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RESEARCH ARTICLE

Reconnecting a stream channel to its floodplain: implications for benthic diatoms and macroinvertebrate trophic structure

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Streams systems draining upland landscapes provide valuable ecosystem services, but they are vulnerable to incision and channelization caused by anthropogenic disturbance. Restoring a degraded stream to its pre-disturbance condition by reconnecting the channel to its historical floodplain aims to recover lost hydro-morphological processes and functions. Seeking evidence to indicate whether that aim is met in practice, we examined diatoms and the stream macroinvertebrate trophic structures in three reaches of Whychus Creek, Oregon, United States. Two reaches were reconnected to their pre-disturbance floodplains in 2012 and 2016. The third, control reach, was not restored and was selected to represent the degraded stream condition prior to restoration. Ordinations showed that benthic diatom species composition shifted from the control reach to the restored reaches. Compared to the control reach, reconnection decreased the percentages of diatoms with nitrogen (N)-fixing cyanobacterial endosymbionts in the 2012 restored reach and decreased diatoms tolerant to low N conditions in both the restored reaches. δ^{15}N values in both stream macroinvertebrates and tree leaves in the riparian zone were higher in the restored reaches. These findings suggest that floodplain reconnection may modify hydro-morphological processes and ecosystem functions in ways that enhance organic matter retention and hyporheic exchange, resulting in increased nutrient availability, improved nutrient cycling, and greater primary productivity. More generally, our results suggest that characterizing diatom species composition and trophic interactions using stable isotopes provides the basis for identifying and evaluating the beneficial effects of stream restoration on ecosystem functions and the food-web.

Key words: benthic diatoms, floodplain connectivity, macroinvertebrates, stable isotopes, stage zero, stream restoration

Implications for Practice

- Documenting the recovery of ecological processes provides evidence that reconnecting a stream to its floodplain is an effective restoration practice.
- Reconnecting artificially incised and disconnected stream channels to their historical floodplain can restore important biogeochemical processes.
- Floodplain reconnection may enhance hyporheic exchange.
- Coupling diatom assemblages and stable isotope data may elucidate the recovery of stream ecosystem processes.

Introduction

Streams in upland landscapes support high levels of biodiversity that provide a multitude of ecosystem services. For example, Ferreira et al. (2022) identified 27 supporting, regulating, and provisioning ecosystem services that headwater streams can provide. Consequently, headwater streams, which usually make up most of a tributary network and cumulative stream length in a watershed (Leopold et al. 1964), support habitats critical for freshwater biodiversity (Meyer et al. 2007). Due to their relatively small size and closely coupled interactions with surrounding riparian and upland zones, headwater streams are highly susceptible to human disturbances resulting from hydro-modification, channelization, and watershed

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development. Approximately, 45% of mountain stream length in the western United States is categorized as mostly (20%) or intermediately (25%) disturbed (Stoddard et al. 2005). Anthropogenically disturbed and degraded streams are increasingly the focus for restoring hydro-geomorphic processes and ecosystem functions to recover lost ecosystem services and provide climate change resilience (Wohl et al. 2021; Jennings et al. 2023). This is exemplified in the Pacific Northwest (PNW), which is one of the epicenters of innovative stream restoration in North America (Bernhardt et al. 2005). In the PNW, the initial focus of stream restoration efforts was aimed at recovering diminished fish populations, particularly salmonids, as specified in Section 7 of the Endangered Species Act (USA 1973). However, restoration best practice subsequently evolved and now takes a more process-based approach. The goal of many restoration projects is recovery of the morphological complexity and habitat diversity necessary to support robust aquatic and riparian ecosystems (Beechie et al. 2010; Wohl et al. 2021; Jennings et al. 2023). Although the evidence base demonstrates that the benefits of process-based stream restoration is growing rapidly (Wohl et al. 2021; Flitcroft et al. 2022), quantifying the direct effects of process-based restoration on hydro-geomorphic processes and ecosystem functions remains a challenge (Jähnig et al. 2011).

Within the gamut of process-based restoration, best practice in the PNW and elsewhere recognizes the importance of fully reconnecting stream channels that have been separated from their historical floodplains through anthropogenically triggered channel incision or levee construction (Cluer & Thorne 2014; Roni et al. 2019; Wohl et al. 2021). This involves either (1) returning the degraded and disconnected channel to its pre-disturbance condition (colloquially referred to as “stage 0”), or (2) prompting the incised stream to continue its response to disturbance by creating a new floodplain nested within the terraces formed by the disconnected, historical floodplain (Cluer & Thorne 2014; Schneider et al. 2022). When a stream is fully reconnected to its floodplain, its simplified, incised, single-thread channel is often replaced by a complex, multi-channel system featuring a braided, island-braided, or anastomosed planform that reduces flow velocities, rehydrates the hyporheic aquifer, and increases the retention of fine sediments, organic matter, and nutrients (Mayer et al. 2022).

Given that the recovery of restored streams is characterized by processes that are nonlinear and complex (Rodriguez-Iturbe et al. 2009), both river scientists and water resource managers need to understand how these complex and highly adaptive fluvial systems evolve during the months, years, and decades following restoration. However, most biological monitoring has focused on structural composition or biomass of a selected group of animals, such as fish or macroinvertebrates (Palmer et al. 2010). While it is generally accepted that increasing habitat heterogeneity promotes biodiversity, a meta-analysis of 78 stream restoration projects based on macroinvertebrate data shows mixed results (Roni et al. 2019). For example, in Finland, where mountain channelized streams were restored by increasing habitat heterogeneity and retention of leaf litter, researchers observed only sparse shredder populations 16 years after the restoration (Laasonen et al. 1998).

Previous research shows that confounding factors such as multiple stressors in watersheds, and regional differences in disturbance regimes and species pools complicate assessment of ecological responses to stream restoration (Palmer et al. 2010). This is an important issue because high-quality, comprehensive post-restoration biological data are essential for better understanding how hydro-geomorphic processes and ecosystem functions respond to process-based stream restoration in general, and floodplain reconnection, in particular.

Recognizing this, the purpose of our study is to evaluate the impact on benthic diatom assemblages and macroinvertebrate trophic structure resulting from reconnecting incised stream channels to their floodplains. In this study, we use a “space for time” substitution to compare three reaches within the middle course of Whychus Creek, Oregon. Pre-restoration conditions were studied in an unrestored, degraded control reach, while short-term post-restoration conditions were studied in a reach that was restored in 2016 and longer-term conditions were studied in a reach that was restored in 2012.

Channel filling and floodplain reconnection directly alter hydro-geomorphic attributes and processes by slowing stream velocity, reducing specific stream power, rehydrating the hyporheic aquifer, and sequestering fine sediment on the floodplain (Roni et al. 2019). Consequently, it is reasonable to expect that benthic diatoms, which are primary producers, will respond to these hydro-geomorphic changes due to their short generation time, rapid dispersal rates, and high sensitivity to a range of environmental factors (Stevenson et al. 2010). While diatoms have been used to assess river restoration (Gray & Vis 2013; Żelazna-Wieczorek & Nowicka-Krawczyk 2015; Edwards et al. 2020), macroinvertebrates are more commonly used to assess the ecological impacts of restorative actions in rivers (Roni et al. 2019). We anticipated that restoration efforts focused on floodplain reconnection would alter nutrient cycling in the stream benthos, thus changing the basal structure of the food-web and having a bottom–up effect on the trophic structure of stream macroinvertebrates. For example, in an arctic river, an in situ experimental phosphorus enrichment increased both benthic algal and bacterial production, resulting in an increase in the size of some dominant macroinvertebrates (Peterson et al. 1985). Stable isotope analyses are increasingly used to assess food-web responses to stream restoration (Lepori et al. 2006; Hering et al. 2015; Kupilas et al. 2016). In our study, we used stable isotope compositions (δ^{15}N and δ^{13}C values) to analyze the food sources of macroinvertebrate taxa in different functional feeding groups. By combining detailed diatom community analysis and characterization of the macroinvertebrate trophic structure using isotope analysis, our study provides novel insights into how stream ecosystems may respond to stream restoration actions.

Methods

Study Region

Whychus Creek drains a 656 km^2 watershed within the Eastern Cascades Slopes and Foothills ecoregion of central Oregon

(Fig. 1). The regional setting is high-elevation volcanic plateaus characterized by xeric ponderosa pine forests and shrubland (Clarke et al. 1991). Whychus Creek is approximately 64 km long and descends approximately 660 m between its source on the flanks of the Three Sisters volcanic range and its confluence with the Deschutes River at an elevation of 640 m. In the control and restored reaches, the active primary channel width of Whychus Creek ranges from 4 to 9 m and the stream slope ranges from 1.0 to 1.6%. The hydrograph is dominated by snow and glacial meltwater run-off during spring and early summer. Discharges generally range between a spring-fed, summer low flow of approximately 1 m^3/s with a 2-year return interval peak flow of approximately 14 m^3/s. The catchment is largely undeveloped and is comprised of wilderness areas, National Forests, and natural private lands, almost half of which are protected as nature preserves (USFS 1998). Whychus Creek is typical of streams in this region, with low nutrient conditions and conductivity. In the only previous study of water quality conditions in Whychus Creek, conducted in the summer of 1981, nitrate and orthophosphate concentrations were 0.11 and 0.04 mg/L, respectively and conductivity was 26 μS/cm (USGS 2016).

Stream Restoration

Historically, Whychus Creek featured a single-thread channel in narrow canyon reaches alternating with wider, less-constrained reaches featuring multi-threaded anastomosed channels within expansive meadows rich in vegetation that provided high-quality spawning and rearing habitat for endangered steelhead and salmon (UDWC 2007). Approximately, 50% of the length of the creek was channelized between the 1960s and 1990s to support cattle ranching activities, such as grazing and hay production (USFS 1998). Channel-straightening and berm construction disconnected stream channels from its riparian zones and floodplain meadows (e.g. Fig. 2, panel C). Post-2000, restoration projects on Whychus Creek initially focused on reaches located at Camp Polk Meadow Preserve and Whychus Canyon Preserve (Fig. 1; UDWC 2007).

At Camp Polk Meadow, 1.9 km of channelized stream was restored between 2009 and 2012. Of this, the lower 1.4 km of the project reach was restored to a single-thread, meandering planform based on the Rosgen natural channel design approach (Rosgen 2011). However, the upstream 0.5 km of the incised channel was restored as an alluvial fan, with the intention that a multi-threaded, river-wetland corridor would develop. For this study, the upstream 0.5 km of Camp Polk Meadow is designated as the "restored 2012" reach (Fig. 2, panel A).

In Whychus Canyon, 2.4 km of channelized stream was reconnected to its floodplain in 2016 using the Geomorphic Grade Line and Relative Elevation Model design approach (Powers et al. 2019), which involves fully reconnecting the stream to its floodplain by filling the simplified, single-thread,

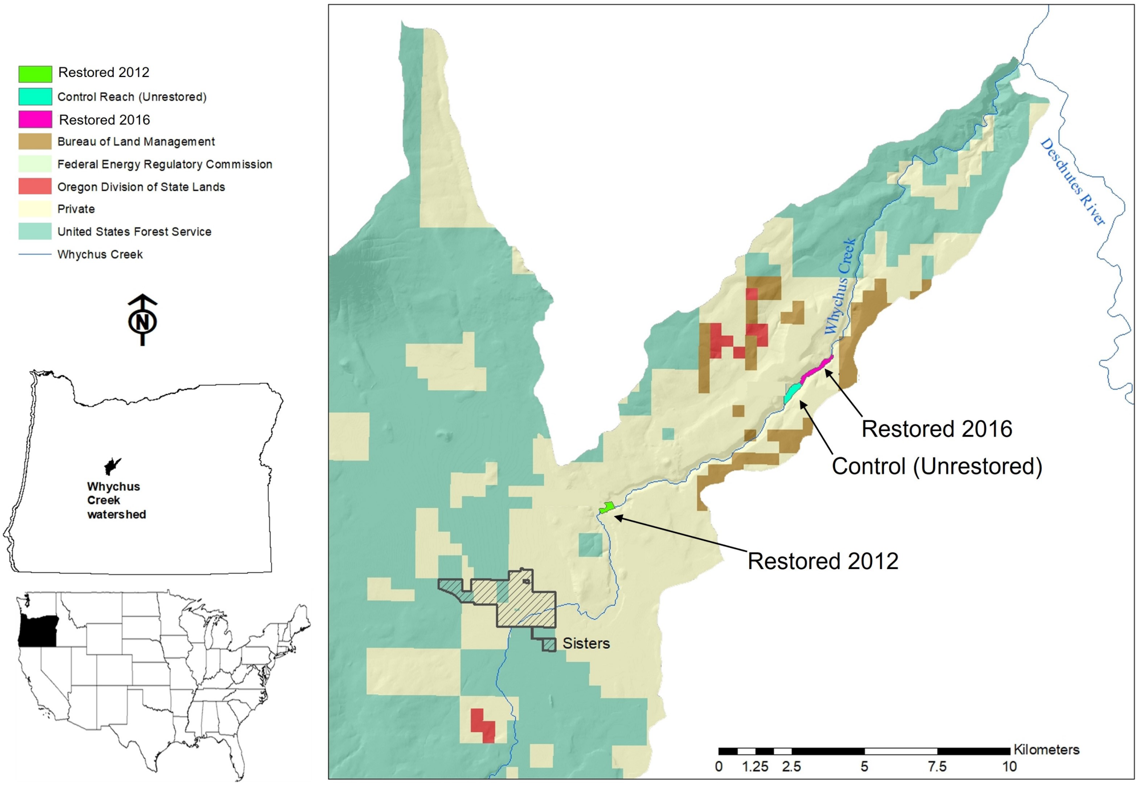

Figure 1. Oregon State, Whychus Creek Watershed and study reach location maps. The control reach is immediately upstream of the restored 2016 reach, with the restored 2012 reach located a further 8 km upstream. Apart from the small urban area of Sisters, the watershed is predominantly rural. Land ownership is mixed. Figure modified from Edwards et al. (2020).

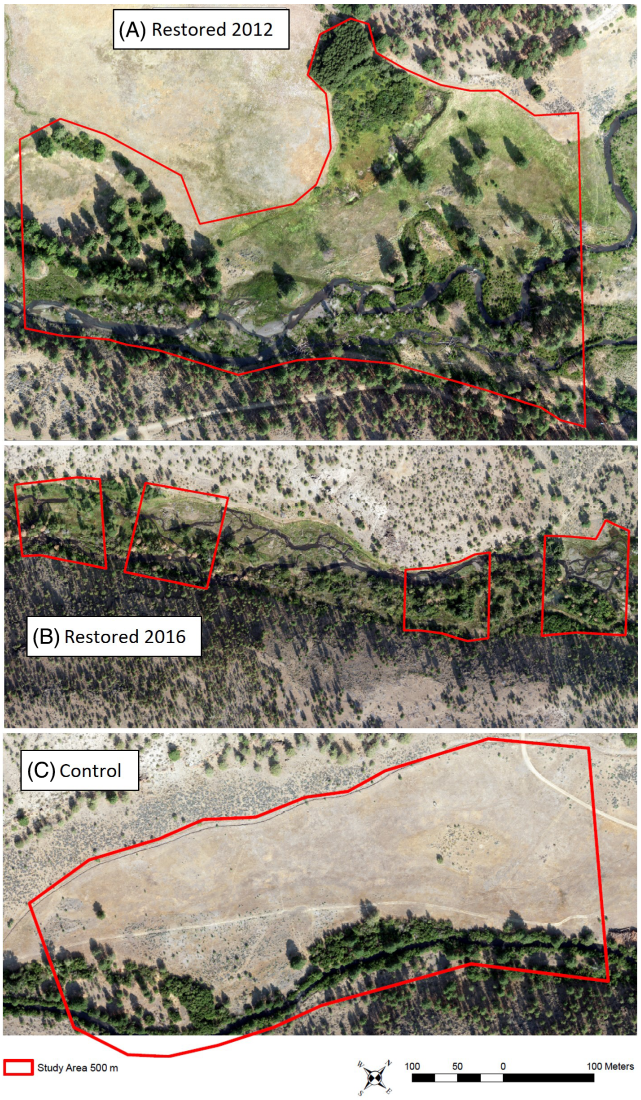

Figure 2. Aerial photos of the Camp Polk Meadow restored 2012 reach (panel A), the Whychus Canyon restored 2016 reach (panel B) and the unrestored control reach (panel C). All three reaches were extensively channelized and straightened during the mid-twentieth Century. Restoration of the restored reaches involved filling in the incised, re-aligned channel, and reconnecting the stream with its pre-disturbance floodplain. Red polygons indicate sampled areas, which extended along 500 m of Whychus Creek in each study reach. The control reach is directly upstream from the restored 2016 reach. The restored 2012 reach is 8 km upstream of the control reach. Figure modified from Edwards et al. (2020). Photo Credit: Upper Deschutes Watershed Council.

incised channel and replacing it with a multi-thread, anastomosed river-wetland corridor. The restoration created 3.76 km^2 of wet meadow with a habitat structure similar to the restored 2012 reach, but 4 years younger. In this study, we designate this section as the "restored 2016" reach (Fig. 2, panel B). The restored 2016 reach is located approximately 8 km downstream of the restored 2012 reach (Fig. 1).

The channelized, unrestored reach within Whychus Canyon is immediately upstream of the restored 2016 reach and retains habitats that are representative of degraded conditions resulting from nearly a century of anthropogenic modification for agriculture and water resource development. The straightened, single-thread channel was shunted to the northern edge of the valley floor and disconnected from the floodplain and is now situated 1–2 m below the narrow remaining riparian corridor. This channelized reach represents the conditions in both the 2012 and 2016 restored reaches prior to their restoration, and hence this section of the stream is designated in this study as the unrestored "control" reach (Fig. 2, panel C).

The riverscape in the restored reaches features a complex network of anastomosed channels, islands, ponds, and floodplains (Fig. 2) with a diversity of aquatic, riparian, wetland, and off-channel habitats (Fig. 3) that are either seasonally or perennially inundated (Mork & UDWC 2013). In-stream habitat in the restored 2012 reach comprises 30% riffles, 53% pools, 2% off-channel habitat, and 15% other habitat (e.g. glides, rapids, and dry units), while the restored 2016 reach features 60% riffles, 31% pools, 3% off-channel habitat, and 6% other habitat (Edwards et al. 2020). In contrast, in-stream habitat in the control reach comprises 92% riffles and 8% pools with no off-channel habitat or other habitat types (Edwards et al. 2020). The canopy in the restored reaches is generally open and stream velocity is highly variable (Noone 2023). The stream canopy in the control reach is relatively closed and there is little variability in stream velocity (Noone 2023). During restoration of both the restored reaches, riparian zones were replanted with native plants, but the plants were not fertilized during or after planting.

Study Design

This study used a Control-Impact design in place of the Before-After-Control-Impact study design, which is often cited as preferable when evaluating the outcomes of ecological restoration (Al-Zankana et al. 2019). We chose Control-Impact because no pre-project data exists for the restored reaches. Data collected in the unrestored control reach immediately adjacent and upstream to the restored 2016 reach in Whychus Creek provided the control data needed to identify restoration impacts in both the restored reaches.

The selection and relative position of the study reaches was prescribed prior to our study by the availability of land for restoration. Due to this logistic constraint, which is common to many stream restoration projects, we decided not to analyze our data statistically because the samples within each reach, as well as between the control and restored 2012 and 2016 reaches, are not spatially independent (Hurlbert 1984). Instead, we used multiple lines of evidence (Mupepele et al. 2016) derived from datasets that included stream habitat, water chemistry, diatom traits, and trophic structure in stream food web.

Samples were collected from a variety of habitats in both the restored reaches and the control reach. Sample locations were selected based on habitat type and accessibility. During the summers of 2019 and 2020, three datasets were collected: water chemistry, benthic diatoms, and stable isotopes. A balanced sampling design was employed except for the off-channel habitat, which did not exist in the control reach ($n = 10$), so only the

Figure 3. Examples of off-channel aquatic and wetland habitats in the restored 2012 reach (panels A and B) and the restored 2016 reach (panels C and D). No similar off-channel habitat was found in the unrestored, control reach. Photo Credit: Portland State University.

restored 2012 ($n = 15$) and restored 2016 reaches ($n = 15$) have off-channel habitat samples.

Diatom Sampling

In 2019, benthic diatom samples were collected from selected riffle, pools, and off-channel habitats along designated 500 m sub-reaches within the three study reaches. Diatoms were collected using standard methods (Kelly et al. 1998; Baird et al. 2017). At five sampling locations for each available habitat, a toothbrush was used to scrape 129 cm^2 of periphyton from each of five cobbles. The cobbles and toothbrush were rinsed with distilled water and composited into a single sample. The sample was split into two 50 mL subsamples, with one preserved with 37% formalin for diatom species identification, while the other was analyzed for chlorophyll *a*.

Stable Isotope Sampling

We used stable isotopes to characterize the base of the food-web and trophic relationships in the restored and control reaches of Whychus Creek. In 2020, three sites in each reach were sampled for stable isotope analysis of macroinvertebrates, fine particulate organic matter (FPOM), periphyton, and macrophytes from three riffle, pool, and off-channel habitats (except in the control reach, which had no off-channel aquatic habitats). Leaves from riparian plants were collected from the stream bank nearest the sampling sites. These variables were chosen to represent the stream food-web, beginning with primary producers and organic matter, and ending with macroinvertebrate predators. Multiple organisms for each macroinvertebrate trophic guild were collected to ensure there was enough material for analysis, but not all taxa were available in all habitats, so some functional groups are represented by different taxa.

FPOM was collected from the stream substrate using a large pipette to suction a sample from the stream bottom. Periphyton was scrubbed from the rocks with a toothbrush. Macroinvertebrates representing the major trophic groups were collected from the substrate using a D-net. Macroinvertebrate grazers (macroinvertebrates that eat algae, Heptageniidae, Glossosomatidae, and Physidae), shredders (macroinvertebrates that eat leaves, Pteronarycidae and Nemouridae), detritivores (Chironomidae and Baetidae) and predators (Perlodidae, Rhyacophilidae, and Gomphidae) were collected from habitats where they were present. Macrophytes (*Elodea*) were collected from the stream substrate. Leaves were collected from alder trees (*Alnus rubra*).

Stream Environmental Data

Water samples (0.5 L) were collected from riffles at the beginning and end of each reach and from five, off-channel habitats in the restored reaches. Stream velocity was measured at the same location and time that diatoms were collected. Stream velocity was collected at 0.6 of the water depth using an electromagnetic velocity meter (Flo Mate, Model 2000). Water samples were frozen and shipped overnight to the Cooperative Chemical Analytical Laboratory at Oregon State University for analysis of soluble reactive phosphorus (SRP, mg/L), total phosphorus (TP, mg/L) and total nitrogen (TN, mg/L). Laboratory analysis of water samples was conducted using persulfate digestion with subsequent analysis by Technicon Auto-Analyzer II Cadmium Reduction Method (APHA 4500-NO_3 F; APHA 4500-P J).

Diatom and Stable Isotope Data

Diatom samples were processed with concentrated HCl using a Microwave Accelerated Reaction System (Model MARS5, CEM Corporation). The digested samples were repeatedly rinsed with distilled water until the pH was neutral and then the cleaned diatom valves were mounted in NAPHRAX mounting medium to make permanent slides for taxa identification and enumeration. Diatom species were counted and identified at 1000× magnification using a Zeiss Axio Scope compound microscope. Diatom taxonomy mainly followed Kramer and Lange-Bertalot (1986, 1988, 1991*a*, 1991*b*, 2000) and Krammer (2003).

Diatom data were analyzed using nonmetric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity to generate two-dimensional ordinations to compare benthic diatom assemblage distribution patterns among the three reaches. NMDS was repeated 20 times each with a random starting configuration and the final solution with the lowest stress value was selected. The lower stress value represents a better NMDS solution to summarize the relationships of diatoms among samples. Diatom taxa were classified in terms of their nitrogen affinity (Tyree et al. 2020). All analyses were performed in R (R, version 4.1.2, Vienna, Austria, R Development Core Team 2021).

Samples for $\delta^{13}C$ and $\delta^{15}N$ values were determined using an elemental analyzer (Costech ECS 4010 Elemental Combustion System using a Zero Blank Autosampler) interfaced to a mass spectrometer (ThermoFinnigan Delta XP). Isotope values are reported as δ-values (‰) relative to Vienna PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen. Ten percent replication of samples and tests using in-house reference materials of known isotopic composition determined that the average accuracies and precisions of all stable isotopic analyses were less than 0.2‰.

Results

Abiotic Factors

The median concentrations of SRP were similar in all three study reaches (Fig. 4, panel A); however, compared to the control reach, the within-reach variability was higher in both restored reaches. Median TN and TP were higher in the both restored reaches compared to the control reach (Fig. 4, panels B & C). The highest median TN and TP concentrations were in the restored 2016 reach, where spatial variation in both nutrients was also comparatively high. Median velocity was highest in the control reach, though within-reach variability was highest in the restored 2016 reach (Fig. 4, panel D).

Diatom Assemblages

The ordination shows that benthic diatom species composition for the control, restored 2016 and restored 2012 reaches shifted sequentially to the left on the NMDS axis I (Fig. 5). Median diatom taxa richness was higher in the restored reaches with the largest increase observed in the restored 2016 reach (Fig. 6, panel A). In contrast, median chlorophyll *a* concentration was slightly higher in the control reach, but more variable in both the restored 2016 and restored 2012 reaches (Fig. 6, panel B).

Median percentages of nitrogen-fixing diatoms were low (<5%) in the control and restored 2016 reaches (Fig. 6, panel C), but even lower (0.4%) in the restored 2012 reach, where diatom taxa with nitrogen-fixing symbionts were entirely absent from eight of the 15 sample sites. Except for one outlier in the control reach, variability was greatest in the restored 2016 reach. The median percentage of diatoms classified as low nitrogen taxa decreased from 63% in the control reach to 38% and 34% in 2016 and 2012 restored reaches, respectively (Fig. 6, panel D).

Diatom assemblages in the control reach were numerically dominated by high flow resistant taxa, characterized by their small size and close attachment to substrates including *Achnanthidium minutissimum*, *Cocconeis placentula*, *Gomphonema rhombicum*, and *G. pumulum*, which together made up 69% of all diatom taxa at the control reach (Fig. 7). These taxa

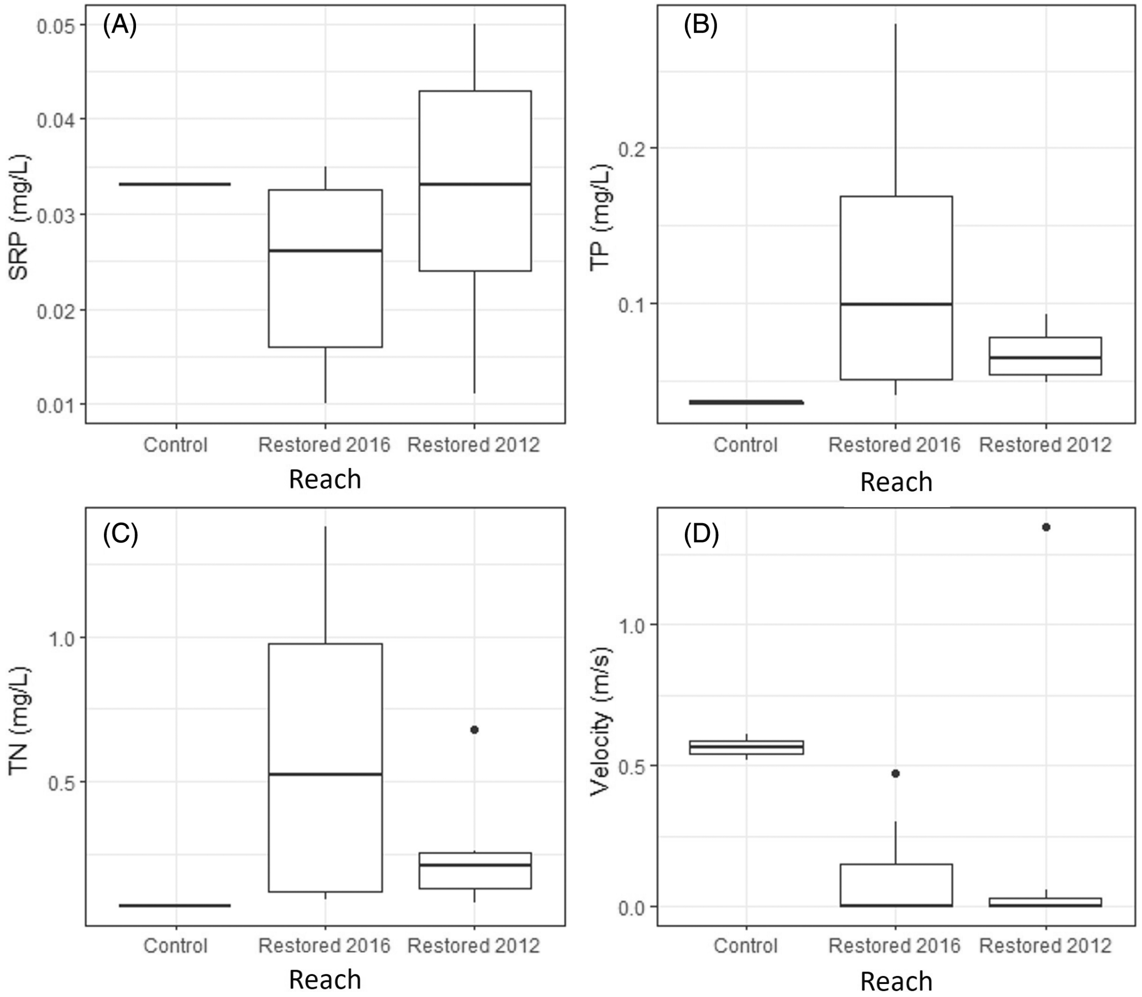

Figure 4. Boxplots of soluble reactive phosphorus (SRP, panel A), total phosphorus (TP, panel B), total nitrogen (TN, panel C) and stream velocity (panel D).

were also found in the restored 2012 reach, but only comprised 6% of the diatom population (Fig. 7), which was dominated by taxa with low resistance to high flow, e.g. *Synedra ulna* (21%), which is a large, colonial taxa forming rosettes or unattached cell aggregates, and taxa tolerant to sediment, e.g. *Nitzschia dissipata* (10%). Other common taxa in the restored 2012 reach included *Rhoicosphenia abbreviata* (8%) and *G. olivaceoides* var. *densestriata* (8%). In the restored 2016 reach, no individual taxa made up more than 10% of the sampled population (Fig. 7).

Stable Isotope Composition

δ^{13}C values of riparian alder leaves (Fig. 8) were generally lower than those of in-stream aquatic carbon (e.g. benthic algae, macrophytes, and FPOM). The difference between these two groups is greatest in the control reach and diminishes in the restored reaches. Overall, δ^{15}N values increased from the control reach to the restored 2012 reach in all biotic groups except FPOM (Fig. 8), which decreased slightly in the restored 2012 reach. It is notable that mean δ^{15}N values in riparian plant leaves in the restored 2012 and restored 2016 reaches (mean = −1.1 and −1.8 ‰, respectively) are considerably higher than those in the control reach (mean = −4.8‰).

Figure 9 shows that median δ^{15}N values in several macroinvertebrate functional feeding groups including predators (panel A), grazers (panel B), and shredders (panel D), were also higher in the restored 2012 reach than in either the control or restored 2016 reaches. For instance, median δ^{15}N values for both the predators Rhyacophilidae and Perlodidae increased by approximately 2‰ from the control reach to the restored 2012 reach, but mean δ^{15}N values for Rhyacophilidae decreased in the restored 2016 reach, while Gomphidae were entirely absent in the control reach.

Discussion

Previous research shows that reconnecting floodplains in the restored reaches of Whychus Creek led to significant changes in hydro-morphological processes (Flitcroft et al. 2022). Our findings suggest that reconnecting these floodplains also altered

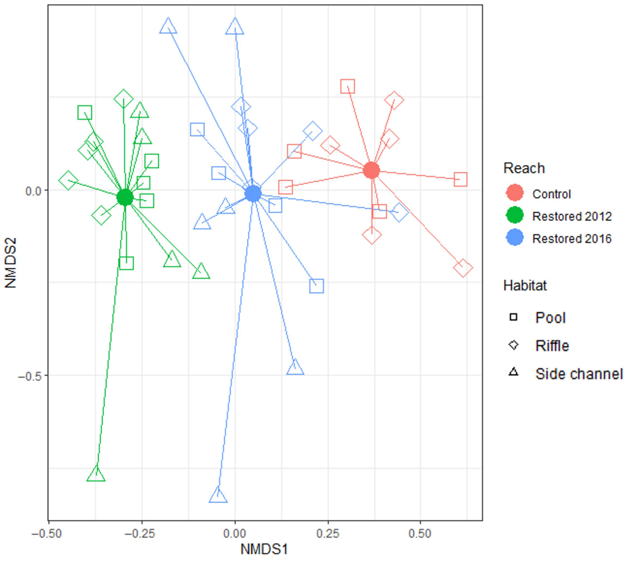

Figure 5. NMDS ordinations based on diatom assemblages for riffle, pool, and side channel habitats in the control, restored 2016, and restored 2012 reaches.

benthic assemblages of diatoms in ways consistent with the hydro-geomorphic changes observed in the earlier studies (Flitcroft et al. 2022). Changes to the benthic diatom community may be indicative of increased nutrient availability and cycling in the restored reaches. Furthermore, carbon and nitrogen isotopic compositions in the biota across trophic levels suggest that increased nutrient availability and primary productivity may be driving bottom–up effects on the higher trophic structure and riparian vegetation in Whychus Creek.

To explain this bottom–up effect, it is necessary to consider that increasing retention of organic matter and dissolved nutrients, as well as hyporheic biogeochemical activities, can enhance dissolved nutrient availability and thereby impact benthic diatom assemblages. Reconnecting stream channels with their floodplains has been found to substantially reduce flow velocities, due to the increased flow resistance, and reduce the hydraulic efficiency of fully connected channel-wetland-floodplain systems, wherein both the relative roughness and wetted perimeter of the stream are high (Flitcroft et al. 2022). These hydrodynamic responses to floodplain reconnection reduce stream power per unit width and thus the stream's capacity and competence to entrain and transport bed material load. The morphodynamic outcome is to promote net sediment deposition and organic matter retention, especially on the floodplain (Lepori et al. 2006). Given these hydro-geomorphic changes, it would be expected that benthic diatom assemblages should reflect the altered lentic and lotic environments within the channel-wetland-riparian-floodplain system.

The four dominant diatom taxa sampled in the control reach are well adapted to fast-moving flow environments found in the anthropogenically straightened, incised, and single-threaded channel. For example, *Cocconeis placentula* can withstand scouring by attaching one valve face to the substrate using mucilage (Peterson 1996), while *Achnanthidium minutissimum* and the two *Gomphonema* taxa adhere to the substrate using a polysaccharide stalk (Hoagland et al. 1993). In contrast, in both the restored reaches, where the median velocity was more than five times lower than in the control reach, the relative abundance of these species decreased substantially.

Stream reaches with low velocity and backwater habitat have long been known to retain more FPOM and nutrients. For example, Lepori et al. (2006) found that addition of boulders and large wood to slow stream velocity doubled detritus retention compared to values observed in channelized reaches. Furthermore, Craig et al. (2008) showed that headwater streams are effective at decreasing nitrogen loads when velocities are reduced during low to moderate flow, while Frainer et al. (2018) found leaf decomposition to be positively related to in-stream habitat heterogeneity in mountain streams.

The restored reaches in Whychus Creek exhibited rapid and sustained rises in water tables beneath the reconnected floodplains (Wu et al. 2021; Flitcroft et al. 2022), indicating full rehydration of the alluvial, hyporheic aquifer. This suggests increases in the lateral extent and connectivity of the hyporheic aquifer increased hyporheic biogeochemical activity within the hyporheic zone and enhanced exchange of water, detritus, and organisms between surface and subsurface water bodies. Such changes would be expected to result in significant changes to the biogeochemistry of the benthos. For example, Henry and Fisher (2003) found that across a sandbar in the bed of a nitrogen-limited stream in the Arizona desert, nitrate concentrations were 3.5 times higher in an area of hyporheic upwelling than in an area of downwelling and that N_2-fixing cyanobacteria were only abundant in the downwelling area.

Watersheds draining the Cascade Range are often naturally high in phosphorus, resulting in nitrogen limitation in streams flowing through unpolluted, wilderness areas (Johnson et al. 2021) and the abundance of N_2-fixing taxa often reflects the overall N environment. For example, Gillett et al. (2016) showed that downstream sites in the Klamath River, with minimal human impacts, featured abundant N_2-fixing diatoms (*Epithemia sorex*, *E. turgida*, and *Rhopalodia gibba*) and N_2-fixing cyanobacteria (*Calothrix* sp). Conversely, Stancheva et al. (2013) found that for N_2-fixing cyanobacteria, relative abundance decreased with an increase in dissolved inorganic nitrogen (NO_3-N > 0.075 mg/L and NH_4-N > 0.04 mg/L).

Our study showed a similar relationship between N_2-fixing diatoms and the availability of dissolved inorganic nitrogen. For example, median percentages of N_2-fixing diatoms in the control and restored 2016 reaches were low (<5%), and these species were almost entirely absent in the restored 2012 reach. The control reach had less than 0.01 mg/L of TN and diatom assemblages were dominated by taxa that prefer low N environments. This contrasts with the results of a pilot study performed in preparation for this investigation Edwards et al. (2020), which found that in the control reach, the median percentage of diatoms with N_2-fixing cyanobacterial endosymbionts was as high as 27%. That earlier finding may have resulted from local variability in the proportion of N_2-fixing cyanobacteria coupled with the limited sampling performed in the pilot study; in the pre more extensive study, we found the relative abundance of N_2-

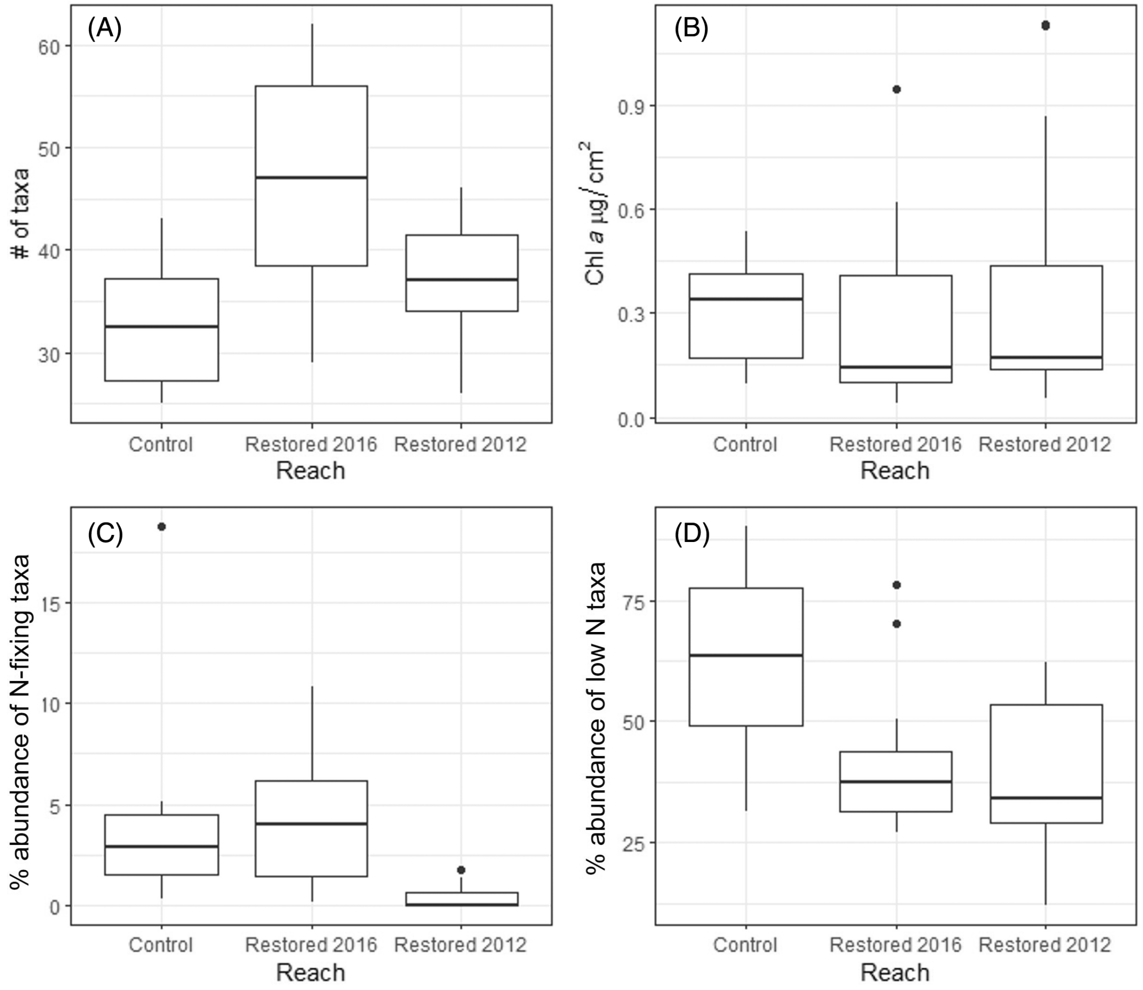

Figure 6. Boxplots of diatom richness (panel A), chlorophyll *a* (Chl *a*, panel B), percentage of diatoms that are nitrogen fixers (panel C) and percentage of diatoms that are tolerant to low nitrogen conditions (panel D).

fixing diatoms at one sample site in the control reach was greater than 20%.

The lower $\delta^{15}N$ values we observed in the leaves of the riparian vegetation in the control reach could indicate disconnection of riparian vegetation roots from the hyporheic aquifer and the biogeochemical processes that transform organic matter into nutrients (Krause et al. 2011). Reconnecting streams with their floodplains and slowing the stream velocity raises the water table and facilitates exchange of surface water with that in the rehydrated hyporheic zone (Brunke & Gonser 1997). This was evident in the restored 2016 reach of Whychus Creek, where depth to the water table decreased by approximately 2 m within 10 days after completion of the restoration project (Flitcroft et al. 2022).

It follows that by raising the water table, restoration enabled the roots of riparian, wetland, and floodplain vegetation to access water and nutrients in the hyporheic aquifer (Boulton et al. 1998; Clarke 2002). Thus, increases in hyporheic extent and activity may explain the differences in $\delta^{15}N$ values for leaves in the control and restored reaches. For example, $\delta^{15}N$ values for leaves increased from about −5‰ in the control reach to values of approximately −0.5 and 1‰ in the restored 2012 and restored 2016 reaches, respectively, which likely reflects several factors related to nutrient availability and uptake. For example, in the deeply incised control reach, alder grow high above the channel bed in the riparian corridor where their roots likely tap into soil moisture that contains little stream water and hence, less nitrogenous nutrients with lower $\delta^{15}N$ values. On the other hand, increased hyporheic exchange and the higher water tables in the restored reaches may affect the nutrient isotopic compositions in the soil moisture available to streamside vegetation. This follows because streams with lower velocities and greater morphological complexity often trap higher levels of organic matter, such as decaying leaves and detritus, which serve as the source of nitrogen for biogeochemical conversion to inorganic forms of nitrogen in the hyporheic zone. Decomposition of organic matter in the stream and its hyporheic zone releases inorganic nitrogen into the stream, making it potentially available for uptake by vegetation in the river-riparian-wetland-floodplain system. In the

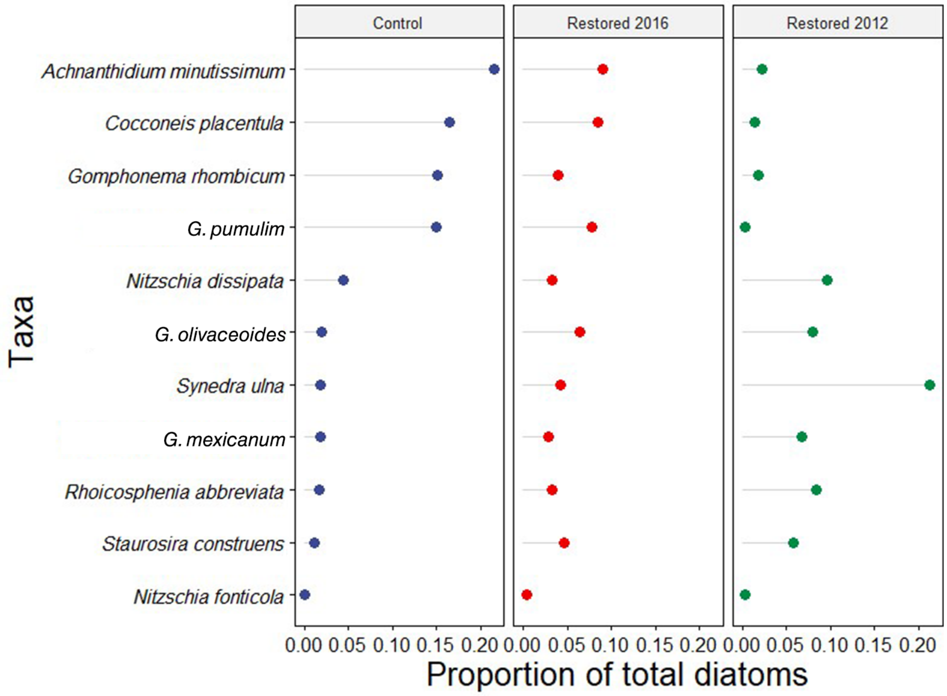

Figure 7. Comparison of the 10 most common diatom taxa among the control, restored 2016, and restored 2012 reaches.

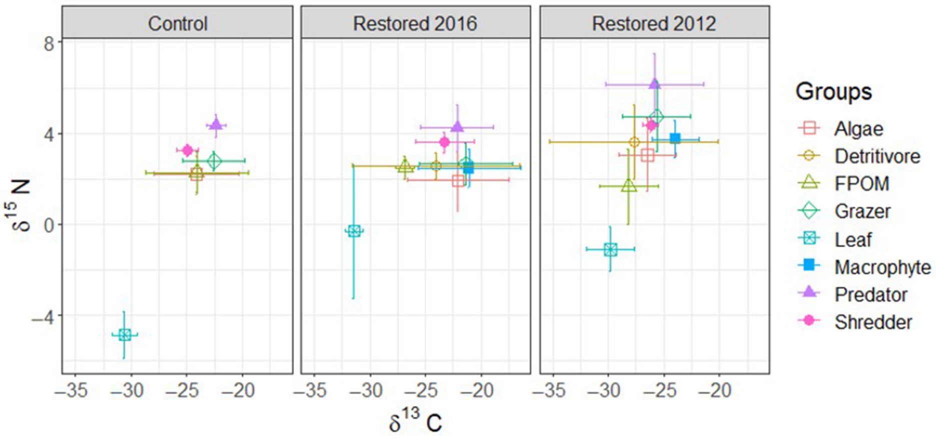

Figure 8. Plots of stable isotope data for the control, restored 2016, and restored 2012 reaches. Groups are periphytic algae (algae), alder leaves (leaf), *Elodea* (macrophytes), and fine particulate organic matter (FPOM). Stream insect groups are detritovores, grazers, predators, and shredders.

restored reaches of Whychus Creek, alders may primarily rely on this nitrogen source, which tends to have higher $\delta^{15}N$ values approaching those of the algae, FPOM and macrophytes whose degradation is the likely source of most of the inorganic nitrogen. Alternatively, the higher nutrient $\delta^{15}N$ values could be affected by partial denitrification in the hyporheic zone because reduction of NO_3 to N_2 results in loss of ^{14}N and thus increases the $\delta^{15}N$ value of the residual NO_3 (Fry 2006).

In the control reach, reduced channel complexity, faster stream velocity, and lack of hyporheic exchange likely resulted in TN concentrations being lower than those in the restored reaches, despite the loss of N due to denitrification expected in the reconnected hyporheic zone. Reduced availability of dissolved nitrogen can limit the nitrogen supply to alder trees. As a result, alder trees growing near channelized streams may adapt by enhancing their nitrogen uptake efficiency. Alders are known for their ability to form symbiotic associations with N_2-fixing bacteria called rhizobia (Bormann et al. 1993). These bacteria convert atmospheric N_2 into biologically available nitrogen (typically ammonium) that can be used by alder. Because the $\delta^{15}N$ value of atmospheric N_2 is lower than that of nitrate or ammonium derived from organic matter

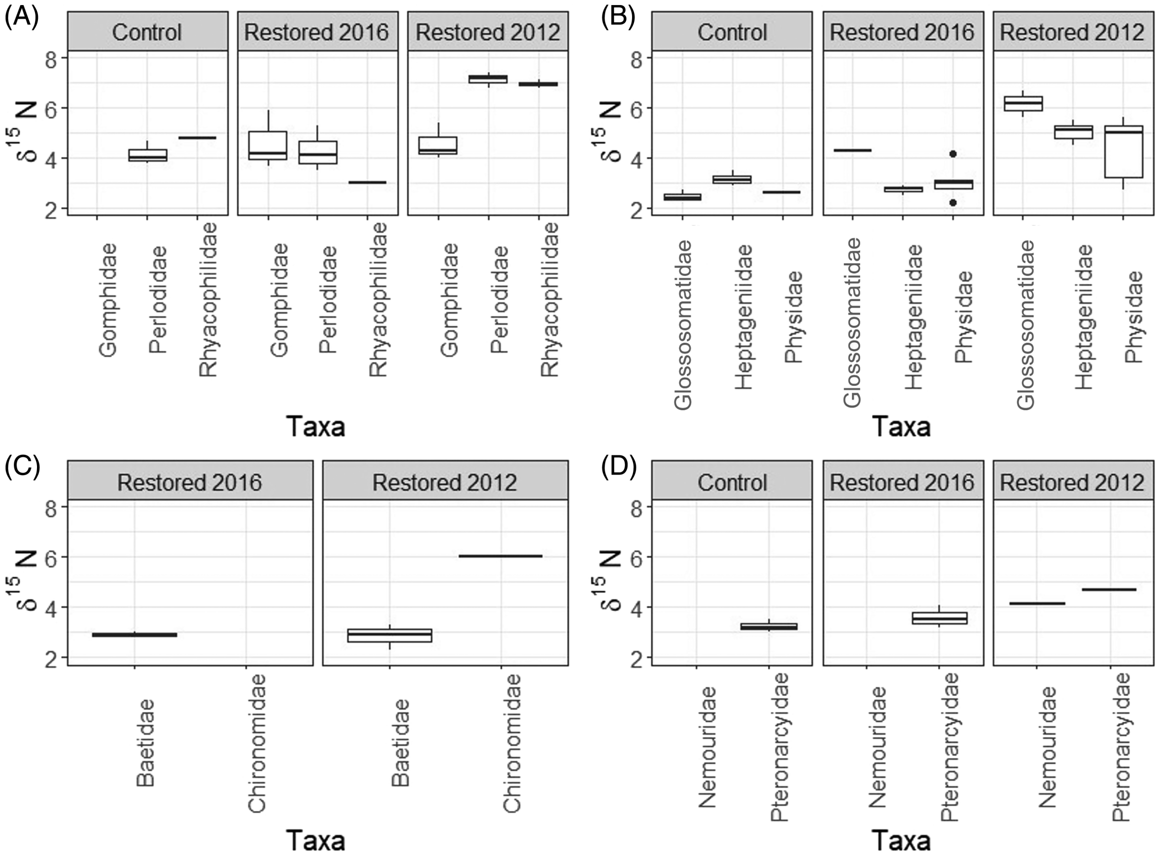

Figure 9. $\delta^{15}N$ values of macroinvertebrate predators (panel A), grazers (panel B), detritivores (panel C), and shredders (panel D) for the control, restored 2016, and restored 2012 reaches. Sample sizes for each organism ranged from one to five organisms. Taxa without boxplots were not observed in that reach.

degradation, rhizobia N_2-fixing activity can lead to lower $\delta^{15}N$ values of foliar nitrogen.

In the slower flowing restored reaches, where organic nitrogen is abundant, alder trees may rely more on the readily available organic nitrogen and allocate fewer resources to N_2 fixation. Alternatively, in fast flowing reaches, lower availability of total dissolved nitrogen makes N_2 fixation more critical for alder trees, thus alder trees growing in the riparian zone of fast flowing reaches may allocate more resources to form symbiotic associations with rhizobia to fix atmospheric N_2. These changes in the $\delta^{15}N$ values of nutrients available to algae, FPOM, and macrophytes are propagated through the stream macroinvertebrate taxa and food-web. These general principles may explain why the highest $\delta^{15}N$ values of grazers, shredders, and predators were found in the restored 2012 reach where a greater proportion of inorganic nitrogen is expected to be sourced from the hyporheic zone.

Restored reaches may have a substantial bottom–up effect on the higher trophic structure through increased nutrient availability and primary productivity. The $\delta^{15}N$ values of a consumer are higher than that of its prey because nitrogen waste has low $\delta^{15}N$ values and thus, the consumer becomes preferentially enriched in ^{15}N relative to the prey that make up its diet (Fry 2006). Northington and Hershey (2006) reported high $\delta^{15}N$ values in primary producers, macroinvertebrates, and fish in forested stream sites impacted by wastewater treatment plant effluent.

However, stable isotope values can also be influenced by other environmental factors, such as substrate composition. For example, when Hering et al. (2015) compared stable isotopes in 10 pairs of nearby restored stream reaches across different European regions, they found that $\delta^{15}N$ values were weakly responsive to restoration but were strongly associated with substrate type. Unlike stream restoration projects in polluted watersheds, Whychus Creek is situated in a predominantly natural, rural basin with minimal anthropogenic impacts on water quality other than temperature, and the three study reaches are within the same stream segment. The $\delta^{15}N$ values of riparian vegetation leaves in the control reach show N-limitation. Similarly, the stable isotopic composition in Lock Creek, a forested stream in the western Cascade Range, shows low $\delta^{15}N$ values in all autotrophs, including riparian vegetation leaves and in-stream algae, reflecting overall nitrogen limitation in volcanic regions (Fry 1991). In Whychus Creek, nearly all sampled biota in both the restored reaches showed an increase in $\delta^{15}N$ values compared to the control reach, with ^{15}N enrichment being particularly pronounced in riparian vegetation leaves and invertebrate predators. ^{15}N enrichment in the restored 2012 reach may also be associated with increased denitrification in the hyporheic zone associated with the rehydrated and more accessible hyporheic aquifer, expanded wetlands, and newly formed, moist, off-channel habitats, as denitrification results in the loss of ^{15}N depleted N_2, leaving residual nitrate with relatively high δ^{15}N values (Kellman & Hillaire-Marcel 1998).

The lack of a corresponding increase in chlorophyll *a* observed in the restored 2012 reach is unexpected. Previous research by Frainer et al. (2018) demonstrated that stream restoration, which enhances habitat heterogeneity, can increase leaf decomposition and FPOM deposition, but does not necessarily increase algal biomass in boreal streams. Valett et al. (1994) found that chlorophyll *a* levels increased in Sycamore Creek, Arizona in response to hyporheic activity and increased dissolved inorganic nitrogen. However, we did not measure hyporheic exchange in our study reaches, and detailed mapping of hyporheic zones in the restored 2012 reach may be required to detect algal biomass changes. Additionally, it is possible that an initial increase in algal biomass following restoration may have subsequently been consumed by grazers, resulting in an increase in secondary production. This supposition is supported by the higher δ^{15}N values in grazers in the restored 2012 reach compared to the control reach.

Evaluating the effects of stream restoration on ecosystem processes can pose a challenge for several reasons, including: the absence of a true reference condition, the dynamic nature of ecosystem processes, changing environmental and climactic conditions, and the lack of adequate independent replication of the treatment effect. The decreased relative abundance of N_2-fixing and low N diatoms, and ^{15}N enrichment in the restored reaches may be partially attributed to leaching of legacy nitrogen in meadow soils and groundwater. The meadows in the restored reaches were used for agriculture and ranching from 1868 until around 1990 and 2000 at the restored 2012 and the restored 2016 reaches, respectively. Basu et al. (2022) reported that legacy nitrogen, particularly soil organic nitrogen in watersheds with highly intensive agricultural activities, can have long-lasting impacts on water quality in streams and rivers. Jones et al. (2015) reported that the nitrogen in a restored stream reach continued to be affected by legacy soil nutrients from past intensive agricultural land use following river–floodplain connection. However, the intensity of agricultural land use in Whychus Creek was substantially lower than that in these case studies.

Alternatively, off-site fertilization of nursery-grown plants used in revegetating the riparian zones of the restored reaches following floodplain reconnection also has the potential to contribute nitrogen to the restored reaches at Whychus Creek. However, planted riparian vegetation may retain most of the fertilizer in their biomass during the growing seasons. For example, in an in situ fertilizing study, Chambers et al. (2004) reported that riparian vegetation in two central Idaho creeks, with similar geology to that of Whychus Creek, retained most of the ^{15}N-labeled fertilizer that had been applied to them.

In conclusion, the benthic diatom species assemblages and nitrogen isotopic composition of diatoms and stream biota were substantially different between the control, restored 2016, and restored 2012 reaches. This result, combined with the other data presented, provides strong evidence (Mupepele et al. 2016) that the restoration of Whychus Creek likely altered stream nutrient cycling. The findings of this study suggest that characterizing the basal structure of the stream food web and using δ^{15}N values to monitor trophic interactions could be used to assess the impact of stream restoration on ecosystem processes.

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