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Variation in riparian and stream assemblages across the primary succession landscape of Mount St. Helens, U.S.A.

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Abstract

1. Although most lotic ecosystems experience frequent and sometimes large disturbances, opportunities are uncommon to study primary succession in streams. Exceptions include new stream channels arising from events such as glacial retreat, volcanism, and catastrophic landslides. In 1980, the eruption and massive landslide at Mount St. Helens (WA, U.S.A.) created an entire landscape with five new catchments undergoing primary succession. We asked if riparian and lotic assemblages at early successional stages (36 years after the eruption) showed predictable change along longitudinal gradients within catchments, and whether assemblages were similar among five replicate catchments.
2. In July 2016, we collected environmental data and characterised riparian, algal, and benthic macroinvertebrate assemblages at 21 stream reaches distributed within and among five neighbouring catchments. We evaluated patterns of richness, abundance, biomass, multivariate taxonomic community structure, and functional traits both longitudinally and among catchments.
3. We found minimal evidence that longitudinal gradients had developed within catchments at 36 years post-eruption. Increases in diatom and macroinvertebrate richness with downstream distance were the only biological responses with longitudinal trends. Conversely, we documented substantial variation in community structure of riparian plants, soft-bodied algae, diatoms, and macroinvertebrates at the among-catchment scale. Among-catchment differences consistently separated two eastern catchments from three western catchments, and these two groups also differed in stream water chemistry, water temperature, and geomorphology.
4. Overall, we documented greater diversity in the young catchments than predicted by ecologists in the years immediately following the eruption, yet functional traits indicate that these catchments are still in relatively early stages of succession. Variation at the among-catchment scale is likely to be driven in part by hydrological source variation, with the two eastern catchments showing environmental signatures associated with glacial ice-melt and the three western catchments probably fed primarily by springs from groundwater aquifers. Contemporary

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flow disturbance regimes also varied among catchments and successional trajectories were probably reset repeatedly in streams experiencing more frequent disturbance.
5. Similar to new stream channels formed following glacial retreat, our results support a tolerance model of succession in streams. However, contrasting abiotic templates among Mount St. Helens catchments appear to be driving different successional trajectories of riparian plant, algal, and macroinvertebrate assemblages among neighbouring small catchments sharing the same catastrophic disturbance history.

KEYWORDS
catchment evolution, community assembly, disturbance, stream succession, volcanic eruption, watershed

1 | INTRODUCTION

Streams are notable for frequent disturbance (Resh et al., 1988; Stanley et al., 2010), and a large body of research has been dedicated to understanding how stream ecosystems and organisms respond and adapt to natural disturbance (e.g. Benda et al., 2005; Fisher, 1983; Lytle & Poff, 2004; Poff et al., 1997). However, even major disturbances in streams in most cases do not devastate entire ecosystems; the physical channel usually remains and recolonisation is often rapid (Bellmore et al., 2019; Foster et al., 2020; Grimm & Fisher, 1989). Most natural disturbances in streams occur within established channels (Resh et al., 1988) and often have short-lived effects, with biotic recovery driven by recolonisation from undisturbed tributaries, upstream reaches, or hyporheic refuges (Blum, 1956; Parkyn & Smith, 2011; Vander Vorste et al., 2015). As such, most recovery trajectories in lotic ecosystems can be classified as secondary succession. Opportunities are relatively rare to study primary succession in streams (Brown & Milner, 2012; Milner et al., 2008), especially following catastrophic disturbance at a scale that creates entire new catchments.

Our most robust understanding of primary succession in streams is associated with channels gradually emerging from beneath receding glaciers (Milner & Robertson, 2010; Milner et al., 2013). Milner and colleagues have demonstrated rapid colonisation of instream and riparian organisms and the development of complex assemblages and food webs within 30 years of natural *daylighting* of new channels from beneath thick ice (Milner et al., 2008, 2011). Based on the well-studied macroinvertebrate assemblages of these streams, Milner and Robertson (2010) proposed a tolerance model of primary succession (Connell & Slatyer, 1977) in which most colonist taxa continue to persist following initial establishment. However, they also noted that successional trajectories can be interrupted frequently by the flow-related disturbances that characterise most stream ecosystems (Milner & Robertson, 2010).

Volcanic eruptions are another not uncommon cause of catastrophic disturbance in which the deposition patterns and amount of violently released ash and larger pyroclastic materials determine the degree of disturbance and whether ecological succession following the impact is classified as primary or secondary. Current understanding of volcanic disturbance effects in streams is mostly associated with ash deposition in pre-existing channels (e.g. Ayris & Delmelle, 2012; Carrillo et al., 2018). Overall effects range from partial loss of taxonomic and functional diversity (e.g. Cushing & Smith, 1982; Mauad et al., 2017) or large-scale disturbance followed by secondary succession (e.g. Fuentes et al., 2020). However, explosive eruptions also have the potential to reset entire landscapes (Meyer & Martinson, 1989), initialising primary succession not only in new stream channels but also at the catchment scale. In such cases, entire catchments can form on new landscapes. Patterns of primary succession at the scale of newly formed catchments have never been documented.

We studied riparian, algal, and macroinvertebrate assemblages in five replicate catchments on the Pumice Plain of Mount St. Helens (MSH; Washington, U.S.A.). This landscape was created by a massive debris avalanche and extensive deposition of pyroclastic material and ash during a series of eruptions starting in 1980. Using a point-in-time study 36 years post-eruption, we addressed two assemblage-level questions in the five young catchments: (1) Had longitudinal patterns developed in the stream channels as expected under the River Continuum Concept (RCC; Vannote et al., 1980) and longitudinal succession models (Fisher, 1983)? For example, local diversity of both taxa and functional traits is expected to increase with distance downstream as headwater streams expand in size (Finn et al., 2011; Finn & Poff, 2005). Mountain streams are also expected to show upstream–downstream gradients in channel slope and substrate stability (Benda et al., 2005), which should influence longitudinal patterns of riparian and instream assemblages. (2) Were spatial patterns of assemblage structure similar among the five replicate catchments? If primary succession is predominantly deterministic, then general patterns of community structure along one stream should be predictive of patterns along neighboring streams that share the same successional age, disturbance history, hydrological sources, and regional colonisation pools. Volcanic eruptions

are common drivers of primary succession globally and our research provides novel ecological insight into the development of stream and riparian assemblages in newly formed catchments.

2 | METHODS

2.1 | Site description

Mount St. Helens (Lawetlat'la in the Cowlitz language) is in the Cascade Range of Washington (U.S.A.) and one of 452 of volcanos in the Pacific Ring of Fire. Its eruption on 18 May 1980 caused an enormous debris avalanche and pyroclastic flows, producing one of the largest landslides in recorded history: 2.8 km^3 of material transformed >600 km^2 of the landscape and decreased the summit elevation of MSH by nearly 400 m. On the north side of the mountain, a thick layer (>100 m in depth) of sterile pumice, ash, and rock incinerated and buried pre-existing forests and streams (Meyer & Martinson, 1989), instantaneously creating an ecological blank slate for primary succession across a 15-km^2 area now known as the Pumice Plain (Crisafulli & Dale, 2018; Dale et al., 2005; Lipman & Mullineaux, 1981). The Pumice Plain landscape was gradually colonised by early successional plants and, by 2005, a few locations had developed riparian cover of Sitka alder (*Alnus viridis* (Chaix) DC. ssp. *sinuata* (Regel) A. Löve & D. Löve) and Sitka willow (*Salix sitchensis*) (Titus & Bishop, 2014). Overall, however, upslope woody vegetation was still sparse and patchy 36 years post-eruption (Chang et al., 2019).

New stream networks began developing on the Pumice Plain following the eruption as rills and gullies formed and were supplied with surface water from precipitation and re-established spring sources, later supplemented by runoff from snowmelt and glaciers. Small headwater streams coalesced, forming larger drainage networks that flow north into Spirit Lake (Swanson & Major, 2005; Figure 1). Following the eruption, Spirit Lake was toxic, anoxic, and water temperature reached 35°C (Larson, 1993). Given the inhospitable state of the lake, the spatial extent of the disturbance, and the lack of local refuge habitat for stream-associated organisms, potential colonists were limited to wind or animal dispersal (attached to mobile animals such as elk and birds). The nearest streams with potential colonists to the new catchments were >5 km distant.

2.2 | Sampling design

From 18 to 27 July 2016, we collected environmental data and characterised riparian, algal, and benthic macroinvertebrate assemblages at 21 reaches. The reaches were distributed along longitudinal gradients within each stream across the five catchments: Camp Creek, Geothermal (Geo) Creek, Clear Creek, Willow Creek, and the combined Forsyth/Redrock Creeks (Figure 1). Stream length between headwaters and outlets into Spirit Lake ranged 1.5–3.5 km. During data collection, all streams were at summer baseflow. Springs feeding Forsyth, Redrock, and Willow had relatively stable flows and emerged from the same location over time. Springs feeding Clear, Geo, and Camp had seasonally variable flow and emerged from a variety of locations along each stream network.

2.3 | Environmental variables

At each of the 21 sites, over a 10-day period, we established reach length as 20 times the average wetted width and measured bankfull width, wetted width, and depth profiles across each stream at five equally spaced transects. Discharge (L/s) was measured once, at the time of biota sampling, with a Flo-Mate Model 2000 Portable Flowmeter (Marsh-McBirney, Inc.) from a single cross-section in each reach. Substrate composition was assessed using

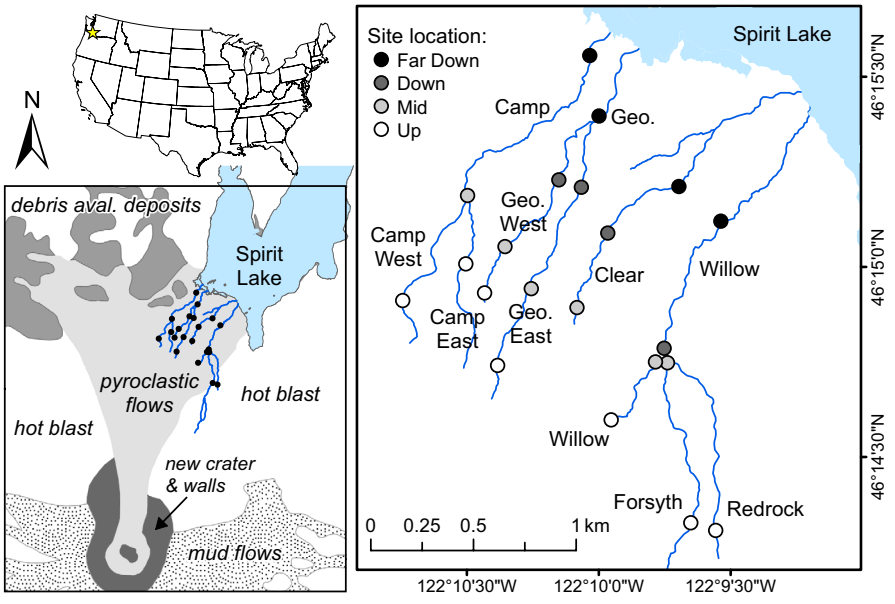

FIGURE 1 Map of 21 study sites on the Pumice Plain of Mount St. Helens, Washington State, U.S.A. Sites were distributed to represent headwaters, midstream reaches, and downstream reaches on each of five catchments (Forsyth/Redrock, Willow, Clear, Geo, Camp). For analyses, Forsyth/Redrock Creeks were treated as a separate catchment from Willow Creek [Colour figure can be viewed at wileyonlinelibrary.com]

a modified pebble-count of 100 particles per reach (Kaufmann et al., 1999). The D_{50} sediment size (median diameter) was calculated for each reach. Slope (%) was measured with a clinometer between each end of the reach at 1-m height. Water temperature (°C) was recorded hourly during the 10-day study period, 18–27 July 2016, with Hobo Pro v2 or Tidbit v2 loggers (±0.2°C accuracy; Onset, Bourne, MA, U.S.A.).

Instantaneous daytime measurements of temperature-compensated pH (Oakton Ion 6+), specific conductance (CON, µS/cm), and dissolved oxygen (DO, mg/L, YSI Professional Plus) were averaged from five locations across each reach. At the same time, water samples were collected for alkalinity (mg $CaCO_3$/L), dissolved organic carbon (DOC, mg/L), ammonia + ammonium (NH_3–N + NH_4–N, µg/L, hereafter referred to as ammonium), nitrite + nitrate (NO_2–N + NO_3–N, µg/L, hereafter referred to as nitrate), and soluble reactive phosphorus (SRP, µg/L). Water samples were filtered in situ (Whatman GF/F, 0.7 µm pore size) and stored in the dark and frozen until laboratory analysis. Within several days after collection, alkalinity titrations were carried out under the USGS alkalinity and acid-neutralising capacity protocol (Section 6.6., Ch. A6, National Field Manual) and quantified following EPA 310.2 (1974; EPA-100-B Rev 0; AQ1 Discrete Analyzer, SEAL). Oregon State University Cooperative Chemical Analytical Laboratory conducted the following analyses: DOC using a combustion-infrared method APHA 5310 B; ammonium using both methods APHA 4500-NH3 G and EPA 350.1; nitrate using cadmium reduction methods APHA 4500-NO3 F and EPA 353.2; and SRP using ascorbic acid methods APHA 4500-P F and EPA 365.1.

2.4 | Riparian plants

Riparian vegetation cover proportions were measured using 1-m^2 plots located immediately adjacent to the channel edge, alternating river-right and river-left at 8 equidistant locations along each sample reach. All plants were identified to the lowest practical taxonomic level given growth and flowering stage at the time of the survey. The total percent cover within a plot could exceed 100% due to overlapping vegetation at different heights. Percent cover of total vegetation and each plant taxon were averaged across the 8 plots.

2.5 | Periphytic diatoms and soft-bodied algae

From each site, a composite periphytic algae sample was collected from 5 random substrates representing the dominant types present (cobbles or sand). The area sampled on cobble was determined by measuring each rock along three axes and calculating the half surface area as described by Dall (1979). Sand was collected from the top layer (1.5 cm depth) using a 6-cm diameter petri dish with a surface area of 28.27 cm^2 and a large spatula. Algae were scrubbed from rocks and sand to create a composite slurry. We measured the total volume of the slurry, then removed the following well-mixed aliquots for analysis: 50 ml each for quantitative analysis of diatoms and soft-bodied algae (both preserved in 2.5% glutaraldehyde), and 10–25 ml filtered for algal biomass as measured using chlorophyll-*a* (Chl-*a*, mg/cm^2). The Chl-*a* aliquots were filtered onto pre-combusted (500°C) and pre-weighed GF/C filters, then stored in the dark and frozen (−80°C) until laboratory analysis. Chl-*a* was determined spectrophotometrically following Steinman et al. (2006).

For *quantitative* analysis of the full algal assemblage at a coarse taxonomic level, each soft-bodied algae sample (described above) was homogenised, and a subsample was pipetted into a Palmer–Maloney counting chamber following Acker (2002). Counts and identifications were done by Rhithron Associates, Inc. and allowed us to compare relative abundances of soft-bodied algae versus live diatoms (with intact organelles) among sites. Soft algae were identified using this method to genus-level or coarser, and diatoms were identified using other methods described below. Three hundred cells (or natural counting units) were identified from each sample. Absolute cell density of each soft-bodied alga and total diatom cells was converted to a relative cell density by dividing the taxon cell density by the total algal cell density recorded for the sample.

We also *qualitatively* characterised all soft-bodied algae at the genus- or species-level for presence/absence. The macro- and microalgae were identified separately following Stancheva et al. (2012). The purpose of the additional qualitative taxonomic analysis of soft-bodied algae was to produce a comprehensive taxonomic list at the species-level without the limitation of the subsamples used for the quantitative analysis. These results were used for comparisons of soft-bodied algae taxa richness and community composition among sites.

For *quantitative* analysis of all diatoms identified at the species-level, an aliquot of the well-mixed diatom sample was treated with 70% nitric acid and rinsed with deionised water following Acker (2002). Subsample volumes were adjusted to obtain adequate densities for slide mounts and a minimum of 600 diatom valves were counted and identified to species. Relative abundances of diatoms were corrected for the number of live diatoms observed in the Palmer–Maloney counting chamber by multiplying the relative abundance of each taxon by the relative abundance of live diatoms (Acker, 2002). Diatom identifications followed standard taxonomic references (Spaulding et al., 2020; Stancheva et al., 2015). These densities were used for comparisons of all diatoms and to evaluate species richness and community composition among sites.

We classified algal taxa into ecological guilds modified from Passy (2007) and described by Rimet and Bouchez (2012): (1) low profile versus high profile; (2) motile versus planktonic; and (3) nitrogen fixers (N_2-fixers). We also classified algal taxa by morphological traits: (1) substratum attachment morphology (not attached, loosely, or firmly attached); (2) lifeform (unicellular, colonial, filamentous; and (3) diatom cell size (micro <300 μm^3, meso 300–600 μm^3, macro >600 μm^3) (Lange et al., 2016; Stancheva et al., 2013).

TABLE 1 Environmental and biotic community metrics per site, mean (range), from five catchments on the Pumice Plain of Mount St. Helens. The catchment For/Red includes Forsyth and Redrock Creeks

	Willow	For/Red	Clear	Geothermal	Camp
Environmental					
Number of sites	4	3	3	7	4
Discharge (L/s)[a]	125 (81–180)	29 (15–42)	63 (9–95)	23 (6–66)	43 (30–67)
Bankfull width (m)	33.9 (6.9–89.5)	16.0 (2.8–42.3)	7.8 (2.1–15.8)	6.2 (1.9–15.7)	7.3 (2.8–9.9)
Wetted width (m)[a]	2.0 (1.9–2.1)	1.1 (0.7–1.4)	1.5 (1.1–2.0)	1.0 (0.6–1.6)	1.1 (0.5–1.7)
D50 (mm)[a]	36 (32–47)	28 (25–32)	29 (18–35)	15 (1.0–24)	17 (4.7–27)
DO (mg/L)[a]	11.4 (10.8–12.7)	11.9 (11.6–12.2)	9.4 (7.5–10.6)	8.5 (4.2–10.2)	9.4 (8.7–9.9)
Temperature (°C)[b,c]	5.7 (4.0–11.0)	5.0 (3.9–7.0)	8.9 (5.6–14.0)	10.6 (6.3–21.6)	13.2 (7.2–24.7)
Slope (%)[b]	4.5 (3.0–6.0)	5.5 (4.5–6.0)	2.5 (1.5–3.0)	2.6 (1.0–4.0)	2.9 (1.0–4.0)
Conductivity (µS/cm)[b]	86 (79–89)	60 (50–68)	296 (256–362)	261 (164–414)	269 (139–531)
Alkalinity (mg $CaCO_3$/L)[b]	50 (47–55)	49 (46–53)	58 (55–60)	60 (54–66)	72 (58–80)
pH[b]	6.4 (6.1–6.7)	6.4 (6.0–6.8)	7.4 (7.2–7.7)	7.2 (6.8–7.7)	7.6 (7.0–7.9)
DOC (mg/L)[b]	0.3 (0.2–0.4)	0.4 (0.4–0.4)	0.5 (0.5–0.5)	0.6 (0.4–0.8)	0.7 (0.3–1.5)
NH_3–N + NH_4–N (µg/L)	5.3 (4–6)	5.3 (4–7)	3.3 (3–4)	5.6 (3–10)	5.0 (4–7)
NO_2–N + NO_3–N(µg/L)	21.5 (1–69)	14.0 (1–31)	1.7 (1–3)	1.3 (0–3)	1.3 (0–2)
PO_4-P (µg/L)	65.3 (59.0–72.8)	62.8 (47.6–79.0)	48.0 (40.0–55.7)	58.5 (45.7–75.5)	60.8 (47.2–75.7)
Biota					
Riparian richness	6 (0–9)	14 (13–16)	14 (12–16)	15 (10–18)	12 (11–14)
Soft-algae richness	3 (2–4)	5 (3–8)	11 (6–17)	8 (1–14)	9 (6–11)
Diatom richness	10 (5–16)	15 (3–23)	26 (25–27)	30 (16–41)	26 (13–36)
Invertebrate richness	13 (8–20)	19 (11–24)	28 (25–32)	25 (16–32)	23 (15–27)
Riparian cover (%)	12 (0–48)	75 (20–160)	125 (75–161)	102 (1–188)	92 (3–273)
Chl-a (mg/m^2)	0.66 (0.35–1.30)	9.08 (2.77–16.19)	0.94 (0.43–1.81)	2.16 (0.03–11.15)	0.52 (0.12–0.79)
Insect density (#/m^2)	405 (133–659)	3,704 (1,589–6,628)	838 (478–1,217)	1,640 (741–2,871)	1,829 (1,196–2,606)
Insect biomass (mg/m^2)	50 (9–110)	314 (235–437)	347 (239–490)	308 (188–457)	361 (306–461)

[a]Discharge was positively correlated with wetted width, substrate D50, and dissolved oxygen (DO).

[b]Water temperature was positively correlated with conductivity, alkalinity, pH, dissolved organic carbon (DOC), and negatively correlated with slope.

[c]Water temperatures recorded hourly during the 10-day study period of 18–27 July 2016.

2.6 | Aquatic macroinvertebrates

We collected benthic macroinvertebrates at each site from 8 randomly distributed, 0.09-m^2 Surber samples (500-µm mesh, 0.72-m^2 total per site), composited in situ, and preserved in 80% ethanol. In the lab, each composited sample was subsampled for a minimum of 600 individuals. Insects and snails were identified to genus or species, except Chironomidae, which were identified to subfamily or tribe (Merritt et al., 2019). Other invertebrates were identified to class. To estimate insect biomass (mg/m^2), the body length of each insect was measured with a micrometer and converted using taxon-specific length-to-dry-mass regressions (Benke et al., 1999). Subsample results were divided by the fraction subsampled to obtain full-sample estimates standardised to 1 m^2. Taxa in the orders Ephemeroptera, Plecoptera, and Trichoptera were used to calculate EPT taxa richness and density per site.

We classified the insect portion of the macroinvertebrate samples into 13 trait categories (Poff et al., 2006) chosen a priori to be related to dispersal, habitat stability, thermal or flow regime, or food resources: (1) voltinism (multi-, uni-, or semi-voltine); (2) seasonal development rate (fast, slow, non-seasonal); (3) adult life span (long >1 month, short <1 month, very short <1 week); (4) desiccation survival (yes, no); (5) adult female dispersal (low <1 km, high >1 km); (6) adult flying strength (weak, strong); (7) drift occurrence (rare, common, abundant); (8) armouring (none, poor, good); (9) body shape (streamlined, not streamlined); (10) mature size (small <9 mm, medium >9 mm);(11) thermal preference (cold stenothermal, cool eurythermal); (12) habit (burrow, climb, sprawl, cling, swim); and (13) functional feeding groups of collector–gatherer (CG), collector–filterer (CF), scraper (SC), shredder (SH), and predator (PR).

2.7 | Statistical analyses

Many of the environmental variables expressed high collinearity; (1) daily mean water temperature was positively correlated with conductivity, alkalinity, pH, DOC, and negatively correlated with slope; and (2) discharge was positively correlated with wetted width, substrate D50, and DO (Table 1, $r > |0.7|$). Therefore, in subsequent analyses, temperature was used as a representative for correlated water quality measures and reach slope, and discharge was representative of stream width, substrate size, and DO. The N and P nutrient measures were not correlated with other variables nor each other and were included independently in subsequent analyses.

To assess among-catchment patterns in the environmental variables and taxa richness, abundance, and/or biomass of each assemblage, we used analysis of variance (ANOVA) and Tukey's post hoc comparisons. To assess longitudinal gradients in environmental variables and community metrics along the stream continuum, we used linear regression models with mixed effects to test for non-zero slopes with stream distance (fixed effect, continuous), grouped by catchment (random effect, categorical). Response variables were tested for normality (Shapiro–Wilk) and ln-transformed if necessary. Analyses were performed in R 4.0.0 with the functions aov and TukeyHSD from the stats package, and the function lmer from the lmerTest package (Kuznetsova et al., 2017; R Core Team, 2020).

Differences in riparian plant, algal, and macroinvertebrate assemblages among sample reaches were examined with non-metric multidimensional scaling (NMDS) ordination and Bray–Curtis distance measures performed in PC-ORD v.7 (McCune et al., 2002). Non-metric multidimensional scaling ordinations were conducted on plant taxa % cover, diatom species cell density (log(n+1)) from quantitative analysis, soft-bodied algae taxa presence/absence from qualitative analysis, and benthic invertebrate taxa density (log(n+1)). Final NMDS ordination stress values are reported on a scale of 0–100 (McCune et al., 2002). Pearson correlations ($r \geq |0.45|$) in ordination space were used to determine which environmental factors, community metrics (e.g. taxa richness, total cover, density, or biomass), or functional traits influenced each assemblage ordination. Differences in community structure among sites grouped by catchment (5 groups) or by downstream distance category (4 groups, Figure 1) were tested with multi-response permutation procedures (MRPP).

3 | RESULTS

3.1 | Environmental variables

Our surveys revealed substantial differences in environmental variables among reaches spanning the five catchments on the Pumice Plain (Table 1). Within each stream or tributary (e.g. Geo-East and Geo-West), temperature and discharge significantly increased with distance downstream (Figure 2) along with conductivity and ammonium (Table S1). Channel slope significantly decreased with distance downstream (Table S1), with upstream reaches in erosional and downstream reaches in depositional settings. No other environmental variables changed significantly along the longitudinal gradient. Concentrations of SRP were similar among streams, but nitrate concentrations in upstream sites in the Willow and Forsyth/Redrock catchments were 30- to 69-fold higher than in the other catchments (Table 1), resulting in high N:P ratio in these streams in contrast to low N:P and N-limiting conditions in the remaining streams. Temperatures were lowest in the Redrock/Forsyth and Willow catchments, whereas discharge was highest in Willow Creek (Figure 2). Temperature and discharge (and their correlated water quality and hydrology variables, respectively) varied more significantly among catchments (Table S2) than along longitudinal gradients within the catchments.

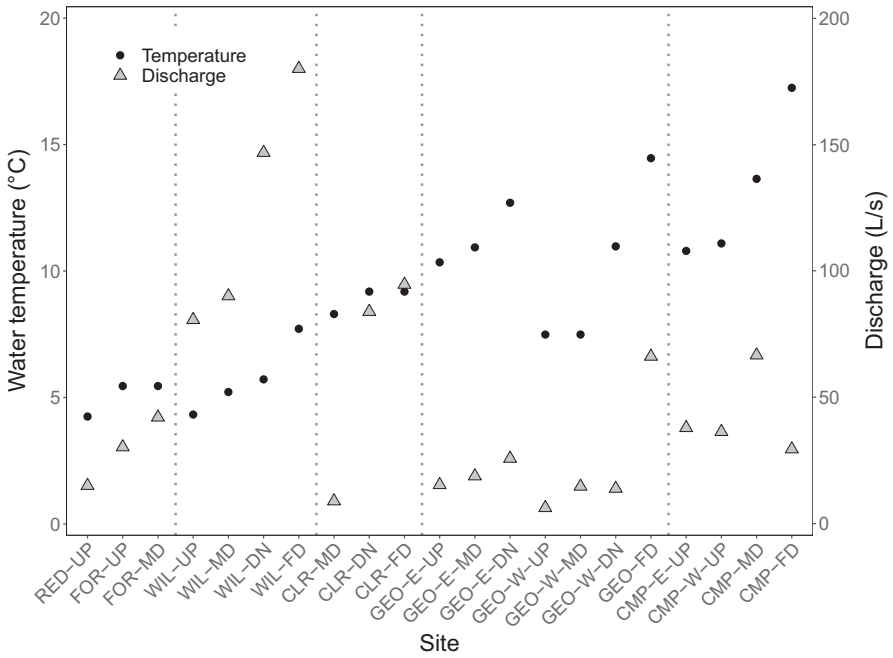

FIGURE 2 Water temperatures (°C, daily average) and discharge (L/s) from 21 sites surveyed July 2016 on the Pumice Plain of Mount St. Helens. Dashed vertical lines separate sites by catchment. Site labels indicate stream name followed by their location in the stream network (UP, upstream; MD, midstream; DN, downstream; FD, far downstream)

3.2 | Riparian plants

In riparian zones, we observed 37 plant taxa (30 native and 10 non-native), including 29 forbs, 4 graminoids, 2 shrubs, moss, and lichen (Table S3). Many of the taxa were unique to a single site (11 forbs) or contributed <2% of total cover. On average, Sitka alder had the greatest cover per site (mean 26%, range 0–88%), closely followed by Sitka willow (mean 17%, range 0–48%). Sitka willow and grasses (Poaceae) were observed at all sites except at the downstream-most site on Willow Creek, where the channel had recently shifted, and no plants were observed in any plot adjacent to the stream channel.

Across the sample reaches, riparian plant taxa richness ranged 0–18, and total cover ranged 0–273%, due to overlapping canopies (Table 1). Neither taxa richness nor % cover changed predictably with downstream distance along stream gradients (Table 2). Willow Creek had significantly lower plant richness than the other catchments and a trend toward lower % cover (Table 3).

The NMDS ordination for plant taxa % cover (Figure 3a; 2D solution, stress = 11.8, total r^2 = 89%, axis 1 = 54%, axis 2 = 35%) revealed some differences among catchments along axis 1. Plant assemblages showed no difference when grouped by downstream distance (MRPP $p > 0.05$). However, assemblages differed significantly among catchments: Willow Creek was different from all of the other catchments except Camp Creek, and Forsyth/Redrock was different from Geo (MRPP pairwise comparisons, $p < 0.05$). In general, the plant assemblages along Willow Creek had greater grass and forb cover and were correlated with higher stream discharge. Forsyth and Redrock Creeks had the highest willow and alder tree cover. Camp, Clear, and Geo catchments had the highest taxa richness, including cover by exotic taxa, and were correlated with warmer water temperatures.

3.3 | Periphytic diatoms and soft-bodied algae

Algal biomass, as determined by Chl-*a* (Table 1), did not vary significantly with downstream distance along stream gradients or among catchments (Tables 2, 3). We recorded 55 soft-bodied algal taxa and 96 diatom taxa representing seven phyla, with 78 taxa unique to just 1 or 2 sites (Tables S4, S5). Soft-bodied algal taxa richness ranged 1–17 and diatom species richness ranged 3–41 (mean 7 and 23, respectively; Table 1). Diatom richness increased with downstream distance, but soft-bodied algal richness did not (Table 2). Soft-bodied algae and diatom richness were generally lowest in Willow Creek but rarely significantly different among catchments. One exception was lower diatom richness in Willow compared to the Geo catchment (Table 3).

Quantitative analysis of periphytic algal cell densities revealed that all stream sites were dominated by cyanobacteria (Cyanophyta) and diatoms (Bacillariophyta), with occasionally high cell densities of green algae (Chlorophyta and Streptophyta) and chrysophyte algae (Ochrophyta: Chrysophyceae; Figure 4a). The yellow-green algae (Xanthophyceae) and euglenoids (e.g. *Trachelomonas* sp.) were recorded rarely and in low densities. The greatest cell densities of cyanobacteria were found in the upstream site on Forsyth Creek; however, subsequent qualitative observations revealed that high cyanobacterial cell numbers were due to their very small cell sizes and the producer with greatest biomass at this site was probably the large colonial diatom *Odontidium* sp. Qualitative observations of the soft-bodied algae also revealed the presence of cyanobacteria and chrysophyte algae at the upstream Redrock site.

The NMDS ordination for soft-bodied algae presence/absence (Figure 3b; 3D solution, stress = 10.6, total r^2 = 76%, axis 1 = 35%, axis 2 = 23%, axis 3 = 18%) and the NMDS ordination for diatom cell densities (Figure 3c; 2D solution, stress = 10.5, total r^2 = 89%, axis 1 = 70%, axis 2 = 19%) revealed significant differences in community

TABLE 2 Linear regression mixed effects model summary for community responses when testing for non-zero slopes with distance downstream (fixed, continuous), grouped by catchment (random, categorical)

	Fixed effect					Random	Residual
Response	Est.	*SE*	*df*	*t*-value	*p*	Variance	Variance
Riparian plants							
Richness	−0.14	0.56	16.0	−0.258	0.8000	12.58	6.91
Cover (ln)	−0.14	0.14	17.3	−0.948	0.3564	0.21	0.48
Periphytic algae							
Soft algae rich	−0.72	0.84	17.0	−0.862	0.4005	7.26	16.25
Diatom rich	+4.45	1.29	16.1	3.456	0.0032*	59.87	36.33
Chl-*a* (ln)	−0.13	0.12	17.2	−1.112	0.2820	0.09	0.32
Benthic invertebrates							
Richness	+3.26	0.95	16.2	3.432	0.0034*	27.54	19.84
Density (ln)	+0.02	0.05	15.7	0.327	0.7480	0.12	0.06
Biomass (ln)	+0.10	0.05	15.5	1.975	0.0663	0.21	0.05

Note: Fixed effect *t*-tests use Satterthwaite approximations of degrees of freedom. Significant *p*-values (*, $\alpha < 0.05$) indicate response variables that increase (positive fixed effect estimate) or decrease (negative fixed effect estimate) along a downstream gradient.

TABLE 3 ANOVA summary for community responses when testing for differences among catchments (Willow, For/Red, Clear, Geo, Camp)

Response	adj. r^2	$F_{(4,16)}$	p	Tukey HSD
Riparian plants:				
Richness	0.62	9.09	0.0005*	Willow < (ALL OTHERS)
Cover (ln)	0.24	2.61	0.0746	
Periphytic algae:				
Soft algae rich.	0.21	2.37	0.0965	
Diatom rich.	0.46	5.19	0.0071*	Willow < Geo
Chl-*a* (ln)	0.25	2.67	0.0703	
Benthic invertebrates:				
Richness	0.40	4.33	0.0145*	Willow < (Clear, Geo)
Density (ln)	0.60	8.37	0.0008*	Willow < (For/Red, Geo, Camp), Clear < For/Red
Biomass (ln)	0.70	12.76	<0.0001*	Willow < (ALL OTHERS)

Note: Response variables with significant differences by catchment (* $\alpha < 0.05$) were tested for all pair-wise contrasts (Tukey's post hoc). Only catchment contrasts found to be significantly different are described.

composition among catchments. For both algal types, assemblages from Willow and Forsyth/Redrock catchments were not significantly different from each other (MRPP $p > 0.48$), but they were different from each of the Camp, Clear, and Geo catchments (MRPP $p < 0.04$). Algal assemblages in the Willow and Forsyth/Redrock catchments were correlated with higher discharge and nitrate levels, whereas assemblages in the Camp, Clear, and Geo catchments were correlated with warmer water temperatures.

Generalising across major taxonomic groups of both soft-bodied algae and diatoms across the Pumice Plain catchments, we see some patterns in characteristic algal assemblages (Table 4). Of the soft-bodied algae, only low-profile and firmly attached cyanobacteria were found in Willow Creek and mainly included the mat-forming cyanobacteria *Chamaesiphon minutus*, *Homoeothrix varians*, and *Microcoleus autumnalis*. The Forsyth/Redrock catchment supported both low- and high-profile, firmly attached soft-bodied algae such as the cyanobacteria *C. minutus* and *H. varians*, the green filamentous algae *Ulothrix zonata* and *U. aequalis*, and the colonial chrysophyte macroalga *Hydrurus foetidus*. In contrast, a more diverse array of soft-bodied algae of different attachment types (firm, loose, or not attached) and ecological guilds (low-profile, high-profile, and motile) were observed at sites in the Camp, Clear, and Geo catchments including N_2-fixing cyanobacterial heterocystous (e.g. *Anabaena*, *Calothrix*, *Nodularia*, *Nostoc*), filamentous free-floating green algae (*Microspora* sp., *Spirogyra* sp., *Zygnema* sp.), and yellow–green *Tribonema* sp.

Of the diatoms, *Planothidium amphibium* (prostrate, non-colonial, low-profile) was found at nearly every site and in every catchment. Forsyth/Redrock sites were dominated by *Odontidium hyemale* (ribbon colony, high-profile), but also included *Odontidium mesodon*, *P. amphibium*, and *Nitzschia soratensis* (non-colonial, motile). These diatom species were also found in Willow Creek but at lower densities, where *Adlafia minuscula* var. *muralis* and *Mayamaea permitis* dominated (both non-colonial, motile). Diatom assemblages in the Camp, Clear, and Geo catchments were more similar to one another with high species richness and biovolume and comprised of a greater variety of lifeforms (e.g. colonial) and guilds (e.g. N_2-fixers and loosely attached). *Achnanthidium minutissimum* is considered to be cosmopolitan and an early coloniser of disturbed sites but was only observed in low abundances at five sites in the Camp, Clear, and Geo catchments.

3.4 | Aquatic macroinvertebrates

We observed 82 benthic macroinvertebrate taxa (74 insects and 8 non-insects, including 2 snails), with 35 taxa unique to just 1 or 2 sites (Table S6). Taxa richness among sites ranged 8–32 (mean 22, Table 1) and significantly increased from headwater to downstream sites (Table 2). However, the downstream-most site on Camp Creek was infested with the invasive New Zealand mud snail (*Potamopyrgus antipodarum*; 9,150/m^2) and was an outlier in terms of very high invertebrate density and biomass. Invertebrate richness, density, and biomass were significantly lower in Willow Creek compared to many of the other catchments including Forsyth/Redrock (Table 3). Insect density was highest at the upstream site on Redrock Creek and was dominated by Orthocladiinae midges, a common taxon found at nearly every site (Figure 4b).

The NMDS ordination for benthic invertebrates (Figure 3d; 2D solution, stress = 11.7, total r^2 = 90%, axis 1 = 82%, axis 2 = 8%) revealed significant differences in community composition among catchments (MRPP $p < 0.02$). Forsyth/Redrock sites were dominated by Orthocladiinae and Diamesinae midges (CG), but also supported *Mesocapnia* sp. (Capniidae, SH), *Clinocera* sp. (Empididae, PR), and *Dicranota* sp. (Tipuloidea Pediciidae, PR). These taxa were also found in Willow Creek but at substantially lower densities. Because of this difference in abundance, the Forsyth/Redrock assemblages align closer to those in Clear Creek. However, invertebrate assemblages in the warmer Camp, Clear, and Geo catchments contained greater taxa richness, density, biomass, and proportions of EPT taxa, clingers, climbers, and shredders than in both Willow or Forsyth/Redrock. Camp, Clear, and Geo sites were commonly colonised by Orthocladiinae and Tanytarsini sp. (CG), *Baetis tricaudatus* complex (Baetidae, CG), Simulidae sp. (CF), and *Malenka* sp. (Nemouridae, SH).

4 | DISCUSSION

Our point-in-time surveys of five MSH Pumice Plain catchments undergoing primary succession revealed consistent and strong

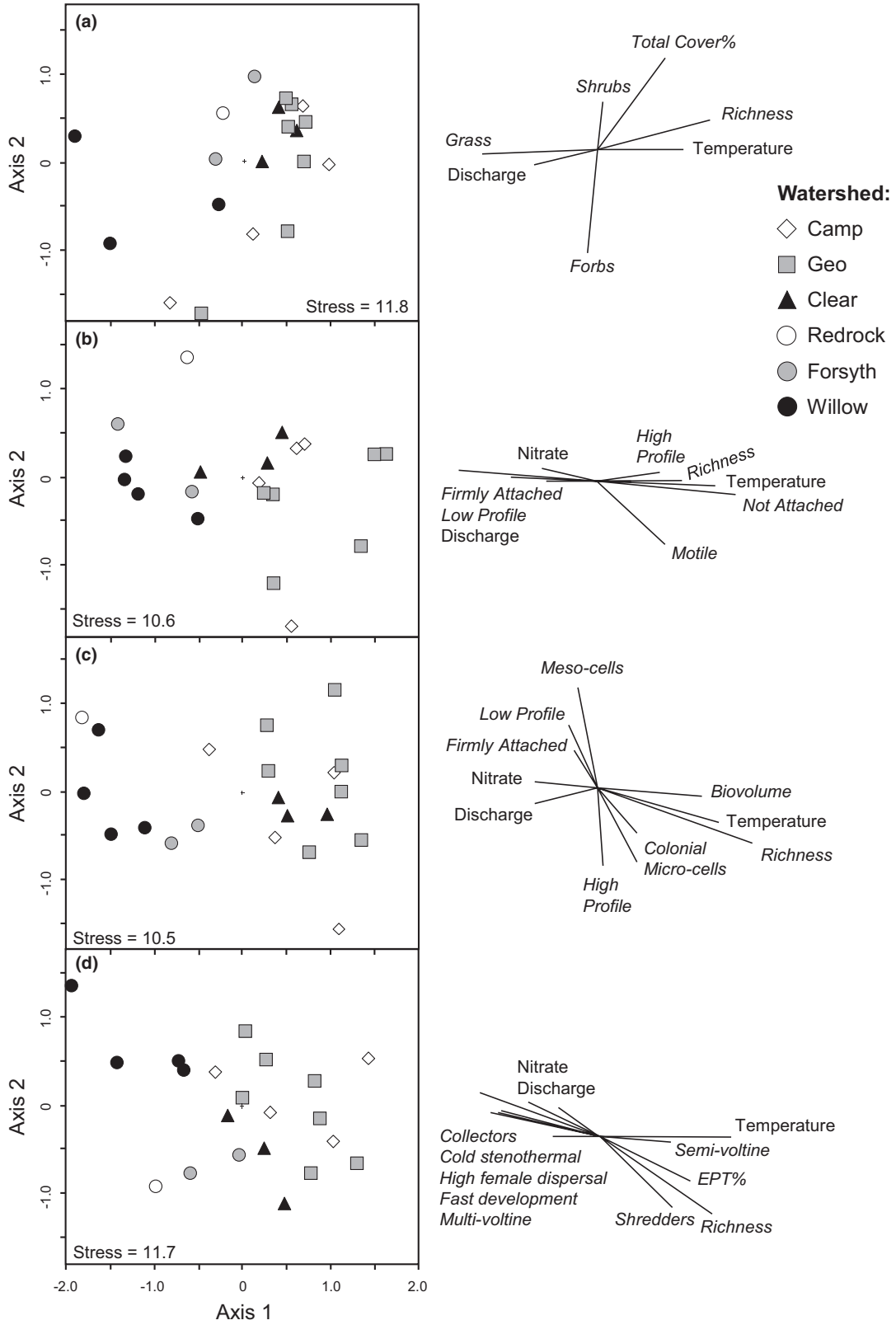

FIGURE 3 Non-metric multidimensional scaling ordination plots of riparian and aquatic assemblages: (a) riparian vegetation cover % of 38 taxa by 20 sites (no Willow–Far Down site due to zero vegetation); (b) soft-algae presence/absence of 55 taxa by 20 sites (no Geo-W-Down site due to only 1 taxa present); (c) diatom cell density of 96 species by 21 sites; and (d) benthic invertebrate density of 82 taxa by 21 sites. Symbols of different shapes and shade represent sites from different catchments. Pearson correlation ($r \geq |0.45|$) vectors for environmental variables and taxa traits (italics) associated with axes 1 or 2 are to the right of each plot. Discharge and temperature are representatives for correlated hydrology and water quality measures, respectively (see Methods—Statistical analyses)

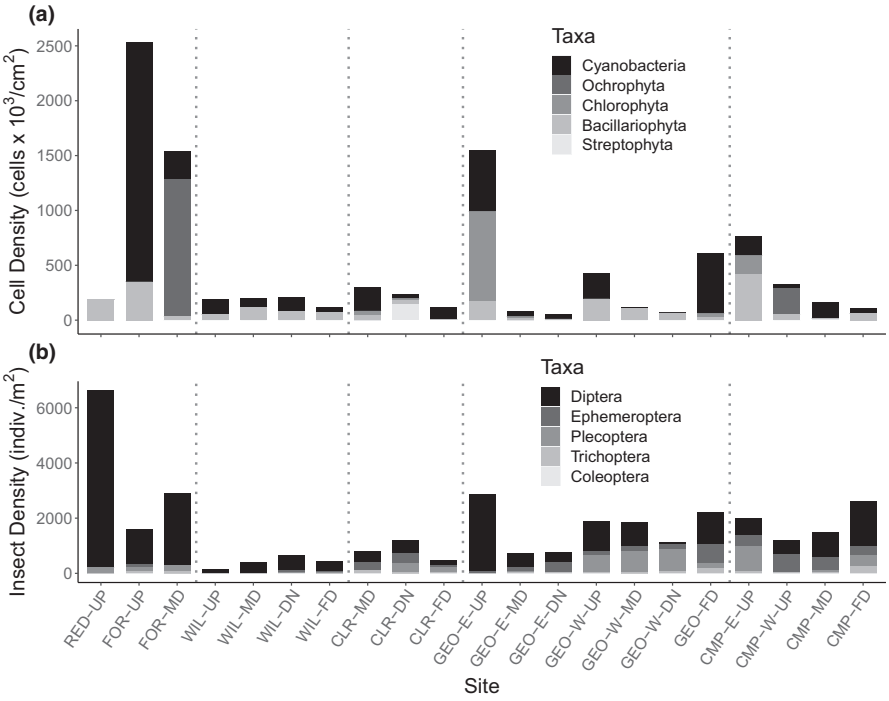

FIGURE 4 (a) Periphytic algae densities (cells × 10^3/cm^2) grouped by taxonomic division, and (b) insect densities (individuals/m^2) grouped by taxonomic order from 21 sites surveyed July 2016 on the Pumice Plain of Mount St. Helens. Qualitative observations of soft-bodied algae also found cyanobacteria and chrysophyte (Ochrophyta) algae at the upstream site on Redrock Creek (RED-UP). Site labels indicate stream name followed by their location in the stream network (UP, upstream; MD, midstream; DN, downstream; FD, far downstream)

TABLE 4 Characteristic algal assemblage for each catchment. N_2-fixing heterocystous cyanobacteria are in bold

Catchment	Creek (site)	Algal assemblage
Willow	Willow	*Microcoleus–Homoeothrix–Chamaesiphon*
For/Red	Forsyth	*Odontidium–Hydrurus–Homoeothrix–Chamaesiphon*
For/Red	Redrock	*Odontidium–Tribonema–Chamaesiphon*
Clear	Clear	***Nostoc –Anabaena –Calothrix*** *Mougeotia–Homoeothrix–Chamaesiphon*
Geo	Geo-East/West	***Nostoc –Anabaena –Calothrix –Nodularia*** *Tribonema–Microspora*
Geo	Geo (Far Down)	***Anabaena –Microspora–Tribonema***
Camp	Camp	***Nostoc –Anabaena –Calothrix*** *Microspora–Tribonema–Trachelomonas–Desmids*

differences at the broader spatial scale among catchments. The most important environmental variables differentiating catchments included discharge (also related to substrate size and DO), water temperature (also related to conductivity, alkalinity, pH, DOC, and slope), and nitrate. Contrary to our first hypothesis, we found little evidence that biological gradients had developed along the longitudinal dimension of individual streams as suggested by the River Continuum Concept (Vannote et al., 1980) and termed longitudinal succession by Fisher (1983).

Thermal and chemical differences broadly separated the five catchments into two major groups: Redrock/Forsyth and Willow Creeks on the eastern portion of the Pumice Plain, and Clear, Geo, and Camp Creeks on the western portion. The strong differences between eastern and western streams point to differences in primary hydrological source. The relatively low conductivity and colder water temperatures in the eastern streams suggest they are sourced in large part by glacier melt (Ilg & Castella, 2006). A glacial source to the eastern streams probably also explains their substantially higher nitrate concentrations, due to diverse microbial assemblages, active nitrogen cycling, and longer-term N deposition on older glacier ice habitat (Fegel et al., 2016; Hotaling et al., 2017). The Forsyth Glacier, located outside and to the east of the MSH crater, probably sources a shallow aquifer with short residence time and springs characteristic of the streams of the eastern Pumice Plain. The spatially and temporally diffuse springs of the three western catchments likely originate from aquifers that have longer residence times and may be influenced by groundwater and processes associated with the volcanically active MSH crater. Despite the shared geologic setting, shared history of catastrophic disturbance, and same successional age, the catchments on the Pumice Plain clearly developed different environmental settings from an early age. As such, contrasting abiotic templates appear to be driving contrasting successional trajectories of riparian plant, algal, and macroinvertebrate assemblages at the catchment scale.

Furthermore, flow disturbance common to stream ecosystems probably has differentially affected each of the five young Pumice Plain catchments. Large and destructive mudflows in 1982, 1983,

and 1984 (Major et al., 2005; Pierson, 1999) and recurrent floods have had variable influence and occurred with variable frequency among catchments. At the time of our study, Willow Creek was the most physically dynamic stream and demonstrated clear evidence of frequent disturbance associated with high flows and massive sediment movement following storms. Willow Creek, on average, had a steeper slope, and the catchment upstream of the springhead was large and a source of substantial sediment during heavy precipitation. Indeed, we observed frequent channel migration of Willow Creek in years immediately prior to and following the current study (unpublished data), and we hypothesise that recurrent flow disturbances have frequently interrupted its successional trajectory, similar to the temporal observations of Milner and Robertson (2010) in glacier retreat streams of Glacier Bay, AK. As such, in a space-for-time framework, riparian and benthic community structure in Willow Creek probably represents *earlier* successional stages than the other less frequently disturbed catchments of the Pumice Plain.

4.1 | Riparian plants

On mudflow deposits in a stream just east of MSH undergoing secondary succession, 18 years of riparian development showed early dominance by red alder (*Alnus rubra*), followed by recruitment into gaps by western hemlock (*Tsuga heterophylla*; Weber et al., 2006). Elsewhere in western WA, two forested streams impacted by catastrophic debris flows (not of volcanic origin) showed red alder with over 50% canopy cover after only 3 years of secondary succession (Foster et al., 2020). In contrast, young riparian zones on the Pumice Plain 36 years after the eruption had only occasional canopy closure (six of the 21 sites had canopy cover ≥50%), and the dominant canopy species were Sitka alder and Sitka willow, with few red alders, and no evidence of recruitment by western hemlock. Slower growth and establishment may be due to slower soil development, frequent flood scour, or limited seed sources. Chronosequences along glacier retreat streams in Glacier Bay show initial growth of moss and the N-fixing forb, *Dryas drummondii*, followed by alder, willow, and cottonwood colonisation after about 50 years, and developing spruce forests (*Picea sitchensis*) after about 100 years (Sidle & Milner, 1989). Pumice Plain catchments seem to have alder/willow riparian zones developing at a faster rate than Glacier Bay streams, but this may be influenced by lower latitude and smaller catchment size.

Across the Pumice Plain we saw wide variation in riparian cover at the reach scale, from 0% at several sites along Willow Creek to over 100% cover due to overlapping layers of vegetation. More broadly, we observed two dominant types of riparian plant assemblages; one assemblage lower in richness and canopy cover along Willow Creek and another assemblage co-dominated by alder and willow, with diverse understories of forbs, grass, and moss in Camp, Geo, Clear, and Forsyth/Redrock Creeks. Both Sitka alder and Sitka willow are early colonisers, and alder adds plant-available nitrogen to the nutrient-poor soils (Robbins et al., 2017). At 36 years post-eruption, it appears that woody plant establishment in the riparian zones relies on initial colonisation by alder and willow, but unstable banks and frequent flow disturbances can continually reset this first stage of woody plant development – as observed along most of the length of Willow Creek. Channel slope alone did not account for riparian cover or flow disturbance differences among catchments. Willow, Forsyth, and Redrock all had similarly steep slopes, but Forsyth/Redrock had more riparian shrubs. The lower frequency of flow disturbance in the Redrock catchment was probably due to its relatively small size, while Forsyth had lower discharge than Willow Creek. The combination of slope and discharge (i.e. stream power) is probably important to the interplay between channel dynamics and riparian plant establishment, with each influencing the other (Sidle & Milner, 1989). The Pumice Plain may be an ideal location for the exploration of this type of *evolutionary geomorphology*, the interplay between biological colonisation and geomorphological development (Steiger & Corenblit, 2012). We did not observe later-successional woody plant species in the riparian zones of our study reaches, although later-successional conifers (*Pseudotsuga menzieszii*, *T. heterophylla*, and *Abies procera*) occur occasionally on the Pumice Plain uplands (Wood & del Moral, 1988).

4.2 | Periphytic diatoms and soft-bodied algae

For several years after the 1980 eruption, algal colonisation of springs and streams on MSH remained in early successional stages, composed mostly of low-profile diatoms and dominated by *Achnathidium minutissimum* (Rushforth et al., 1986). Six years post-eruption, taxa richness of cyanobacteria and green algae increased, suggesting that successional processes were occurring (Steinman & Lamberti, 1988). In catchments undergoing primary succession on the Pumice Plain, we found that cyanobacteria and diatoms were common at all sites 36 years post-eruption and that filamentous green and yellow–green algae were only common at two headwater sites (Camp-East and Geo-East). Similar to the successional trajectory of riparian plants, algal assemblages in the Pumice Plain streams also appeared to be mostly in relatively early successional stages in 2016. The most common algal association was cyanobacteria-diatom, dominated by the low-profile and firmly attached cyanobacteria *Chamaesiphon minutus* and *Homoeothrix varians*, and diatom *Planothidium amphibium*, which are commonly encountered at sites experiencing frequent disturbance, low nutrients, and low conductivity (Wetzel et al., 2014).

Overall, diatom richness significantly increased with downstream distance in all catchments. This was one of just two longitudinal patterns we documented. Far downstream reaches were depositional with lower slope gradients, higher discharges, and warmer temperatures than upstream reaches. Nonetheless, diatom community structure also varied considerably among catchments. Algal assemblages in Willow Creek were different than other streams and were characterised by low taxa richness, a dearth of N_2-fixing algae, and common occurrence of the mat-forming cyanobacterium *Microcoleus autimnalis*. Dominant species in Willow Creek were the small, low-profile diatoms *Adlafia minuscula* var. *muralis* and *Mayamaea permitis*.

Frequent high-flow and bed-moving disturbances in Willow Creek, associated with high discharge and steeper slopes, have probably precluded development of algae with larger growth forms.

The absence of N_2-fixing algae in both the Willow and Forsyth/Redrock catchments, in combination with high N:P ratios, suggests that nitrogen was not a limiting factor for algal growth in these streams of the eastern section of the Pumice Plain. Relatively high nitrate concentrations in most reaches of these streams support that hypothesis and may be due to N deposition and microbial processing in glaciers melting into streams. Nitrate concentrations have been shown to strongly affect diatoms in other systems (Slemmons et al., 2017). Furthermore, the ion content and dissolved organic carbon in these catchments were lower than in the other catchments, suggesting lower riparian contributions (Robbins et al., 2017). Algal assemblages in the three western catchments were more diverse, including N_2-fixers and motile taxa, such as the euglenoid *Trachelomonas*, planktonic and tychoplanktonic diatoms (i.e. *Aulacoseira* sp., *Staurosira* sp., *Staurosirella* sp., *Pseudostaurosira* sp.) and free-floating filamentous green and yellow-green algae, which have an advantage in low-flow depositional conditions. These algal assemblages developed under contrasting water chemistry conditions (i.e. low N:P ratio and N-limitation, increased pH, organics and ion content) and higher water temperatures than the streams in the two eastern catchments. Although detailed algal results from Glacier Bay streams do not appear to be available, the development of filamentous algae and moss was observed in the more stable channels and contributed to food-web dynamics and low-flow microhabitat (Milner et al., 2000).

4.3 | Aquatic macroinvertebrates

This is the first study of lotic macroinvertebrates from the pyroclastic flow disturbance zone of MSH, but several early studies focused on streams outside of the Pumice Plain that experienced ashfall, forest blowdown, or mudflows. At these less disturbed sites, fast-colonising aquatic insects (chironomids and baetid mayflies) were abundant within several years of the disturbance, but the absence of taxa that require stable substrate for attachment, such as filter-feeding collectors or large mayfly or caddisfly scrapers, reflected substrate instability (Anderson & Wisseman, 1987; Fusté, 1981; Wilzbach et al., 1983). The presence of intra- and inter-stream refuge habitat also played an important role in helping to rebuild aquatic insect populations in peripheral streams undergoing secondary succession (Anderson, 1992; Hawkins & Sedell, 1990).

On the Pumice Plain, we suspect that stream macroinvertebrate assemblages took longer to develop and diversify than in peripheral streams due to the large deposits of sterile parent material, more distant sources for colonists, lack of refuge habitat, and a longer period of channel instability. Benthic macroinvertebrate taxa richness increased with distance downstream, but as with algae, there were also significant differences in richness, density, and biomass among catchments.

In general, the most abundant insects collected from all of the catchments had functional traits associated with an ability to colonise new environments or survive variable conditions. These included: (1) common in drift; (2) strong swimmers; (3) strong adult fliers; (4) desiccation resistant; and (5) strong female dispersers. The macroinvertebrate assemblages in Willow Creek were dominated by disturbance-tolerant chironomids, with low EPT taxa richness and low functional feeding group diversity compared to the other Pumice Plain catchments. As with riparian vegetation, the combination of high discharge and steep slopes may have reduced macroinvertebrate density and diversity in Willow Creek. Like Willow, Forsyth and Redrock also had cold temperatures, but their assemblages were more similar to Clear Creek, which had warmer temperatures and lower discharge. Forsyth and Redrock may also benefit from allochthonous inputs of riparian litter. Overall, though, flow disturbance regimes appear to be the primary influence on invertebrate communities, more so than water temperature. However, further research should focus on how water source influences macroinvertebrate assemblages across the Pumice Plain since several recent studies have found significant differences in glacier-fed streams compared to streams with other sources (Finn et al., 2013; Tronstad et al., 2020).

Interestingly, across the Pumice Plain catchments, we encountered very few representatives of common regional taxa that tend to be associated with hyporheic habitat during some life-cycle stages, such as Amphipoda and Leuctridae (Plecoptera). Amphipods are likely to be strongly dispersal limited (Hatley & Murphy, 2016; Zickovich & Bohonak, 2007) such that colonists may not have arrived, but the scarcity of leuctrid stoneflies might also reflect minimally developed hyporheic zones at this early stage of channel evolution. However, stoneflies in the genus *Mesocapnia* commonly use the hyporheic zone during nymphal stages (Bogan, 2017; Jacobi & Cary, 1996) and their prevalence in Redrock and Forsyth Creeks, along with observations of variable hyporheic development across the Pumice Plain (unpublished data), suggests that hyporheic zones in the young streams may be developing at a faster rate in Redrock/Forsyth sections of the Willow Creek catchment.

The development of benthic macroinvertebrate assemblages across catchments on the Pumice Plain shows some similarities with macroinvertebrates in streams exposed from glacial retreat in Glacier Bay. For example, both sites were colonised early by chironomid, baetid, and capniid benthic taxa (Brown & Milner, 2012). Similar to the Glacier Bay streams, most of the Pumice Plain catchments share the same dominant taxa, adding some support to the tolerance model of succession in streams (Connell & Slatyer, 1977; Milner & Robertson, 2010). In glacier retreat streams, macroinvertebrate community assembly was initially deterministic due to low water temperatures, then increasingly stochastic as water temperatures increased (Brown & Milner, 2012; Milner et al., 2011). Similarly, at MSH, the Willow Creek sites have consistently colder water temperatures, unstable substrates, and aquatic macroinvertebrate assemblages with reduced taxonomic and functional trait diversities that are dominated by the cold stenothermic Diamesinae larvae (Niedrist & Füreder, 2017). These

results suggest that environmental niche filtering is probably an important process (Brown & Milner, 2012) and provide additional evidence that glacier melt could be a key hydrological source for Willow Creek. Wolf Point Creek, a stream formed by glacial retreat in Alaska, was colonised by 24 macroinvertebrate taxa over 28 years (Milner et al., 2008). In contrast, individual streams on the Pumice Plain have been colonised by 38–58 taxa in 36 years. Differences in disturbance history, geology, and biogeography are probably part of this discrepancy, but the macroinvertebrate assemblage post-eruption is much more complex both taxonomically and functionally even though deterministic community assembly processes appear to be in effect in both systems.

5 | CONCLUSION

Early studies following the 1980 eruption speculated that ecological development of new streams on the Pumice Plain would take decades to centuries (Steinman & Lamberti, 1988). Overall, however, we documented unexpectedly high diversity in these young catchments after only 36 years of primary succession, despite a scarcity of nearby sources of colonists. At the same time, the dominant taxa and traits suggest that these catchments were still in early stages of succession, with the most frequently disturbed catchment (Willow Creek) having evidence of continual interruption as documented by lower diversity and biomass of biota and a dominance of disturbance-associated traits. We saw little evidence for predictable upstream–downstream gradients in community structure for riparian plants, algal, or invertebrates, with the exception of increasing richness of algae and invertebrates downstream. By contrast, we did find substantial evidence that community structure of riparian plants, algae, and macroinvertebrates varied among catchments.

At the broadest scale of study, Pumice Plain catchments formed two major groups that are likely to be driven by substantial differences in hydrological sources and disturbance regimes. Willow Creek and Forsyth/Redrock catchments overall grouped together, and these streams had a chemical and thermal signature of meltwater from glaciers. These hydrological differences were unexpected, and more research is needed to tease apart hydrological differences among the Pumice Plain catchments and to evaluate the influence of these differences on patterns of ecological succession in the streams.

Overall, we anticipate that physical dynamism of the landscape will continue to affect the evolution of Pumice Plain catchments and interrupt successional trajectories. Frequent avulsion events over the past 40 years indicate that unpredictable physical dynamism is still occurring at MSH (Major et al., 2019). The combination of disturbance magnitude/frequency and hydrological source variation appears to have driven the divergent successional trajectories across Pumice Plain catchments of similar age, geology, and colonist pools.

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AUTHOR CONTRIBUTIONS

S.M.C. and C.J.L. collaborated closely on all aspects of this research project. S.M.C. collected, quality-checked, and analysed data, and wrote major sections of the manuscript. C.J.L. coordinated student collaborators, organised field trips, collected data, and wrote major sections of the manuscript. D.S.F. wrote major sections of the manuscript. R.S. identified species from algal samples and wrote sections of the manuscript. E.R.W. collaborated in the field, collected data, and analysed preliminary datasets in support of this project. All authors edited multiple drafts of this manuscript.

DATA AVAILABILITY STATEMENT

If you would like to use any of these data for subsequent analyses or meta-analyses, please go to this site for access to the data: https://github.com/carrileroy/MSH_2016.

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SUPPORTING INFORMATION

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

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