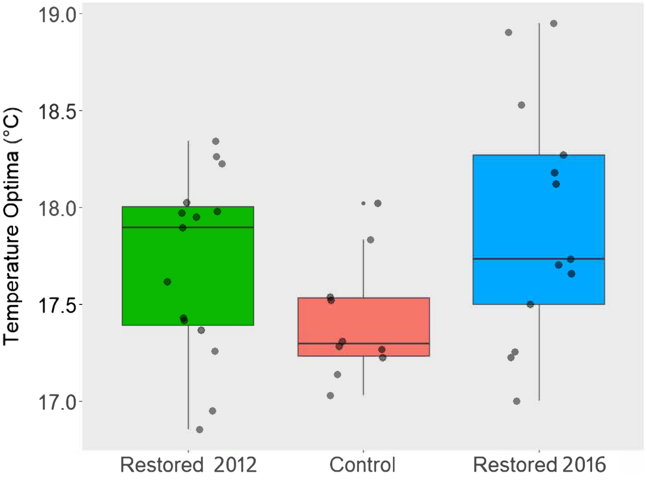

FIGURE 7 | Boxplot for weighted average macroinvertebrate temperature optima. The colored region shows the upper and lower quartiles, the dark bar shows the median, and the lines extend to the upper and lower deciles. Points represent values of individual samples and are shown to aid in visualizing the distribution of the data. The restored reach ($n = 15$) and transition reach ($n = 13$) included samples from riffle, pool, and off-channel habitat types. The control reach ($n = 10$) included samples from riffle and pool habitat types only. [Color figure can be viewed at wileyonlinelibrary.com]

4 | Discussion

This is the first study that we are aware of in Stage 0/8 restoration settings to evaluate the reach level geomorphic habitat diversity, measure differences in water temperature variations in different restored habitats for macroinvertebrates, and collect biota simultaneously to interpret different temperature variations in restored habitats and the impact on macroinvertebrate assemblage and their temperature associations. When compared to an unrestored, channelized reach, reaches with fully reconnected floodplains have higher geomorphic habitat diversity (i.e., pools and off-channel habitats for biota), higher spatial variability in water temperatures, more effective numbers of macroinvertebrate taxa, and a broader range of thermal optima. Our findings also demonstrate that the macroinvertebrate communities in the two restored reaches were different and more diverse (thanks largely to the addition of the off-channel habitats and species) and contain low to moderate proportions of coldwater stenothermic or cool eurythermal taxa. The proportions of coldwater stenothermic or cool eurythermal taxa are less in the off-channel habitats found in restored reaches, compared to riffles and pools. Last, macroinvertebrates in restored reaches displayed a broad range of thermal optima that reflect the environmental conditions of the habitats they occupy. In the remainder of this paper, we discuss specific points raised by our findings as well as their wider implications.

4.1 | Habitat Diversity

Results from the geomorphic habitat diversity index show that habitat diversity in the two restored reaches compares well with each other even though they differed in time since restoration. This finding agrees with the predictions of the Stream Evolution Model (Cluer and Thorne 2014) that habitat complexity increases as streams proceed from middle stages (channelized) to early (Stage 0) and late stages (Stage 8). A notable difference in the habitat types of the restored reaches, however, is the restored 2016 reach has double the percent of riffle area compared to the restored 2012 reach. These differences may change under functioning floodplain conditions over time (Wohl et al. 2021) due to the presence of large wood. Collins et al. (2012) described the effects of the "floodplain large wood cycle" including an increase in the number and depth of pools in a river, influencing the development of additional channels, and creating more diverse habitat types. The presence of large wood in the restored 2016 (field photos) reach suggests that slow-moving pools will form (Kirkland and Flitcroft 2020).

Pools and riffles in the two restored reaches of the present study have lower velocities compared to the control reach due to the straightened and constrained nature of the control reach. Our findings of lower velocity in the habitats of restored reaches were consistent with Flitcroft et al. (2022) who modeled the increase in pre and post-restoration low-velocity habitat for juvenile salmonids in the restored 2016 reach. High velocity can lead to wash out of some fish life stages (i.e., during egg development) and is not a desirable rearing habitat for juvenile fish that require low-velocity off-channel habitats during high flow events (Jeffres, Opperman, and Moyle 2008). Edwards et al. (2020) suggested the slowing of flow in restored floodplains as a mechanism to increase primary productivity and observations in macroinvertebrate communities suggest so (Flitcroft et al. 2022).

4.2 | Water Temperature and Macroinvertebrate Temperature Associations

Overall, the variability in water temperatures in the restored reaches is higher compared to the control. Within a broader floodplain restoration context, maximum water temperatures in the restored reaches of the present study were within 1°C of Five mile-Bell Creek, Oregon (Stage 0, Flitcroft et al. 2022), and the range of maximum water temperatures in the present study are comparable to those of Weber et al. (2017) in a nearby watershed Bridge Creek, Oregon (710 km^2) restored with beavers. High maximum summertime water temperatures, and low percent canopy cover in restored reaches, are consistent with maximum water temperature increases observed in streams with reduced canopy cover in Oregon (Ringler and Hall 1975; Harris 1977; Warren et al. 2022). The water temperature data from the control reach in the present study contradicts the results of Weber et al. (2017) who found higher water temperatures in their control reach versus their restored reach. We attribute the divergence of our results to differences in the control reach used in this study, which was heavily shaded (and undisturbed over the last 60 years) compared to the control reach in the Weber et al. (2017) study. Orzetti, Jones, and Murphy (2010) suggested that both riparian buffer age and past land use, in conjunction, will determine the trajectory, or time required, for measurable improvement in water quality and temperature, which typically achieves full water quality function in 15–20 years. Due to our control reach having high velocity, high canopy cover, and a simplified channel, it is likely that water temperatures are artificially lower compared to pre-settlement conditions and the restored reaches are more representative of actual historic (pre-settlement) conditions.

Collectively, our results and the literature describing aquatic floodplain habitats (Jeffres, Opperman, and Moyle 2008; Flitcroft et al. 2022) suggest that high maximum water temperatures are common in restored floodplains and their associated aquatic habitats, at least in post-restoration appraisal studies conducted after short durations (<10 years). However, the present study shows differences in the thermal variations in the off-channel, in two sites, equating to 0.13 cold water patches (<3°C relative to ambient stream conditions) per 100 m of stream channel length (approximate total stream length sampled ~1.5 km). The two cold water patches are separated by more than 8 km and share similarities in their water quality properties—elevated conductance (>80 μS/cm) and low dissolved oxygen (<15% DO saturation) and are likely connected by long (>100 m) hyporheic flow paths based on the range of temperatures. Ebersole, Liss, and Frissell (2003) calculated 0.39 cold water patches per 100 m stream length for an unrestored Eastern Oregon stream with a functioning floodplain (with a greater sampling effort). Within the context of stream restoration, we caution those who undervalue seasonally warm water habitats because of the benefits to biota during the non-peak summertime water temperature period and the influence on ecological functions (Armstrong et al. 2021).

We recognize several limitations of the water temperature data, particularly the uncertainty associated with the measurements due to the lack of a calibration procedure on the data loggers. The study was conducted during the hottest month of the year with a very limited duration, and we did not measure the extent of hyporheic activities, which may be the most effective way to address the effects of restoration on stream temperatures. However, it was good to do the study in the summer as it was more likely to capture the upper temperatures that may be the thermal limits of some macroinvertebrates, and this was our objective. Our study did not do a heat budget of stream and groundwater impacts on each reach thus, it may be difficult to assess the exact impact of stream restoration on stream temperatures over longer periods of time based on our data. Unlike the temperature studies which only measure temperature, we also assessed resident macroinvertebrates that provide an ultimate response to the restoration effects on temperature.

The taxa with the lowest thermal optima are examples of taxa whose distribution may be limited by the temperature variations (and maximum temperatures) recorded in this study. Take, for example, two Ephemeroptera taxa *Caudatella* and *Ephemerella* with thermal optima values of 13.6 and 14.4°C and the Plecoptera taxa *Pternonacys*, whose thermal optima is 15.2°C. *Caudatella*, a cold stenotherm or cool eurytherm, that exhibits high performance in a narrower range of temperatures, was only found in three samples from the restored 2012 reach (in all three habitat types). *Ephemerella*, a eurytherm, can maintain optimal performance over a wide range of temperatures throughout its annual life cycle and was found in 12 samples from this study (in all three reaches). Uno and Stillman (2020) found that for *Ephemerella* sp., each life stage exhibits phenotypic variation matching ambient temperatures typically experienced in that stage. *Pternonacys*, a cold stenotherm or cool eurytherm was only found in nine pool and riffle samples in the control and restored 2016 reaches. *Skwala*, in contrast, a Plecoptera a cold stenotherm or cool eurytherm taxa whose thermal optima was higher (18.6°C), was found in 21 pool and riffle samples and all three reaches.

Mazzacano (2021) found a wide range of temperature associations for macroinvertebrates in the same restored reaches used in our study, with weighted averages for temperature optima between 16.3 and 18.2°C compared to ours 16.8 and 19.0°C. This discrepancy in the calculated range of thermal optima is likely due to differences in sampling sites and identification procedures used (proportional multihabitat and riffle targeted sampling, NWSTE Level 2) or optima values for specific taxa. However, the median temperature optima of the three reaches in the present study compares well to the mean of their 17.3°C.

4.3 | Macroinvertebrate Assemblage Structure

Efforts in Whychus Creek to restore a Stage 0 condition appear favorable to the macroinvertebrate community. Overall, higher diversity in restored reaches (total taxa per reach and number of EPT taxa) in the present study is attributed to contributions of taxa in the off-channel that possess a variety of adaptations for low dissolved oxygen conditions (e.g., Aeshnidae, *Sialis*, *Sigara*, *Siphlonurus*). Aeshnidae, a family of dragonflies, are predators that are typically associated with lentic habitats (McCafferty 1981). *Sialis* is a genus of alderfly in the order Megoloptera, typically associated with slow-moving pools and backwaters with accumulations of detritus and debris, and are highly predacious (McCafferty 1981). *Sigara* is a genus of water boatman in the order Hemiptera and is a notable herbivore (McCafferty 1981). *Siphlonurus* is a large swimming mayfly described as inhabiting isolated pools with silty bottoms, sometimes found in pools of “seepage water” (Edmunds, Jensen, and Berner 1976) as mature nymphs. The genus *Siphlonurus* is classified as collector-gatherers, however, McCafferty (1981) notes they feed opportunistically on small aquatic insects. Overall, the off-channel taxa found herein represent a shift in food resources (high abundance of collector-gatherer and predator functional feeding group, presence of copepods and zooplankton), change in stream habitat availability (lentic off-channel habitat), and adaptations to diverse thermal regimes as predicted by the conceptual model of Poff et al. (2006).

In the context of Poff et al. (2006), there were limitations to using macroinvertebrate thermal preference and thermal optima to interpret differences in the macroinvertebrate communities between the reaches. Clustering of cold stenothermal or cool eurythermal macroinvertebrates in ordination space is correlated with %EPT taxa and velocity due to the high presence of *Rhithrogena* taxa in fast-flowing habitats. However, pairing a qualitative measure of thermal preference with a quantitative measure of thermal optima made the relationships between the macroinvertebrates and the temperatures they experience in different habitats easier to interpret, particularly when the thermal optima were plotted with contours in ordinations. These ordinations revealed that there is considerable variation in the thermal optima of individual samples within the reaches and the habitats studied. There is a recognition of the limitations of the three categories of thermal preference described in Poff et al. (2006) and since the time of this study, Hubler et al. (2024) have modeled temperature relationships for macroinvertebrates in the Pacific Northwest with seven categories for thermal preference. Future appraisal studies may be enhanced by these regionally based thermal optima categories.

Our habitat-specific sampling approach was a benefit to our analysis. While other studies have been done in floodplains restored to similar conditions as in the present study, limitations in their study design (i.e., riffle samples only), or large-scale impairments in the watershed (i.e., excess sediment) led to conclusions that there was no effect on the macroinvertebrate community (Smith et al. 2020). When we included pool samples in our analysis and controlled for the variability of the macroinvertebrates within the habitats, our results showed significant differences in the assemblages of restored and unrestored reaches within 5 years since restoration. However, we caution the interpretation of our test results with concerns about the significance level of $\alpha = 0.05$ raised by Anderson (2001).

Besides restoration, basin-scale factors like in stream flow restoration (which provides the greatest improvements in water temperature), decommissioning of roads, wildfire, and climate change impacts (USFS 2013) all affect macroinvertebrates in Whychus Creek. Flow underneath the surface of the stream (hyporheic) also contributes to the overall habitat area and availability of resources for macroinvertebrates (Hauer et al. 2016). There are limitations in our study design because we did not measure hyporheic exchange or other basin-scale factors that exert selective pressures on the macroinvertebrate community. In addition, we assume that the macroinvertebrate assemblage was primarily driven by environmental factors rather than biotic factors like competition.

5 | Implications

The results of this study demonstrate the temperature variations of streams in Stage 0/8 conditions and the diverse macroinvertebrate communities they support. An important objective of any temperature monitoring in restored reaches should be to adequately characterize thermal heterogeneity. Spatial assessment of temperature variations in the habitats of restored reaches (>5 temperature loggers in each habitat type) can more accurately characterize the temperature variability within habitats and identify areas of coldwater refugia (as we did in the off-channel habitats) and more work should be done on the temporal variation in temperature over longer time scales. These data can be important when communicating with stakeholders to show that new methods of restoration can achieve results for coldwater species like salmon and certain taxa of macroinvertebrates. An additional implication for effective appraisal is that macroinvertebrate sampling should separate samples collected from different habitat types. This is important because when samples are composited, as is done with routine bioassessments of floodplains, the off-channel macroinvertebrate community is combined with pool and riffle macroinvertebrates. This compositing of samples ultimately confounds the macroinvertebrate response to the creation of off-channel habitats and coldwater patches found in these habitats. Bioassessment in restored floodplains should adequately characterize the trajectory of macroinvertebrate communities in the off-channel habitats, as these are potential hotspots for biodiversity and productivity in the system.

Acknowledgments

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors confirm that the data supporting the findings of this study are available within the supplementary materials. Scripts used to run the analysis are available upon reasonable request from the corresponding author.

References

Allan, J. D., and M. M. Castillo. 2007. *Stream Ecology: Structure and Function of Running Waters*, 436. Dordrecht: Springer.

Al-Zankana, A. F. A., T. Matheson, and D. M. Harper. 2020. "How Strong is the Evidence – Based on Macroinvertebrate Community Responses – That River Restoration Works?" *Ecohydrology & Hydrobiology* 20: 196–214.

Anderson, M. J. 2001. "A New Method for Non-Parametric Multivariate Analysis of Variance." *Austral Ecology* 26: 32–46.

Armstrong, J. B., A. H. Fullerton, C. E. Jordan, et al. 2021. "The Importance of Warm Habitat to the Growth Regime of Cold-Water Fishes." *Nature Climate Change* 11: 354–361. https://doi.org/10.1038/s41558-021-00994-y.

Aylward, B., and R. O'Connor. 2017. "Whychus Flow Restoration: An Environmental Water Transactions Case Study." http://www.ampinsights.com/s/Whychus.pdf.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. *Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates, and Fish*. Second ed|Bioassessment|US EPA. Washington, D.C.: United States Environmental Protection Agency; Office of Water. https://archive.epa.gov/water/archive/web/html/index-14.html.

Beechie, T. J., D. A. Sear, J. D. Olden, et al. 2010. "Process-Based Principles for Restoring River Ecosystems." *Bioscience* 60: 209–222. https://doi.org/10.1525/bio.2010.60.3.7.

Benson, B. B., and D. Krause. 1984. "The Concentration and Isotopic Fractionation of Oxygen Dissolved in Freshwater and Seawater in Equilibrium With the Atmosphere." *Limnology and Oceanography* 29: 620–632.

Bernhardt, E. S., and M. A. Palmer. 2011. "River Restoration: The Fuzzy Logic of Repairing Reaches to Reverse Catchment Scale Degradation." *Ecological Applications* 21: 1926–1931.

Biron, P. M., T. Buffin-Bélanger, M. Larocque, et al. 2014. "Freedom Space for Rivers: A Sustainable Management Approach to Enhance River Resilience." *Environmental Management* 54: 1056–1073. https://doi.org/10.1007/s00267-014-0366-z.

Bouwes, N., N. Weber, C. E. Jordan, et al. 2016. "Ecosystem Experiment Reveals Benefits of Natural and Simulated Beaver Dams to a Threatened Population of Steelhead (*Oncorhynchus mykiss*)." *Scientific Reports* 6: 28581. https://doi.org/10.1038/srep28581.

Braccia, A., J. Lau, J. Robinson, M. Croasdaile, J. Park, and A. Parola. 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.

Caissie, D. 2006. "The Thermal Regime of Rivers: A Review." *Freshwater Biology* 51: 1389–1406.

Cluer, B., and C. Thorne. 2014. "A Stream Evolution Model Integrating Habitat and Ecosystem Benefits: SEM Incorporating Habitat and Ecosystem Benefits." *River Research and Applications* 30: 135–154. https://doi.org/10.1002/rra.2631.

Collins, B. D., D. R. Montgomery, K. L. Fetherston, and T. B. Abbe. 2012. "The Floodplain Large-Wood Cycle Hypothesis: A Mechanism for the Physical and Biotic Structuring of Temperate Forested Alluvial Valleys in the North Pacific Coastal Ecoregion." *Geomorphology* 139–140: 460–470. https://doi.org/10.1016/j.geomorph.2011.11.011.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2003. "Thermal Heterogeneity, Stream Channel Morphology, and Salmonid Abundance in Northeastern Oregon Streams." *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1266–1280. https://doi.org/10.1139/f03-107.

Edmunds, G. F., S. L. Jensen, and L. Berner. 1976. "The Mayflies of North and Central America. George F. Edmunds, Jr., Steven L. Jensen, Lewis Berner." *Quarterly Review of Biology* 52: 440. https://doi.org/10.1086/410240.

Edwards, P. M., Y. Pan, L. Mork, and C. Thorne. 2020. "Using Diatoms to Assess River Restoration: A Pilot Study in Whychus Creek, Oregon, USA." *River Research and Applications* 36: 2089–2095. https://doi.org/10.1002/rra.3712.

England, J., N. Angelopoulos, S. Cooksley, et al. 2021. "Best Practices for Monitoring and Assessing the Ecological Response to River Restoration." *Watermark* 13: 3352. https://doi.org/10.3390/w13233352.

Flitcroft, R. L., W. R. Brignon, B. Staab, 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.

Gotelli, N. J., and A. M. Ellison. 2012. *A Primer of Ecological Statistics*. Sunderland, MA: Sinauer Associates Inc. https://harvardforest.fas.harvard.edu/ellison/pubs/primer/datafiles2e.

Harris, D. D. 1977. "Hydrologic Changes After Logging in Two Small Oregon Coastal Watersheds." 2037. http://pubs.er.usgs.gov/publication/wsp2037.

Hauer, F. R., H. Locke, V. J. Dreitz, et al. 2016. "Gravel-Bed River Floodplains Are the Ecological Nexus of Glaciated Mountain Landscapes." *Science Advances* 2: e1600026. https://doi.org/10.1126/sciadv.1600026.

Hill, M. O. 1973. "Diversity and Evenness: A Unifying Notation and Its Consequences." *Ecology* 54: 427–432. https://doi.org/10.2307/1934352.

HOBO. 2014. "Pendant Temperature Data Logger (UA-001-xx) Manual."

Hubler, S., J. Stamp, S. P. Sullivan, et al. 2024. "Improved Thermal Preferences and a Stressor Index Derived from Modeled Stream Temperatures and Regional Taxonomic Standards for Freshwater Macroinvertebrates of the Pacific Northwest, USA." *Ecological Indicators* 160: 111869.

Huff, D. D., S. L. Hubler, Y. Pan, and D. L. Drake. 2008. "Detecting Shifts in Macroinvertebrate Community Requirements: Implicating Causes of Impairment in Streams."

Hurlbert, S. H. 1984. "Pseudoreplication and the Design of Ecological Field Experiments." *Ecological Monographs* 54: 187–211. https://doi.org/10.2307/1942661.

Jeffres, C. A., J. J. Opperman, and P. B. Moyle. 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.

Jost, L. 2006. "Entropy and Diversity." *Oikos* 113: 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x.

Kennedy, T. L., and T. F. Turner. 2011. "River Channelization Reduces Nutrient Flow and Macroinvertebrate Diversity at the Aquatic Terrestrial Transition Zone." *Ecosphere* 2: art35. https://doi.org/10.1890/ES11-00047.1.

Kirkland, J., and R. Flitcroft. 2020. "Location, Location, Location: For Coho Salmon, It's all About the Neighborhood." In *Science Findings 224*, vol. 224, 1–5. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Laliberté, E., P. Legendre, and B. Shipley. 2009. "FD: Measuring Functional Diversity (FD) From Multiple Traits, and Other Tools for Functional Ecology."

Lemmon, P. E. 1956. "A Spherical Densiometer for Estimating Forest Overstory Density." *Forest Science* 2: 314–320. https://doi.org/10.1093/forestscience/2.4.314.

Martinez Arbizu, P. 2020. "GitHub – Pmartinezarbizu/PairwiseAdonis: Pairwise Multilevel Comparison Using Adonis. R package Version 0.4." http://www.github.com/pmartinezarbizu/pairwiseAdonis.

Marsh-McBirney Inc. 1990. *Model 2000 Installation and Operations Manual*. Frederick, MD: Marsh-McBirney Inc. www.marsh-mcbirney.com.

Mazzacano, C. 2021. "Macroinvertebrate Monitoring at Selected Sites in Whychus Creek, Sisters, OR." https://www.upperdeschuteswatershedcouncil.org/wp-content/uploads/2023/04/2020-Whychus-Creek-Macroinvertebrate-Montoring-Final-Report_CASM-Environmental.pdf.

McCafferty, W. P. 1981. *Aquatic Entomology: The Fishermen's and Ecologists' Illustrated Guide to Insects and Their Relatives*, 502. Sudbury, Massachusetts: Jones and Bartlett Learning.

McCaffrey, C. M. 2021. *The Use of Mayflies Stoneflies and Caddisflies as Indicators of Fine Sediment Pollution in Salmon-Bearing Streams of the Pacific Northwest*. Portland, Oregon: Portland State University.

McCune, B., J. B. Grace, and D. L. Urban. 2002. *Analysis of Ecological Communities*, 300. Gleneden Beach, Oregon: MjM Software Design.

Merritt, R. W., and K. W. Cummins. 1996. *An Introduction to the Aquatic Insects of North America*. References – Scientific Research Publishing. Vol. 862. Dubuque, IA: Kendall/Hunt Publishing Company. https://www.scirp.org/reference/referencespapers?referenceid=2971142.

Mork, L., and R. Houston. 2016. *2015 Whychus Creek Monitoring Report*. Bend: Upper Deschutes Watershed Council.

Nash, C. S., G. E. Grant, S. Charnley, et al. 2021. "Great Expectations: Deconstructing the Process Pathways Underlying Beaver-Related Restoration." *Bioscience* 71: 249–267. https://doi.org/10.1093/biosci/biaa165.

Oksanen, J., G. L. Simpson, F. G. Blanchet, et al. 2024. "Vegan: Community Ecology Package." https://cran.r-project.org/web/packages/vegan/vegan.pdf.

Olden, J. D., and R. J. Naiman. 2010. "Incorporating Thermal Regimes Into Environmental Flows Assessments: Modifying dam Operations to Restore Freshwater Ecosystem Integrity." *Freshwater Biology* 55: 86–107. https://doi.org/10.1111/j.1365-2427.2009.02179.x.

Oregon Department of Environmental Quality (ODEQ). 2013. "Data Validation Criteria for Water Quality Parameters Measured in the Field."

Orr, M. R., N. P. Weber, W. N. Noone, M. G. Mooney, T. M. Oakes, and H. M. Broughton. 2020. "Short-Term Stream and Riparian Responses to Beaver Dam Analogs on a Low-Gradient Channel Lacking Woody Riparian Vegetation." *Northwest Science* 93: 171. https://doi.org/10.3955/046.093.0302.

Orzetti, L. L., R. C. Jones, and R. F. Murphy. 2010. "Stream Condition in Piedmont Streams With Restored Riparian Buffers in the Chesapeake Bay Watershed 1." *JAWRA Journal of the American Water Resources Association* 46: 473–485. https://doi.org/10.1111/j.1752-1688.2009.00414.x.

Pacific Northwest Aquatic Monitoring Partnership (PNAMP). 2015. "2015 DRAFT Northwest Standard Taxonomic Effort Taxa Lists 2015-11-03."

Poff, N. L., J. D. Olden, N. K. M. Vieira, D. S. Finn, M. P. Simmons, and B. C. Kondratieff. 2006. "Functional Trait Niches of North American Lotic Insects: Traits-Based Ecological Applications in Light of Phylogenetic Relationships." *Journal of the North American Benthological Society* 25: 730–755. https://doi.org/10.1899/0887-3593(2006)025[0730:FTNONA]2.0.CO;2.

Powers, P. D., M. Helstab, and S. L. Niezgoda. 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.

R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: Foundation for Statistical Computing.

Rader, R. B., N. J. Voelz, and J. V. Ward. 2007. "Post-Flood Recovery of a Macroinvertebrate Community in a Regulated River: Resilience of an Anthropogenically Altered Ecosystem." *Restoration Ecology* 16: 24–33. https://doi.org/10.1111/j.1526-100X.2007.00258.x.

Ringler, N. H., and J. D. Hall. 1975. "Effects of Logging on Water Temperature, and Dissolved Oxygen in Spawning Beds." *Transactions of the American Fisheries Society* 104: 111–121. https://doi.org/10.1577/1548-8659(1975)104<111:EOLOWT>2.0.CO;2.

Sánchez-Bayo, F., and K. A. G. Wyckhuys. 2019. "Worldwide Decline of the Entomofauna: A Review of Its Drivers." *Biological Conservation* 232: 8–27. https://doi.org/10.1016/j.biocon.2019.01.020.

Scott, D. N. 2024. "Widespread Wood Placement and Regrading Drive Lateral Connectivity and Reworking of the Channel and Floodplain in a Valley Bottom Reset to Stage 0." *Geomorphology* 446: 108987.

Smith, R. F., E. C. Neideigh, A. M. Rittle, and J. R. Wallace. 2020. "Assessing Macroinvertebrate Community Response to Restoration of Big Spring Run: Expanded Analysis of Before-After-Control-Impact Sampling Designs." *River Research and Applications* 36: 79–90. https://doi.org/10.1002/rra.3556.

Tonina, D., and J. M. Buffington. 2007. "Hyporheic Exchange in Gravel Bed Rivers With Pool-Riffle Morphology: Laboratory Experiments and Three-Dimensional Modeling." *Water Resources Research* 43: 1–16. https://doi.org/10.1029/2005WR004328.

Uno, H., and J. H. Stillman. 2020. "Lifetime Eurythermy by Seasonally Matched Thermal Performance of Developmental Stages in An Annual Aquatic Insect." *Oecologia* 192: 647–656.

U.S. Forest Service (USFS). 2013. "Whychus Watershed Analysis Update."

Voelz, N. J., and J. V. Ward. 1991. "Biotic Responses Along the Recovery Gradient of a Regulated Stream." *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2477–2490. https://doi.org/10.1139/f91-289.

Wagner, R. J., R. W. B. Jr, C. J. Oblinger, and B. A. Smith. 2006. "Guidelines and Standard Procedures for Continuous Water-Quality Monitors: Station Operation, Record Computation, and Data Reporting." 1-D3.

Waite, I. R., Y. Pan, and P. M. Edwards. 2020. "Assessment of Multi-Stressors on Compositional Turnover of Diatom, Invertebrate and Fish Assemblages Along an Urban Gradient in Pacific Northwest Streams (USA)." *Ecological Indicators* 112: 106047. https://doi.org/10.1016/j.ecolind.2019.106047.

Walters, D. M., M. A. Ford, and R. E. Zuellig. 2017. "A Digital Reference Collection for Aquatic Macroinvertebrates of North America." *Freshwater Science* 36: 693–697. https://doi.org/10.1086/694539.

Warren, D. R., D. A. Roon, A. G. Swartz, and K. D. Bladon. 2022. "Loss of Riparian Forests From Wildfire Led to Increased Stream Temperatures in Summer, Yet Salmonid Fish Persisted." *Ecosphere* 13: e4233. https://doi.org/10.1002/ecs2.4233.

Weber, N., N. Bouwes, M. M. Pollock, et al. 2017. "Alteration of Stream Temperature by Natural and Artificial Beaver Dams." *PLoS One* 12: e0176313. https://doi.org/10.1371/journal.pone.0176313.

Wheaton, J., S. Bennett, N. Bouwes, J. Maestas, and S. Shahverdian. 2019. "Low-Tech Process-Based Restoration of Riverscapes: Design Manual Version 1.0."

Wickham, H., M. Averick, J. Bryan, et al. 2019. "Welcome to the Tidyverse." *Journal of Open Source Software* 4: 1686. https://doi.org/10.21105/joss.01686.

Wohl, E., J. Castro, B. Cluer, et al. 2021. "Rediscovering, Reevaluating, and Restoring Lost River-Wetland Corridors." *Frontiers in Earth Science* 9: 653623. https://doi.org/10.3389/feart.2021.653623.

YSI. 2012. *YSI 600 OMS V2 Optical Monitoring System*. OH: YSI, Yellow Springs. https://www.ysi.com/File%20Library/Documents/Specification%20Sheets/E16-600OMS-V2.pdf.

YSI. 2017. *YSI EC300A EC300M Manual*. OH: YSI, Yellow Springs. https://www.ysi.com/File%20Library/Documents/Manuals/YSI-EC300A-EC300M-Manual-English.pdf.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Appendix A

Sample Protocol and Descriptions of Field Methods

Our sampling methodology for macroinvertebrates that we describe in the text was developed by McCaffrey (2021) and he tested the efficacy of the method in Clear Creek, Oregon. Macroinvertebrates collected in the D-frame net were transferred to a white plastic container to minimize field debris in the sample and then the macroinvertebrates were preserved with 70% ethanol and placed into a plastic container with a lid. Macroinvertebrate samples were sorted and enumerated in the lab using references for identification (Merritt and Cummins 1996; Walters, Ford, and Zuellig 2017). The whole sample was counted and identified with a dissecting microscope (20–40× magnification, model: ST-30C, Motic brand); no sub-sampling procedures were used, and we made estimates for the number of unique species (in R with the specpool function in vegan; Oksanen et al. 2024) with a subset of samples ($n=21$) that supports the adequacy of our sampling (Chao mean 93.5 ± 22.2 SE; Bootstrap 69.5 ± 3.4 SE). Taxonomy was resolved to Northwest Standard Taxonomic Effort Level 1, typically genus or family (for some orders), with the following exceptions. Due to their small size, dipteran taxa were typically identified to the family level for Chironomidae. Diptera pupae were classified by sub-order because of their small size. Odonata taxa were identified to family level except for small specimens for which we used order level classification. Mollusca and Oligochaeta taxa were not resolved to higher taxonomy because they were not the focus of this study and were omitted from the analysis, calculations of relative abundance, and estimates of diversity. Abundance data for terrestrial and semi-aquatic insects, and zooplankton were included as incidental information in the Data S1 but were omitted from analysis, calculations of relative abundance, or estimates of diversity.

To measure water quality and temperature, we used a water quality datasonde (model: 600 OMS V2 and EcoSense EC300A, YSI brand) to collect the water temperature, dissolved oxygen concentration, and specific conductance of the sampling site. A rebar was hammered into the streambed and a temperature logger (model: Pendant, Onset HOBO brand) was deployed to collect water temperature at 30 min intervals. The logger was secured to the rebar near the streambed using a Ziptie. Field audits were done on the loggers (with the datasonde), and the accuracy was within 1.5°C. Calibration of the datasonde was verified with methods described by Wagner et al. (2006). Dissolved oxygen saturation was calculated with an equation developed by Benson and Krause (1984). The temperature loggers were left in situ for a minimum of 48 h to capture diel fluctuations in water temperature.

A densiometer (model: Spherical Crown Densiometer, Convex Model A, Forestry Suppliers brand) was used to estimate canopy cover by counting the number of empty “dots” (those with open sky) within each grid square. The counting procedure was repeated instream, at the location of the temperature logger, in the direction of North, East, South, and West, followed by averaging the four measurements for an estimate of percent canopy cover. To compare hydraulics between habitats, a velocity (model: 2000, Flo-Mate) measurement was taken at the site location using a top setting wading rod facing the direction of the current at a depth of 60% from the water surface while standing downstream of the rod to avoid interfering with the current. Depth measurements were recorded at the time of the velocity measurement. Rock measurements were taken by selecting six rocks and length recorded along their longest axis. For rocks too large to measure, we noted their presence but did not measure them. We averaged the rock measurements into a single variable called mean rock to estimate substrate size of the sample site.

Appendix B

Water Temperature Quality Assurance Procedures

For the control reach, one temperature logger measured unrealistic values in a pool (>100°C), so the data were not used, and one logger was observed to have risen to the water surface; however, the data compared well with other data from the reach and was used. The restored 2016 reach had one temperature logger that collected only several data points prior to the logger's deployment, so the data for that riffle was not used, and two loggers had risen from the stream bottom in pools; however, only one data set of those loggers compared well with other data from the reach (similar maximum temperatures) and was used. Two additional temperature loggers in the restored 2016 reach off-channel habitats failed to collect sufficient data during deployment. In total, five temperature loggers did not collect data, or the data were erroneous, for four transition sites, one pool, one riffle, two off-channel, and one control site that was a pool.

The accuracy of the temperature loggers was verified with the following quality control procedure. A handheld thermometer was used to record the water temperature at the location of each temperature logger at the time the logger was deployed and, at the end of deployment. Water temperature, date, and time of the field check were recorded Data (S1). The measured water temperature (field check) was compared to the corresponding recorded data on the temperature logger. Field checks were within 1.0°C for 30 data loggers and within 1.5°C for five data loggers. The five data loggers that were compared within 1.5°C had poor field check comparisons because the comparison reading was taken 5–22 min after the data logger recorded the measurement.

All the recorded temperature data that was collected at the sampling sites overlapped from a period that began on August 17, 2021, at 2100 h through August 20, 2021, at 900 h in the days immediately following the macroinvertebrate sampling. Water temperature data was summarized from each site for this period into three descriptive metrics for each site: minimum, mean, and maximum water temperature. Furthermore, we took the average of the minimum, mean, and maximum water temperature for each habitat type in the respective reach to deal with data gaps in the five sites with no temperature data. For example, for the two missing water temperature datasets in the transition reach off-channel sites, we used the average minimum of three off-channel sites in the transition reach to calculate their minimum temperatures, and so forth for maximum and mean temperature. This step, to fill the data gaps, was necessary to plot environmental variables in ordination space.

Appendix C

Taxa List

Order	Family	Final ID	Restored 2012	Control reach	Restored 2016
Ephemeroptera	Baetidae	Acentrella	x	x	x
	Ephemerellidae	Attenella	x	x	x
	Baetidae	Baetidae			x
	Baetidae	Baetis	x	x	x
	Caenidae	Caenidae	x		
	Ephemerellidae	Caudatella	x		
	Heptageniidae	Cinygma	x		
	Heptageniidae	Cinygmula	x		x
	Heptageniidae	Epeorus			x
	Ephemerellidae	Ephemerella	x	x	x
	Heptageniidae	Heptageniidae			x
	Leptophlebiidae	Paraleptophlebia	x	x	x
	Heptageniidae	Rhithrogena	x	x	x
	Ephemerellidae	Serratella	x	x	x
	Siphlonuridae	Siphlonurus	x		x
Trichoptera	Glossosomatidae	Agapetus	x	x	x
	Hydroptilidae	Agraylea	x		
	Glossosomatidae	Anagapetus	x		
	Brachycentridae	Brachycentrus	x	x	x
	Limnephilidae	Dicosmoecus	x	x	
	Glossosomatidae	Glossosoma	x	x	x
	Hydropsychidae	Hydropsyche	x	x	x
	Hydroptilidae	Hydroptila	x		
	Brachycentridae	Micrasema	x		x
	Leptoceridae	Mystacides	x		
	Hydroptilidae	Ochrotrichia	x		
	Philopotamidae	Philopotamidae	x		
	Phryganeidae	Yphria californica	x		
	Polycentropodidae	Polycentropodidae	x		
	Limnephilidae	Psychoglypha	x		
	Rhyacophilidae	Rhyacophila	x	x	x
Plecoptera	Perlodidae	Isoperla	x	x	x
	Pteronarcyidae	Pteronarcys		x	x
	Perlodidae	Skwala	x	x	x
	Chloroperlidae	Suwallia	x	x	x
	Chloroperlidae	Sweltsa	x		
	Nemouridae	Zapada	x	x	x

(Continues)

Order	Family	Final ID	Restored 2012	Control reach	Restored 2016
Diptera	Simuliidae	Simuliidae	x	x	x
	Athericidae	Atherix	x	x	x
	Chironomidae	Chironomidae	x	x	x
	Culicidae	Culicidae	x		x
	Empididae	Empididae	x		
	Ephydridae	Ephydridae	x	x	x
	Thamaleidae	Thamaleidae	x		
	Tipulidae	Tipulidae	x	x	x
(s) Brachycera[a]		Brachycera	x	x	x
(s) Nematocera[a]		Nematocera	x	x	x
	Ceratopogonidae	Ceratopogonidae	x	x	x
Coleoptera	Elmidae	Ampumixis	x	x	x
	Amphizoidae	Amphizoidae		x	
	Elmidae	Ancyronyx	x		x
	Elmidae	Cleptelmis	x		x
	Dryopidae	Dryopidae			x
	Haliplidae	Haliplidae	x		
	Haliplidae	Haliplus	x		
	Elmidae	Heterlimnius	x		x
	Dytiscidae	Hydroporinae	x		
	Elmidae	Lara	x	x	x
	Elmidae	Narpus	x	x	x
	Elmidae	Optioservus	x	x	x
	Elmidae	Oreodytes	x		
	Elmidae	Zaitzevia	x	x	x
	Hydrophilidae	Laccophilus			x
	Dytiscidae	Dytiscidae	x		
	Dytiscidae	Neoclypeodytes	x		x
	Hydrophilidae	Tropisternus	x		x
Trombidiformes		Trombidiformes	x	x	x
Odonata	Aeshnidae	Aeshnidae	x		x
	Corduliidae	Corduliidae	x		
		Odonata[a]	x		x
Lepidoptera	Pyralidae	Petrophila	x	x	x
Hemiptera	Corixidae	Sigara	x		x
		Hemiptera	x	x	x
Megaloptera	Sialidae	Sialis	x		x
Decapoda[a]		Decapoda	x		

Note: Taxa not included in the analysis include Hymeneptera Chrysomelidae, Salpingidae, zooplankton, Flatworm, Mollusca, Oligocheata, Collembola, Spider.
(s) = suborder.
[a] Not resolved to NWSTE Level 1.