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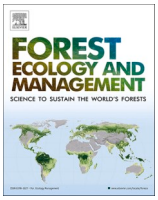

Macroinvertebrate responses to differing riparian treatments following forest harvest in the headwaters of Trask River watershed

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ABSTRACT

Although it is well-established that macroinvertebrates are an integral part of a healthy stream ecosystem, studies designed to inform forest harvest best management practices for sustainability of macroinvertebrate communities in small streams have been limited. Current riparian management practices for headwater streams generally focus on providing adequate wood supply, reducing debris flows and transport of sediment, and maintaining water quality in larger streams that contain fish. Here we studied the effects of contemporary forest harvest practices on benthic macroinvertebrate density and community composition in 12 small headwater streams as part of the Trask River Watershed Study. To account for seasonal and year-to-year variability in macroinvertebrate densities, we sampled each site at the same time of year for six years before and four years after harvest. Three watersheds were clearcut with variable riparian buffers, three were clearcut with 12 m riparian buffers, and one was thinned with 15 m buffers. Five adjacent watersheds were not treated and were studied as reference sites. All sites had approximately 50 yr old conifer and alder forests, which had revegetated following fires and harvest in prior decades.

In these steep mountain streams, benthic macroinvertebrate density and community composition were generally similar across watersheds prior to harvest. Collectors were the most abundant functional feeding group, followed by shredders; scrapers were the least abundant. After harvest, in two of the three clearcut watersheds with variable buffers, the total benthic density and percentage of collectors increased, primarily due to greater numbers of Chironomidae. We also observed more abundant emergence post-harvest at these two watersheds. In the third clearcut watershed with a variable buffer and in the three clearcut watersheds with uniform 12 m riparian buffers, we did not see changes in density or functional feeding groups after harvest. We explored the spatial and temporal aspects of the data using both non-parametric and parametric statistical methods. High variability swamped the treatment effect when watersheds were grouped by riparian treatment for the repeated measure analyses, while NMDS showed a significant shift post-harvest for the watersheds with variable buffers. In the clearcut watersheds with uniform buffers, macroinvertebrates densities and community composition did not shift. At two of the clearcut watersheds with variable buffers, we observed increased density for the first two years after harvest, and chironomids comprised up to 80% of the abundance in samples. In the subsequent years, we documented mixed responses for two watersheds. It was invaluable to have multiple pre- and post-harvest sampling periods in both harvested and reference watersheds in order to better identify site specific responses to treatment and to separate background variability from responses to harvest. We show that retention of riparian vegetation on headwater streams during clearcut harvesting minimized changes in total macroinvertebrate densities and community composition. Small buffers may be key to maintenance of diverse stream invertebrate communities in headwaters.

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1. Introduction

Many of the early studies of effects of forest management on instream communities in the Pacific Northwest occurred during harvest of old growth conifer forests between the 1960′s and 1980′s (Hawkins et al., 1982, Stednick, 2008). Now, these second growth forests are being harvested, and new methods of harvest coupled with recent stricter forest management guidelines have resulted in new questions about the effectiveness of current best management practices. To address these information needs, the multiyear Trask River Watershed Study and associated study of Hinkle Creek (Gerth et al., 2022) were designed and implemented. Multi-disciplinary teams of scientists worked in cooperation with private landowners and managers from state and federal agencies to evaluate the effectiveness of the current forest practice regulations in minimizing the impacts of forest harvest on aquatic resources. Here, we describe the responses of aquatic macroinvertebrates in the fishless headwater streams of the Trask Watershed, before and after forest harvest with differing riparian treatments.

Headwater streams are biologically and hydrologically important systems (Meyer & Wallace, 2001; Naiman & Latterell, 2005; Richardson & Danehy, 2007) forming critical habitats for a high diversity of macroinvertebrates (Li et al., 2001; Robinson et al., 2001). The macroinvertebrate communities are an integral part of healthy stream ecosystems (Cummins et al., 1984). Intimate connections between headwater streams and their riparian zones make aquatic ecosystems particularly responsive to disturbances or harvest activities close to the stream (Newbold et al., 1980; Murphy et al., 1981; Danehy et al., 2021; Gerth et al., 2022). However, in many regions, headwater streams without fish have minimal requirements for retention of riparian vegetation during harvest (ODF, 2010b; Cristan et al., 2016).

To date, meta-analyses of effects of riparian forest harvest on streams and stream macroinvertebrates (Richardson & Béraud, 2014; Cristan et al., 2016; Lunn et al., 2017) have revealed contradictory responses of macroinvertebrates to forest harvest. Multiple factors can lead to distinctively different macroinvertebrate communities in small streams (Li et al., 2001), including differences in riparian forest vegetation (Romero et al., 2005; but see McConigley et al., 2017), hydrology (Moore & Wondzell, 2005), size of stream (Richardson & Béraud, 2014), substrate and microhabitats (Murphy et al., 1981), and geographic isolation and elevation (Robinson et al., 2001). During forest harvest, the type of harvest, amount of retention of upslope and riparian trees, extent of soil disturbance as well as the magnitude and frequency of prior disturbances all have the potential to influence instream responses (Jackson et al., 2007; Cole & Newton, 2013). These multiple sources of variation in responses to harvest highlight the potential importance of controlling for multiple factors when examining macroinvertebrate responses to forest management. Studies that are able to conduct comparisons of responses to riparian and upslope harvest across as similar as possible physical and climatic headwater conditions could be valuable in minimizing the variability and evaluating best management practices.

The timing and duration of studies are also crucial factors in successfully identifying relationships between forest management and instream responses. Many studies use post-harvest surveys that maximize sample size across a broad spatial distribution of sites (Cole et al., 2003; Calvao et al., 2016; McConigley et al., 2017; Jyvasjarvi et al., 2020). These are informative, but at the expense of being able to account for background differences related to pre-harvest conditions in each watershed. Given the high variability in spatial and temporal densities of macroinvertebrates (Frady et al., 2007; Gravelle et al., 2009), without pre-disturbance data it can be difficult to separate disturbance responses from the confounding influence of site-to-site and year-to-year natural variability.

Experimental studies have long played a role in the formulation and application of forest management techniques and regulations (Stednick, 2008). Reach and watershed scale studies have been implemented extensively as a means of quantifying impacts of forest management on water quality and quantity (see example summaries in Campbell et al., 2021; Guillen et al., 2021; Johnson et al., 2021), stream temperature standards (Groom et al., 2017), the role of riparian buffers and fish responses (Naiman & Latterell, 2005; Stednick, 2008; Kaylor et al., 2018). The understanding gained from prior studies has led to updates in harvest methodology and watershed and forest management guidelines on both public and private lands (Cristan et al., 2016). Harvest guidelines vary across forest ownerships, with publicly owned forests generally having more rigorous regulations for retention of riparian buffers than private timberlands in the US. Although there have been recent evaluations of updated best management practices to protect riparian and aquatic ecosystems in fish bearing streams (Groom et al., 2017; Cristan et al., 2016), guidelines for harvest along small, perennial, non-fish-bearing streams are less stringent than along fish bearing streams or streams designated for drinking water use (ODF, 2010a, 2010b) and are beginning to be re-examined (Estrella & Ehinger, 2018).

To increase our understanding of effects of forest harvest on small, fishless streams, we implemented a study of macroinvertebrate responses to differing forest harvest guidelines before and after forest harvest. We sampled a total of 10 years pre- and post-harvest in adjacent treated and reference watersheds, selected to minimize macroscale differences in climate, forest type, forest age, geology and photoperiod. Harvest prescriptions included clearcut harvest of forested watersheds. In the three watersheds owned by private forest companies, riparian buffers were not required along fishless streams. In three clearcut watersheds on state forest lands, riparian buffers were required along the full extent of the perennial streams. An additional harvest treatment in a federal watershed involved thinning with wider riparian buffers than on state forests.

Our objectives for this study were to quantify whether contemporary forest harvest and retention of riparian buffers affects density and community composition of headwater stream macroinvertebrates. This required that we evaluate the spatial and temporal variability of macroinvertebrate densities and community composition across the treated and reference small watersheds. We used multiple, separate statistical methods to assess the effects of forest harvest on macroinvertebrates and the spatial and temporal variability of responses. Using this weight-of-evidence approach, we were able to compare the results from repeated measures analyses of treatment groups pre- and post-harvest with findings from multivariate ordinations and permutation tests across reference and treated watersheds.

2. Methods

2.1. Study site and experimental design

Twelve headwater study sites were located within the Trask River Watershed Study area, which encompasses the upper 25 km^2 of the East Fork of the South Fork of the Trask River (Fig. 1), in the northern Coast Range of Oregon. These highly dissected watersheds drain westward to the Pacific Ocean. The underlying geology is a mixture of both sedimentary deposits and volcanic basalt intrusions (Bywater-Reyes et al., 2017). Annual rainfall in the Trask study area averages 200 cm per year, with most of the precipitation falling as rain between October and May, and occasional snow at the higher elevation sites.

Historically the Trask River Watershed has been subject to severe disturbances, including a series of wildfires between 1933 and 1951 collectively referred to as the Tillamook Burn. Following those fires, all remaining timber was harvested, and hillslopes were replanted, primarily with Douglas-fir. Additional legacies from wildfire and harvest include high densities of logging roads, minimal downed wood in streams and riparian areas, and a greatly simplified understory and overstory vegetation community. As a result, at the beginning of our study, the Trask River Watershed Study area was a plantation of 50 year-old Douglas-fir (*Pseudotsuga menziesii*), with Douglas-fir, red alder (*Alnus rubra*) and big leaf maple (*Acer macrophyllum*) in riparian zones.

The Trask Watershed Study employed a nested (hierarchical) design that consisted of four larger catchments - Rock Creek (RK), Pothole (PH), Gus (GS), and Upper Main (UM) - with up to four small study watersheds within each (Fig. 1). For our BACI design, one watershed (PH3, GS1, UM1) in each larger catchment was not harvested and served an internal or adjacent reference, in addition to two reference watersheds in Rock Creek (RK1, RK3; Table 1). The "before" or pre-harvest sampling occurred from 2006 to 2011. Road upgrade and road construction activities started in summer 2011, after the annual sampling in June. During forest harvest in 2012, access to the catchment was restricted and no sampling occurred. The "after" or post-harvest sampling started in 2013 and continued through 2016.

Forest harvest in the seven treated watersheds was planned for the full watershed area, to the extent practical (Table 1, Supplemental Figure S1). Riparian treatments followed the Oregon Forest Practices Act for private forests (ODF (Oregon Department of Forestry), 2010b) and Forest Management Plan for State Forests (ODF (Oregon Department of Forestry), 2010a). Watersheds UM3, UM2, and GS3, were owned by a private forest company (Weyerhaeuser). Riparian buffers were not required along small streams on private forest lands where the streams did not serve as habitat for trout or salmon (ODF, 2010b). However, forest managers have discretion to leave additional trees within harvest units (aerial photos, Supplemental Figure S1) and often group these together for operational purposes. In these watersheds, the 'leave trees' were a mix of species (alder, maple and Douglas-fir) and were not cut because either they stabilized stream banks or were located on soils that were too wet for harvest machinery. This resulted in selected riparian trees not being harvested immediately adjacent to downstream portions of our study reaches at UM2 and UM3. Because the landowner chose to leave portions of buffers in some reaches and remove any buffer in other

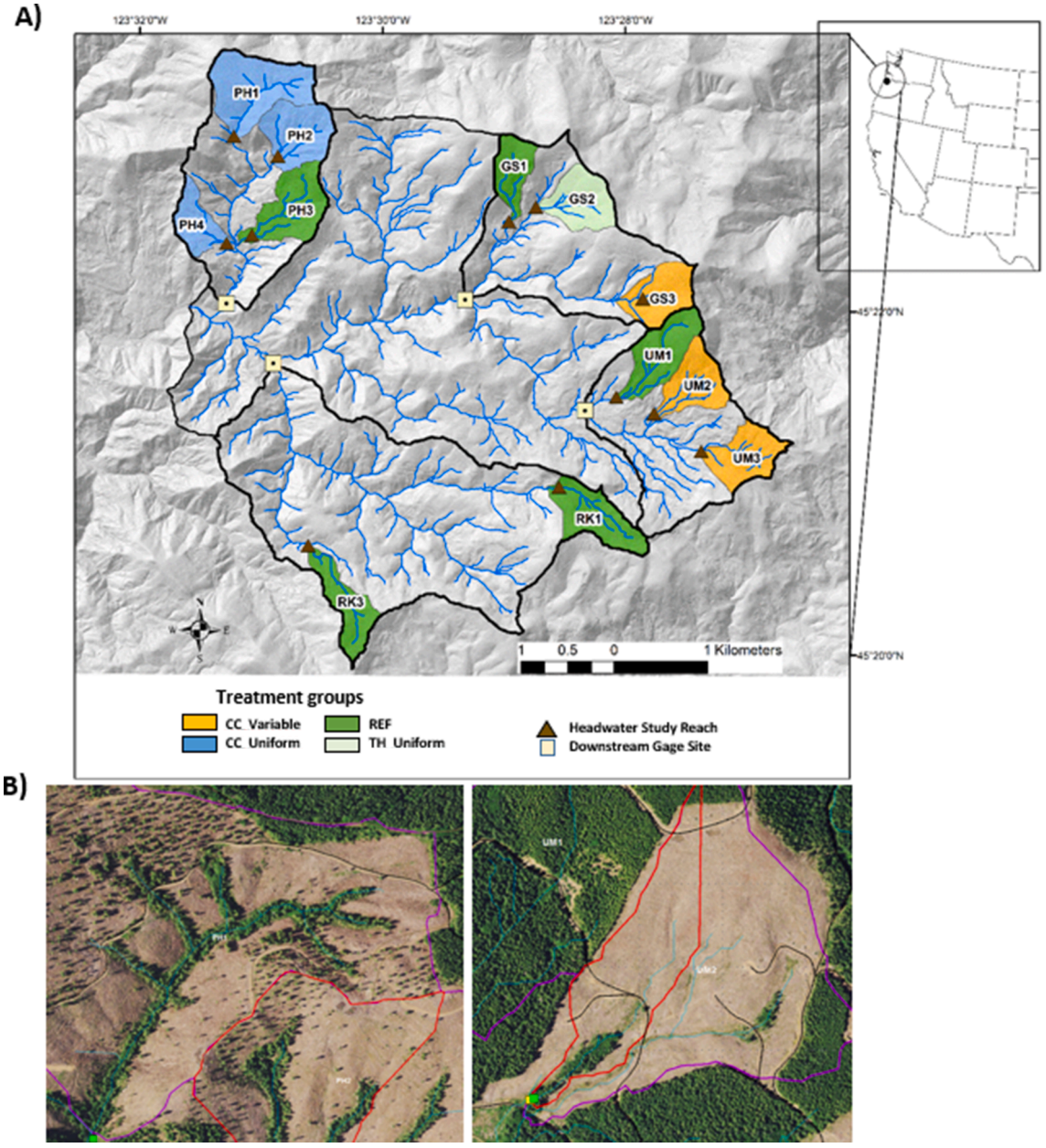

Fig. 1. A) Map of study sites in the Trask River Watershed Study in western Oregon, USA. Sampling reaches were located at the most downstream portion of each watershed, shown as brown triangles. Reference watersheds (REF) are shown in dark green, clearcut with uniform 12 m buffers (CC_B) are shown as blue and clearcut with variable buffers (CC_VB) are show as orange. The BLM site that was thinned with uniform 15 m buffers (TH_B) is shown in light green. B) Aerial photos showing an example of modified clearcut with uniform buffers in PH1 on the left and clearcut with variable buffers in UM2 on the right.

Table 1
Characteristics for the study watersheds (WS). Ownerships are private forest industry (Weyerhaeuser Company; WeyCo), federal (Bureau of Land Management; BLM) and state (Oregon Department of Forestry; ODF). Forest harvest prescriptions vary by ownership for small streams without fish. Elevations were measured at the most downstream point of each study site. Measurements of wetted widths occurred in late June at same time as other sampling.

Watershed	WS and Buffer Treatment	Ownership	Elevation (m)	Average channel slope (%)	Wetted widths (m)	WS Area (ha)	WS area treated in 2012[A]	Percent shade		Average maximum June temperature (°C)	
								Pre	*Post*	*Pre*	*Post*
GS3	CC_Variable	WeyCo	789	22.4	1.20	20.4	94%	89	5	7.5	11.6
UM2	CC_Variable	WeyCo	685	18.4	1.16	17.1	83%	95	75	7.5	10.0
UM3	CC_Variable	WeyCo	728	11.8	1.34	39.2	56% [B]	94	82	9.6	12.7
PH1	CC_Uniform	ODF	531	13.6	1.99	67.1	77%	91	91	9.6	10.7
PH2	CC_Uniform	ODF	493	13.7	1.00	20.4	78%	94	94	9.3	10.0
PH4	CC_Uniform	ODF	370	13.8	0.79	23.6	92%	95	94	9.6	10.6
GS2	TH_Uniform	BLM	638	14.5	1.82	39.0	91%	96	94	9.0	10.2
GS1	REF	WeyCo	611	12.1	1.32	26.5	0%	97	95	9.4	10.8
UM1	REF	WeyCo	658	18.7	1.47	44.2	0%	94	93	7.0	8.1
PH3	REF	ODF	390	12.8	0.93	45.4	0%	98	97	9.6	10.3
RK1	REF	WeyCo	680	7.6	1.36	42.2	0%	87	87	7.5	8.6
RK3	REF	ODF	548	16.2	1.66	35.3	0%	94	95	8.7	9.6

*Details of watershed and buffer treatments:
CC_Variable: Clearcut watershed with variable buffers. A riparian buffer was not required on these sites, and during harvest, some leave trees remained in downstream riparian areas of UM2 and UM3.
CC_Uniform: Clearcut or modified clearcut watershed with uniform 12 m riparian buffer on each side of stream.
TH_Uniform: Thinned watershed with 15 m riparian buffer on each side of stream.
REF: Reference watersheds, not harvested in 2012.
A: Treated area does not include area of riparian buffers or leave trees.
B: A portion of the watershed had been harvested 6 yrs previously.

reaches, we refer to the study sites on private forest lands as clearcut with variable buffers (CC_Variable).

On publicly-owned State Forest land, managed by Oregon Department of Forestry, the required minimum riparian buffer prescription for small fishless streams was 7.6 m no-cut zone from each edge of the stream. In addition, based on site-specific criteria (ODF, 2010a, Appendix J), no-cut riparian zones have potential to be required up to 15.2 m from the stream banks. In this study, the resulting buffer widths on state lands (i.e. watersheds starting with PH) were 12 m each side of the length of the perennial streams, measured in horizontal distance. The clearcuts for the Pothole catchment were considered modified because selected trees throughout the watershed were not harvested (Fig. 1B, Supplemental Figure S1) to meet green tree retention requirements. We characterized these State Forest sites as clearcut with uniform 12 m buffers (CC_Uniform).

The only watershed on federal land was GS2, which was managed by the Bureau of Land Management. Based on federal requirements for harvest, a 15 m no-cut buffer remained on each side of the perennial portions of the stream when the watershed was being thinned. We classified this site as thinned with 15 m uniform buffer (TH_Uniform). More harvest details are available online (https://traskstudy.forestry.oregonstate.edu).

2.2. Data collection

All headwater stream sampling reaches (n=12) were 30 m long. At watersheds designated for harvest, the sampling reaches were located within the most downstream portion of the planned harvested area. Study reach locations and sampling periods were coordinated to overlap with collaborative studies of other stream ecosystem dynamics (Haxton, 2010; Bywater-Reyes et al., 2017; Steadman, 2017; Arismendi et al., 2017; Chelgren & Adams, 2017; Reiter et al., 2020).

Invertebrate sampling was conducted each year over a four-day period in mid- to late-June, when streamflow was stable but with sufficient flow to permit Surber sampling. Basic measurements of stream physical characteristics, including wetted stream width, water depths, and substrate were collected at multiple points within each study reach as part of each year's sampling. Average percent shade over each study reach was measured using a handheld concave densiometer; measurements were collected in all four directions from the center of the stream at 5 transects. Stream temperature measurements at half hour intervals were collected June-September using continuously recording thermistors (Onset Computer Corporation, model U22-001), protected from direct radiation.

Six Surber samples (mesh size 500 μm) were collected in each study reach. Sample locations were chosen using a random number generator of distance upstream; collecting locations alternated between left and right sides of the channel so that the samples reflected the site invertebrate assemblages overall. In 2007 and 2008, samples were individually preserved in ethanol, pooled upon return to the lab, and subsampled for 500 individuals (or the complete sample) using a Caton tray sampler. Starting in 2009, samples were pooled in the field and immediately frozen using dry ice to allow for evaluation of both whole community biomass and density of each taxa. In the lab, we thawed the composited sample, mixed it to ensure random distribution of sample components and divided it in half. The half for density was preserved in ethanol and individuals were immediately identified and counted. Depending on the maturity and physical condition of the macroinvertebrates, we identified individuals to a standard level of genus; for Chironomidae, we only identified to tribe. Because freezing macroinvertebrate samples can damage fragile body parts, genus-level identification was limited for the Ephemerellidae family of mayflies and not possible for the flatworm Turbellaria. All identification and counts were converted to number of individuals per square meter.

We also quantified aquatic emergence at three treated headwater sites (GS3, UM2 and PH2) and three reference sites (GS1, UM1 and PH3). Four emergence traps (Banks et al., 2007) were set above each stream from mid-July through early August in 2010 (pre-harvest) and from late June through early August in 2013 and 2014 (post-harvest) and collected weekly. Differences in timing of the collections was due to a late storm that occurred after benthic sampling in June 2010. All adult aquatic macroinvertebrates were identified and counted. Ephemeroptera, Plecoptera, and Trichoptera were identified to genus. For consistency, the same researcher conducted all insect identifications

throughout the 10-year study.

2.3. Data analyses

2.3.1. Community analyses

To minimize potential biases in quantifying taxa diversity, we used EcoSimR 1.00 (http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html) to rarify samples to a 300-minimum count. Samples with less than 300 individuals (6 of 114) were assessed for validity and sample error; all were included after assessment.

To examine community patterns in pre- and post-harvest macroinvertebrate assemblages, we used Non-Metric Multidimensional Scaling (NMDS, R version 3.6.1, R. Core Team, 2019). We used the "vegan" package (Oksanen et al., 2020) for NMDS analyses of community structure with the Bray-Curtis dissimilarity index. All NMDS analyses used proportional macroinvertebrate abundance to reduce the influence of highly abundant taxa. Separate NMDS ordinations were constructed for each treatment group to evaluate changes in the macroinvertebrate community pre- and post-harvest at the same sites. We also performed an NMDS analysis on all the post-harvest samples to determine how the macroinvertebrate assemblages differed among sites after treatment. Beginning with a 4-dimensional NMDS, we reduced dimensionality by 1 to find a NMDS with a suitable number of dimensions to represent variation while limiting stress to <0.2. For each NMDS subset, we fit explanatory variables into the ordination space using the 'envfit' function available from the "vegan" package and ran 4999 permutations. Explanatory variables included the environmental variables of width, depth, percent shade, average daily minimum and daily maximum water temperatures in June. We also assessed correlations with explanatory variables of functional feeding groups, percent chironomid, total density, and taxa richness. Explanatory variables with a P-value < 0.05 were noted.

We performed a permutational multivariate analysis (PERMANOVA) on each NMDS subset to determine whether the invertebrate proportional communities differed pre- and post-harvest within a group, using the 'adonis' function available in the "vegan" package. We performed 999 permutations and ran the analysis with multiple set seeds to ensure consistent results. An assumption of the permutational multivariate analysis is homogenous dispersion, which we established with the 'betadisper' function prior to running 'adonis'. We performed pairwise 'adonis' analyses for each treatment group with a Bonferroni correction to adjust for multiple statistical tests performed on the dataset. An alpha-value of 0.05 was used to determine which treatment groups differed in their macroinvertebrate proportional compositions from pre-harvest to post-harvest. We used Kendall Tau correlations to determine if any particular species were likely to explain separation between samples in the NMDS ordination space.

2.3.2. Repeated measures analysis

We used repeated measures analysis to evaluate post-harvest changes in mean benthic invertebrate densities, including total, Ephemeroptera, Plecoptera, Trichoptera (EPT taxa), Chironomidae, and functional feeding groups. For each post-harvest year (2013–2016), data from harvested sites, grouped as clearcut watersheds with variable buffers and as clearcut watersheds with 12 m uniform buffers were compared after adjusting for data from the pre-harvest period and reference watersheds.

All densities were log-transformed to meet assumption of normally distributed residuals. Because we measured the same sites through time, it was necessary to include a temporal variance structure in our model to address autocorrelation within sites. Models with different variance structures were compared and the model with the lowest AIC score was selected for analysis. All models included fixed effects for years and harvest treatments.

Estimates of mean benthic invertebrate densities were calculated for each year post-harvest. We adjusted for pre-treatment conditions by subtracting the average densities over all pre-harvest years from the densities in the post-harvest year. For example:

$$\text{2013 Estimate} = (Y_{T13} - ((\overline{Y}_{T06} + \overline{Y}_{T07} + \overline{Y}_{T08} + \overline{Y}_{T09} + \overline{Y}_{T10} + \overline{Y}_{T11})/6))) - (\overline{Y}_{R13} - ((\overline{Y}_{R06} + \overline{Y}_{R07} + \overline{Y}_{R08} + \overline{Y}_{R09} + \overline{Y}_{R10} + \overline{Y}_{R11})/6)))$$

where $\overline{Y}$ = average value for that group for the indicated year, T = treatment group (clearcut_variable; clearcut_uniform) and R = reference, and the subscript number is calendar year. The Bonferroni method was used to correct the 95% confidence interval; because eight comparisons were made, 99.4% confidence intervals were used. All analyses were conducted in R (version 3.6.1, R. Core Team, 2019). The GS2 watershed that was thinned was excluded from these analyses because that treatment only occurred in one watershed.

2.3.3. Permutation analysis

We also employed a series of permutation tests to examine forest harvest effects on total macroinvertebrate densities for each harvested site. Our method was based on procedures described for paired BACI designs (Stewart-Oaten et al., 1986; Underwood, 1992) and permutation tests (Manly 2007) forming an overall approach similar to a randomized intervention analysis (Carpenter et al., 1989; Bried & Ervin, 2011). As in the paired BACI approach, the difference between the densities in treated and reference sites was calculated for each year (Stewart-Oaten et al., 1986). There were multiple references available for each treatment and for consistency, we selected two from the reference catchment, Rock Creek, and used data from an additional reference watershed within the specific catchment. Using these three references, we calculated three separate difference sets for each of the seven harvested watersheds. These served as the data used in a series of permutation tests.

The permutation tests were 1-sided tests for evaluating an increase in macroinvertebrate densities. The tests randomly assigned the annual difference data (i.e. treated minus reference) for the whole study period to either a pre- or post-treatment group. The mean annual difference was then calculated for each group and compared to the mean annual difference of all other possible reshufflings. The strength of the null hypothesis was evaluated using the proportion of permutations equal to or greater than the observed case. Watersheds with 6 years pre-treatment and 4 years post-treatment would have 210 permutations possible. Then, if there were 10 permutations equal to or more extreme than the observed instance, the exact 1-sided P-value would be 10/210 or 0.0476. To test for a lag in response or a return to pre-harvest levels during the post-harvest period, we varied both the starting year in conjunction with the number of consecutive years (1–4) in the treatment group for a total 10 tests for each treated watershed. We conducted a set of three permutation tests for each of the ten tests for each of the seven treated watersheds. To be consistent with the study design (Fig. 1), the three reference reaches used for a given test variant included the reference reach within its treatment catchment (e.g., PH3 in Pothole, GS1 in Gus, and UM1 in Upper Main), and the two reference reaches in the Rock Creek reference catchment. The combined result for each group of permutation tests was the probability of obtaining the number of permutations equal to or more extreme than the observed value from 3 independent events. This was analogous to throwing 3 dice, each representing one of the permutation test results. Thus, the exact, 1-sided P-value reported here represents the proportion of all possible combinations of three dice that were equal to or greater than the observed "dice roll" (AnyDice.com).

3. Results

Headwater stream channels in the study watersheds were steep (slopes ranged from 8% to 22%; Table 1); streams flowed over cascades underlain by primarily large cobbles and gravels. There were very few pools or other distinct habitat characteristics. Large wood was rare (Haxton 2010), likely a function of the young riparian forests and the

multiple prior fires over previous decades (Juday 1976). Wetted channel widths during sampling periods in early summer averaged 1.3 m, with a range of 0.8–2.0 m. Average watershed area was 35 ha, though one site (PH1) was much larger. The treated area of the harvested watersheds averaged 26 ha and ranged from 56 - 94% of the watershed. UM3 had the lowest proportion of area treated in 2012; that watershed contained a small recent clearcut (2005–06), a frequently-cleared powerline corridor, as well as an unharvested portion in the southwest corner (Supplemental Figure S1D). The total proportion of UM3 recently treated (including the area of powerline corridor, 2005 clear-cut, and 2012 clear-cut) was approximately 80%; the 56% listed in Table 1 reflects only the 2012 treatment. The watersheds on private land had aerial application of herbicides in 2012, and the State and private harvested watersheds were replanted with Douglas-fir seedlings during the winter of 2012. The clearcut watersheds with uniform buffers and the thinned watershed showed 1–2% change in percent shade post-harvest, similar to the background variability at reference watersheds (Table 1). Meanwhile, the percent shade at GS3 decreased from 89% to 5% and at UM2 from 95% to 75%. Average maximum June temperatures increased 4.0 and 2.5 °C, respectively. Temperatures in UM3 also increased 3.1 °C post-harvest although the percent shade only decreased to 82%. As noted in Reiter et al. (2020), beavers constructed a pond and occupied an upstream reach of UM3 during the post-harvest study period. Maximum June temperatures at reference sites also increased an average of 1.0 °C in the post-harvest period, associated with drought conditions.

3.1. Macroinvertebrate densities and richness

During the six years of sampling before harvest, we observed wide spatial and temporal variability in macroinvertebrate densities across these headwater streams (Fig. 2). Across watersheds pre-harvest, densities showed somewhat synchronous increases and decreases year-to-year with high average densities in 2007 and generally low densities across sites in 2008. The greatest site-to-site variation pre-harvest occurred in 2009. Collectors were the most numerically dominant functional feeding group with a pre-harvest average across sites of 54% (Table 2). Average percentage of shredders across sites was 19%,

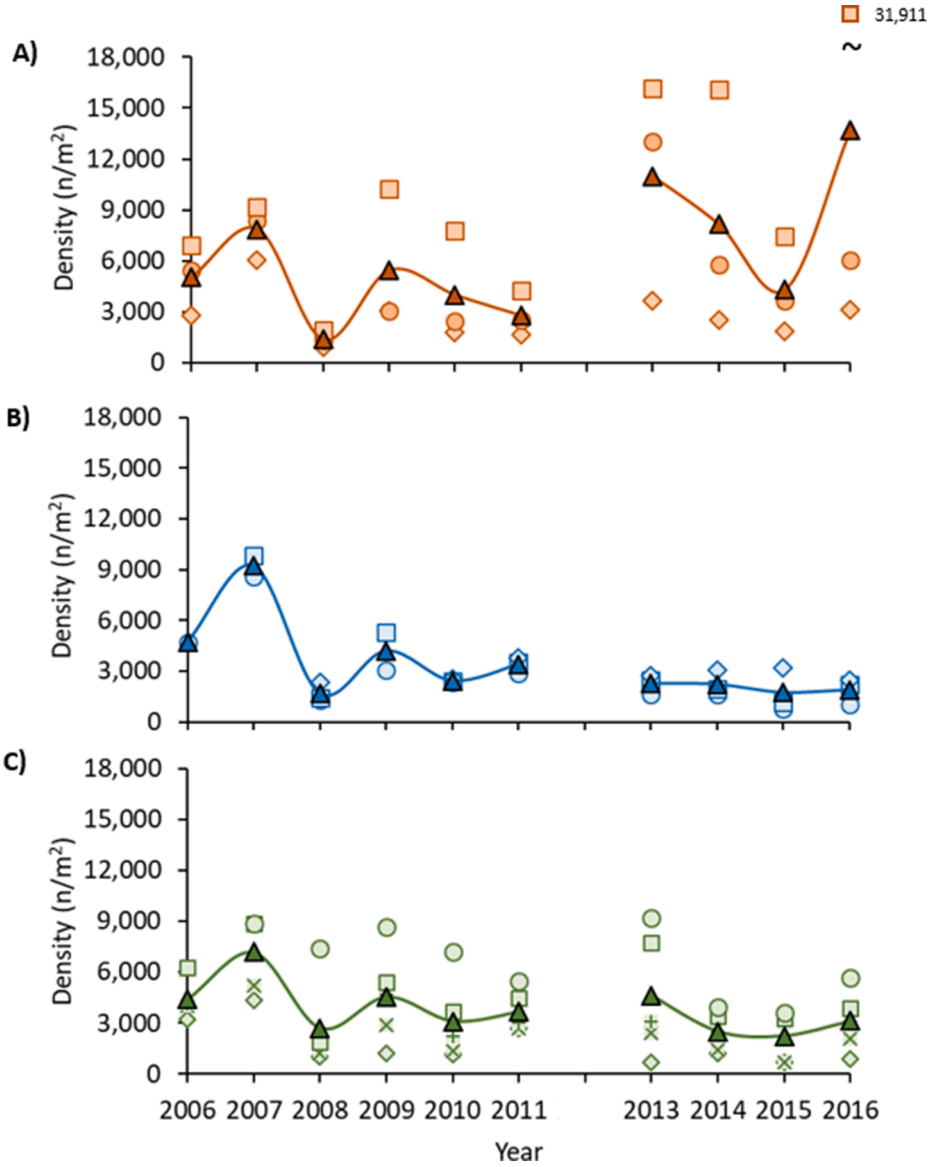

Fig. 2. Macroinvertebrate densities in clearcut and reference watersheds. A) Clearcut watersheds with variable buffers; B) Clearcut watersheds with uniform buffers; C) Reference watersheds. Average annual densities for each group are shown as triangles, connected by smoothed lines. Observed densities for sites are shown as individual points. Harvest occurred in 2012 and no sampling was conducted that year.

Table 2
Average percentage of macroinvertebrate functional feeding groups pre-harvest. The change in percentage from pre- to post-harvest are in brackets [ ]. Increases or decreases of 10% or greater are highlighted by bold text.

Watershed	WS_Buffer Treatment	Collectors	Shredders	Predators	Scrapers
GS3	CC_Variable	54% [+**19%**]	23% [−**19%**]	14% [−5%]	8% [+6%]
UM2	CC_Variable	55% [+**22%**]	15% [−7%]	8% [0%]	21% [−**14%**]
UM3	CC_Variable	51% [−1%]	26% [−2%]	14% [+2%]	9% [+1%]
PH1	CC_Uniform	50% [−3%]	21% [+5%]	13% [0%]	16% [−2%]
PH2	CC_Uniform	53% [−4%]	21% [0%]	18% [−1%]	7% [+5%]
PH4	CC_Uniform	55% [−6%]	20% [+7%]	19% [+1%]	7% [−3%]
GS2	TH_Uniform	53% [+9%]	13% [0%]	17% [−4%]	17% [−5%]
GS1	REF	51% [−6%]	29% [+4%]	11% [+5%]	8% [−3%]
UM1	REF	51% [−3%]	15% [0%]	14% [+2%]	20% [+1%]
PH3	REF	72% [−7%]	11% [+4%]	13% [+4%]	4% [0%]
RK1	REF	44% [−2%]	15% [+5%]	14% [0%]	28% [−3%]
RK3	REF	55% [−1%]	17% [+5%]	17% [+2%]	12% [−6%]

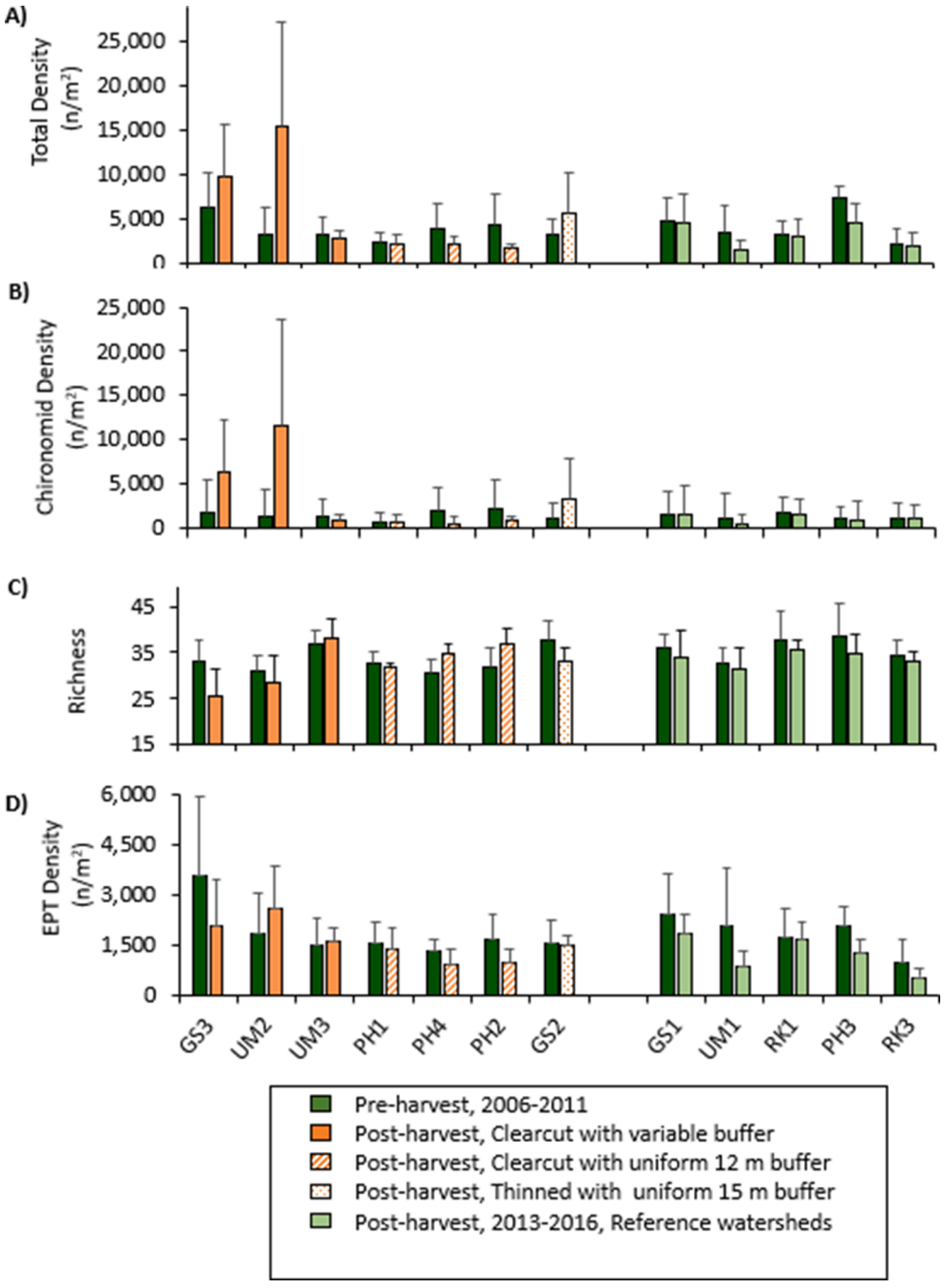

Fig. 3. Average densities and richness of macroinvertebrates pre- and post-harvest in the headwaters of the Trask River Watershed Study. A) Total density of macroinvertebrates; B) Abundances of Chironomidae; C) Taxa richness; D) Combined densities of Ephemeroptera, Plecoptera and Trichoptera (EPT). Error bars show standard deviation. Treated watersheds are displayed along x axis in increasing amount of percent shade post-harvest. GS3 had the least amount of shade after harvest.

predators 14% and scrapers 13%.

Post-harvest, average total macroinvertebrate densities substantially increased at two of the watersheds that were clearcut with variable buffers (Fig. 2A, Fig. 3A). The total densities at the clearcut-variable sites were low with small variation post-harvest (Fig. 2B). Densities at reference sites were mixed; they decreased from 2013 through 2014 and 2015 (Fig. 2C).

The increased densities at two of the clearcut with variable buffer sites involved greater densities of Chironomidae (Fig. 3B). The largest decrease pre- to post-harvest in taxa richness occurred at GS3, where richness decreased from 33 pre-harvest to 26 post-harvest while richness at PH2 increased from 32 to 37 (Fig. 3C). Post-harvest, average EPT densities decreased at GS3 and increased at UM2 (Fig. 3D). Concomitantly, the average percentage of collectors post-harvest increased at GS3 and UM2 to 73% and 77%, respectively (Table 2). Percentages of shredders and scrapers decreased at these two sites, which had the most change in stream shade after harvest (Table 1).

3.2. Comparison of benthic responses by treatment groups and individual watersheds

Macroinvertebrate assemblages at reference watersheds were similar pre- and post-harvest (Fig. 4A). Total density and temperatures were significant and associated with Axis 1, while percent chironomids were negatively associated with Axis 2. Taxa that correlated >0.35 in the NMDS ordination reflected the available stream habitat and thermal conditions in those reference watersheds (Supplemental Table 1). The silty and warmer stream conditions at PH3 likely helped structure the ordination space along Axis 1, as all PH3 samples were grouped together on the right side of the NMDS. Long-lived *Lara* beetle larvae that occur in decomposing wood, and also Nematoda and small Pisidiidae clams that reflect silty conditions, were positively correlated along Axis 1 in the direction of PH3 samples. These and other taxa correlated with the right side of reference watersheds Axis 1 prefer cool to warm eurythemic situations. The opposing end of Axis 1, where UM1 and RK1 samples occur, correlated with four mayfly species, immature Ephemerellidae, and two caddisflies; these are characteristically clingers who would use gravelly substrates found there. Axis 2 of the reference watershed NMDS was associated with several different taxa. Semi-voltine *Yoraperla* was the only taxa with a strong positive correlation along Axis 2, while Chironomidae and planktonic Harpacticoids were strongly negatively correlated with Axis 2. The RK3 and GS1 watersheds were distributed along Axis 2, suggesting that annual shifts in the relative abundance of Chironomidae, Harpacticoids, and *Yoraperla* were likely driving the positions of these samples.

After harvest at the clearcut watersheds with uniform buffers, macroinvertebrate assemblages were less variable but similar to pre-harvest communities (Fig. 4B). Density, percent chironomids and channel widths and depths were significant explanatory factors (Supplemental Table 1). The collector-gatherer chironomid, *Tanysarsini*, was strongly correlated with Axis 1, while the predatory chironomid, *Orthocladinae*, was less strongly correlated. In related analyses of invertebrate metrics, there were lower total abundances and numbers of EPT at PH4 and PH2 (Fig. 3), though richness increased slightly. GS2, which was the thinned watershed with buffers, had high chironomid density in 2016, and this sample influenced the convex hull post-harvest (Fig. 4D, Fig. 5). The centroids for the pre-and post-harvest comparison of the thinned site appeared to be distant and hulls had limited overlap, but because the stress was very low, they were not significantly different.

The most dramatic post-harvest changes occurred in clearcut watersheds with variable buffers (Fig. 4C). The post-harvest communities were significantly different than pre-harvest and multiple explanatory variables were strongly positively (density and percent chironomids) and negatively (percent shade) correlated with Axis 1 (Supplemental

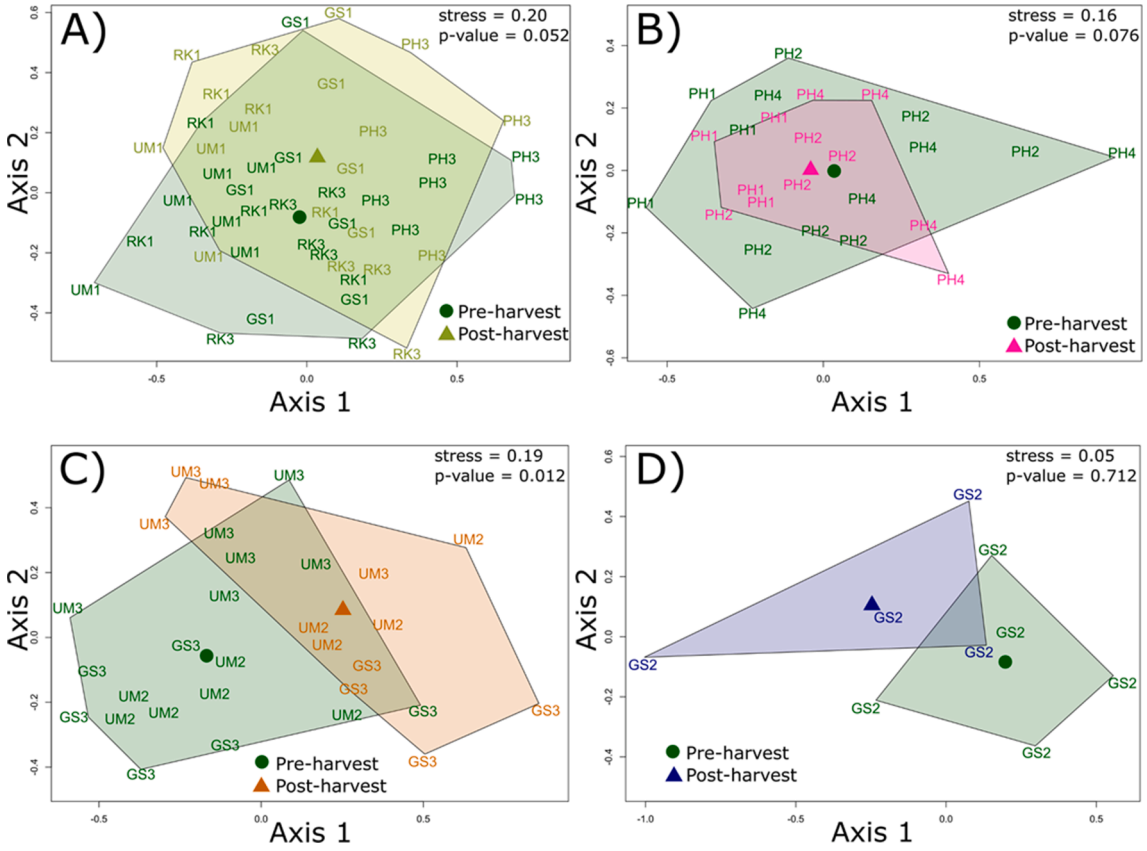

Fig. 4. Non-metric Multidimensional Scaling (NMDS) ordinations of macroinvertebrate community structure in headwater sites, comparing pre-and post-harvest periods within treatment groups. A) Reference; B) Clearcut with uniform buffer; C) Clearcut with variable buffer; D) Thinned with 15 m buffer.

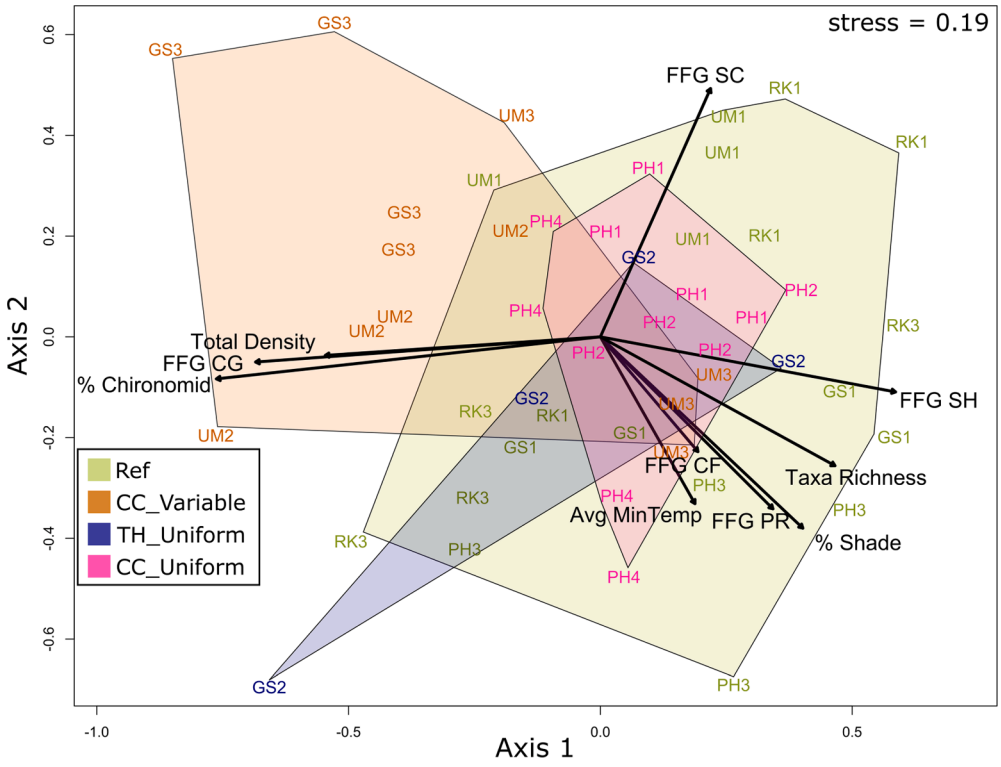

Fig. 5. Non-metric Multidimensional Scaling (NMDS) ordination of macroinvertebrate community structure in headwater sites post-harvest period for all treatment groups. Axes of significant explanitory factors overlay the convex hulls outlining each treatment group. Treatment groups shown are clearcut watersheds with variable buffers (CC_Variable), clearcut watersheds with uniform 12 m buffers (CC_Uniform), thinned watershed with uniform 15 m buffer (TH_Uniform), and reference watersheds (REF).

Table 1). *Orthocladinae* midges, with the only highly dispersive females among these taxa, were highly and positively correlated with Axis 1. Temperature was positively correlated with Axis 2, where UM3 communities clustered. P-values for several functional feeding groups were also significant and had mixed association with both axes.

The effects of harvest with variable buffers were apparent in the NMDS ordination comparing all sites post-harvest (Fig. 5). Three treatment groups (reference, thinned with buffer and clearcut with uniform buffers) had considerable overlap while the convex hull for the clearcut watersheds with variable buffers showed that GS3 and UM2 were outside the convex hulls of the other treatment groups. The biological variables significantly correlated with negative Axis 1 were percent chironomids, total density, and the functional feeding group collector-gatherers. The two tribes of chironomids were negatively correlated with Axis 1, where GS3 and UM2 occurred. In contrast, elmid beetles, predacious *Rhyacophila* caddisflies and shredder *Yoraperla* stoneflies, which are clingers with low dispersal tendencies, were correlated with positive Axis 1, where samples from reference sites occurred.

We found the distribution of sites in the ordination space (i.e. dispersion of the convex hulls) to be significantly different among post-harvest treatment groups (P-value 0.047). However, groups were not different after removing the clearcut with uniform buffers treatment (P-value 0.583). Therefore, we only consider pairwise comparisons among the reference, thinned with buffer, and clearcut with variable buffers treatments since the permutational multivariate analysis may not be capable of distinguishing differences in dispersion from differences in position. The reference and clearcut with variable buffers were significantly different (P-value 0.006) while there was no evidence for differences among the other paired comparisons of reference and thinned (P-value 0.999) or thinned and clearcut with variable buffers (P-value 0.222).

We further explored post-harvest relationships for percent chironomids and taxa richness against two significant explanatory variables, percent shade and average daily minimum temperature (Fig. 6). Except for taxa richness versus percent shade (R^2 = 0.50), correlation coefficients were very low for the comparisons. Values for percent shade, collected using densiometers at each sampling time, were clumped between 80 and 100%, except for clearcut with variable buffer sites, which were much lower.

Our evaluations of invertebrate responses also used two analyses that incorporated data from reference watersheds throughout the full study period as well as multiple years of pre-harvest data in treated watersheds. Our repeated measures analyses were designed to build on BACI sampling design to evaluate responses by treatment group for total density, and densities of chironomids, EPT and functional feeding groups. These analyses did not detect any significant differences in any test for each year post-harvest (Supplemental Table 2). No P-values were 0.05 or less; only two years had P-values less than 0.10. In 2014, the P-value was 0.06 for chironomid density at clearcut with variable buffer watersheds and in 2015, total density at clearcut with uniform buffer watersheds had a P-value of 0.08.

Using a permutation analysis, we then examined site specific responses to harvest using differences in total densities in individual harvested watersheds against multiple reference watersheds (Supplemental Fig. 2). We identified significant responses in three of the seven harvested watersheds (Table 3). In the initial year post-harvest, UM2 showed increased densities and in the second year post-harvest, in 2014, densities in GS3 significantly increased compared to reference watersheds. No post-harvest differences were detected at UM3, or at the three sites with uniform riparian buffers (Table 3). In 2016, GS2, the thinned watershed with 15 m buffer and UM2 both showed significant increases. Except for UM2 in 2013, when the period of the post-harvest analysis included a year where the individual year differences were significant, those multi-year tests tended to also be significant. For example, for GS3, tests that included the year 2014 (tests 5, 6, 8, and 10) were also significant. In UM2, all tests that included 2016 were significant. Being able to examine the timing of post-harvest responses at multiple time steps was useful in refining our understanding of the timing and duration of responses to treatments.

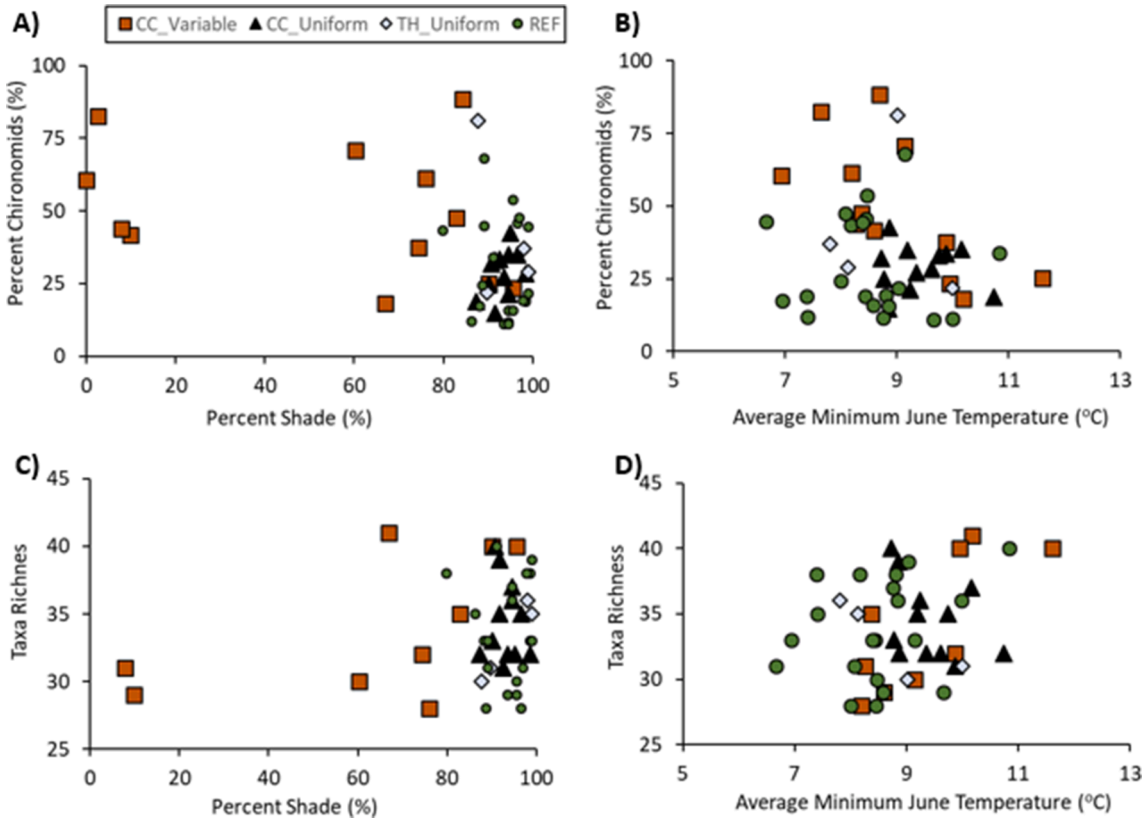

Fig. 6. Correlations for key explanatory factors for post-harvest period; A) Percent of chironomids versus percent shade; B) Percent of chironomids versus temperature; C) Taxa richness versus percent shade; D) Taxa richness versus temperature. Treatment groups are shown as different symbols: clearcut watersheds with variable buffers (CC_Variable), clearcut watersheds with uniform 12 m buffers (CC_Uniform), thinned watershed with uniform 15 m buffer (TH_Uniform), and reference watersheds (REF).

Table 3
Permutation test results of total macroinvertebrate density for the seven treated watersheds. Proportions of permutations that were equal to or more extreme than the observed value are shown for each treated watershed in columns under the watershed name (P-values < 0.025 are shown in bold; 1-sided tests). Each proportion was the combination of three separate permutation tests, each comparing ranks of differences in densities between a treated watershed and three reference watersheds. A total of 10 variations of the permutation test was conducted for each treated watershed. Each test was defined by the years indicated in column post-harvest period, with the remaining years assigned to the pre-treatment group.

Test #	Post-harvest period	Number of years in analysis	CC_Variable			CC_Uniform			TH_Uniform
			GS3	UM2	UM3	PH1	PH2	PH4	GS2
1	2013	1	0.093	**0.022***	0.093	0.341	0.867	0.835	0.624
2	2014	1	**0.001***	0.183	0.384	0.058	0.461	0.542	0.298
3	2015	1	0.817	0.133	0.384	0.898	0.757	0.115	0.624
4	2016	1	0.817	**0.001***	0.757	0.898	0.907	0.973	**0.001***
5	2013–2014	2	**<0.001***	0.062	0.040	0.031	0.865	0.720	0.521
6	2014–2015	2	**0.016***	0.295	0.264	0.376	0.751	0.245	0.458
7	2015–2016	2	0.910	**<0.001***	0.606	0.912	0.893	0.788	**0.006***
8	2013–2015	3	**0.003***	0.141	0.031	0.153	0.918	0.318	0.597
9	2014–2016	3	0.107	**0.002***	0.548	0.770	0.875	0.760	**0.006***
10	2013–2016	4	**0.008***	**<0.001***	0.142	0.575	0.971	0.845	**0.015***

3.3. Emergence

We captured summer emerging insects at a subset of sites for several years. In 2013, during the first summer post-harvest, peak emergence rates of 350 individuals/m^2/day were documented in GS3, a clearcut with variable buffer site (Fig. 7A). Maximum rates in UM2 peaked at 120 individuals/m^2/day. In 2014, peak emergence at GS3 occurred early in the summer, then declined through late June and July. Reference watersheds and a clearcut watershed with uniform buffers, PH2, had much lower peak emergence rates, from 10 to 57 individuals/m^2/day (Fig. 7B, C). Comparisons of potential changes in timing of peak emergence between pre- and post-harvest periods were not possible because pre-harvest emergence sampling was delayed in 2010.

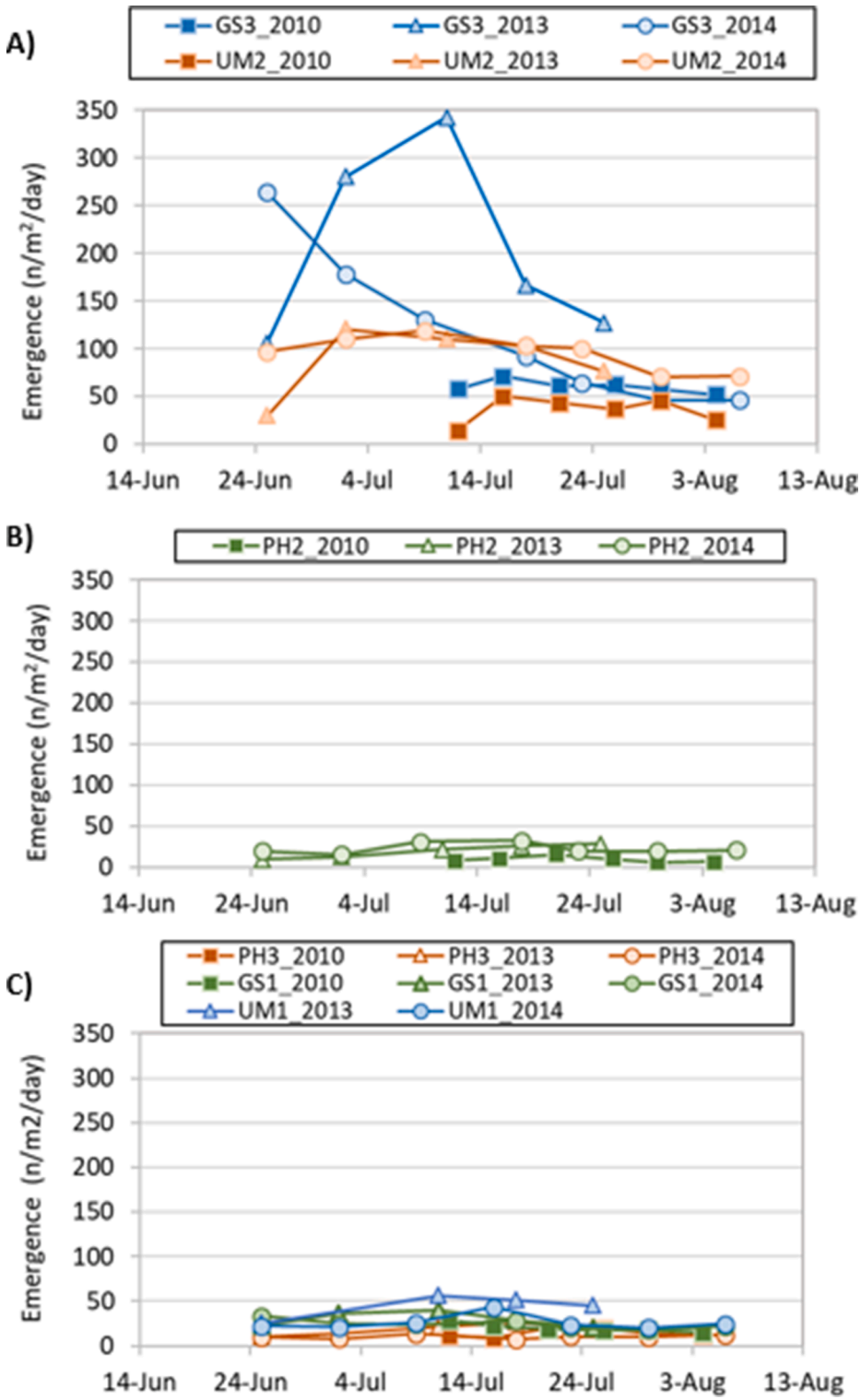

Fig. 7. Average rates of emergence of adult aquatic macroinvertebrates during summer for pre-harvest (2010) and post-harvest (2013–2014). A) Clearcut watersheds with variable buffers; B) Clearcut watershed with uniform 12 m buffer; C) Reference watersheds.

4. Discussion

Our multi-year study of twelve headwater streams in the Trask River Watershed Study before and after forest harvest revealed that major changes to riparian forests were mirrored by short-term changes to macroinvertebrate densities and assemblage structure. Retention of riparian vegetation during clearcut harvesting minimized the shifts in macroinvertebrate densities and community composition. Study of pre-harvest and reference sites over time provided additional supporting information for separating site-specific factors that influence communities from harvest responses. Evaluation of year-by-year responses showed that large changes occurred in the first and second years after harvest and that analyses that evaluate groups of multiple years have the potential to create the perception of extended duration of responses.

Similarly, responses evaluated by treatment groups can mask watershed specific harvest or environmental factors. Where riparian leave trees were retained along the downstream portion of the study reach, we found mixed responses by macroinvertebrates, which highlighted how local factors can influence outcomes from seemingly similar forest and riparian treatments.

Close links between macroinvertebrate responsiveness to disturbances in their adjacent riparian zones have been observed following harvest (Kiffney et al., 2003; Danehy et al., 2007; Gerth et al., 2022). Our findings of macroinvertebrate responses at two of the clearcut watersheds with variable buffers paralleled results of studies that observed increased numbers of benthic chironomids after harvest (Newbold et al., 1980; Chizinski et al., 2010; Reid et al., 2010; Richardson & Béraud, 2014; Danehy et al., 2021; Gerth et al., 2022) as well as greater rates of emergence (Banks et al., 2007; Moldenke & Ver Linden, 2007). Pulses of these multivoltine taxa, which comprised up to 80% of the total density after harvest, result in increased variation in year-to-year total densities. The changes in percent shade and increase in stream temperatures at the clearcut watersheds with variable buffers (Reiter et al., 2020) could have contributed to faster developmental times, leading to increased density of benthic invertebrates and high rates of emergence.

As with many macroinvertebrate studies, we observed spatial and temporal variability in the magnitude of responses to removal of riparian vegetation. Maintenance of canopy closure (Kiffney et al., 2003; Richardson et al., 2012, Jyvasjarvi et al., 2020), such as retention of 12 m riparian buffers on the three Pothole streams, was an important aspect of minimizing changes to instream conditions and macroinvertebrate communities. At most of the clearcut sites, percent shade remained above 75% and we observed minimal macroinvertebrate responses immediately following harvest, suggesting that small areas of riparian vegetation remaining next to headwater streams may be able to partially mitigate harvest impacts for macroinvertebrates. However, other site-specific factors also appeared to influence community composition in this study. Because we observed pulses of chironomids in 2016 at both GS2, where the harvest treatment was thinning with 15 m buffers, and UM2, a clearcut site, there is a strong possibility that these instances of increased density were in response to other site-specific disturbances. We noted a new toppled tree in the upper portion of the study reach at UM2 and a short section of channel switching at GS2; both of these small disturbances would have created new habitat and rearranged sediment – conditions which chironomids can quickly colonize.

When our study began, the broader Trask catchment and adjacent watersheds were covered by 45–55-year-old, second growth, Douglas-fir forests with patches of red alder trees. This portion of northwestern Oregon has had extensive prior forest harvest and repeated forest fires; in the early 1950s, there was minimal forest cover across much of this region. In this study we compare reference watersheds against watersheds recently harvested, yet our reference watersheds in the Trask catchment reflected the legacy of previous disturbances. This legacy included, among other factors, homogenous-aged young forests, limited instream wood and greatly simplified riparian vegetation communities (Haxton, 2010). Although some studies of headwater streams have shown recovery of water temperatures and nutrients 10–15 years after harvest or other disturbances (Johnson and Jones, 2000; Reid et al., 2010), others have documented strong macroinvertebrate responses continuing more than 10 years after harvest (Hawkins et al., 1982; Progar & Moldenke, 2009). The richness or species diversity in this study was low in comparison to the minimally impaired western Oregon streams studied by Herlihy et al. (2005), where richness ranged up to 71 in intensively sampled sites , and those studied by Cole et al. (2003) who noted an average richness of 45. Richness in the Trask streams was similar to that found in other headwater communities following repeated exposure to prior disturbances (Danehy et al., 2007). The spatial scale of prior disturbances and proximity to undisturbed areas are likely major factors affecting structure, function and recovery of stream communities after harvest or disturbances (Frady et al., 2007; Reid et al., 2010; Gladstone-Gallagher et al., 2019). Because large extents of forested watersheds across the northwestern and central Oregon Coast Range have been harvested repeatedly and/or burned in major wildfires few watersheds with old growth vegetation remain (Juday, 1976) and our baseline understanding of pre-disturbance community composition and richness is limited.

Having data for the full ten year study duration from both the pre-harvest period and from reference streams during the post-harvest period was crucial for evaluating the spatial and temporal dynamics of macroinvertebrate responses to forest management. Generally, streams exposed to harvest treatments across a landscape are sampled only after treatment, or only for a year or two pre- and post- disturbance. Some comparisons employ a space-for-time substitution, where pre-treatment conditions are assumed using data from nearby undisturbed sites (Murphy et al., 1981; Danehy et al., 2007; Cole & Newton, 2013; Calvao et al., 2016). Only a small number of studies have been conducted for multiple years before and after harvest (as reviewed in Richardson & Béraud, 2014; Gravelle et al., 2009). In the Trask, we employed a BACI design to integrate temporal and spatial background variability and allow us to account for year-to-year climatic differences. Given the confounding information in the literature about macroinvertebrate responses to disturbances, and because forest harvest methods in this region have been updated, we fully anticipated that the responses we were to be evaluating in this study might be small, especially in comparison to what was observed in studies of older, less restrictive forest management practices and harvest of previously undisturbed old growth forests (Hawkins et al., 1982; Stednick, 2008; Yeung et al., 2017). Our use of multiple statistical approaches facilitated our exploration of treatment groups as well as site specific responses. And even with our attention to landscape conditions, proximity of sites and background variability, we were not able to implement a fully balanced study design where all treatments were randomly assigned, and baseline conditions were homogenous. The implementation of the harvests, especially for the clearcut watersheds with variable buffers, varied due to logistics of harvest activities and landowner preferences, and this resulted in a mix of post-harvest riparian conditions and macroinvertebrate responses. And as frequently happens with field experiments over time, data only met the assumptions of parametric analyses (including normal distribution and residuals) after extensive transformation. The permutation analyses were an alternative non-parametric approach that allowed us to evaluate site-specific, year-by-year responses to harvest using multiple reference sites. Due to the inherent variation in densities, even at reference sites, the inclusion of several reference watersheds proved to be important for characterizing temporal variability, especially because the post-harvest period included a drought. The duration of responses can be masked (in the repeated measures analyses) or exaggerated (graphical comparison of means or NMDS plots) if we had only evaluated a four year response period. Comparing pre- and post-harvest results for individual sites, year by year, was useful in recognizing the resilience of headwater biota to differences in riparian management treatments (Richardson & Danehy, 2007).

Increased densities of more tolerant taxa, such as chironomids, after harvest can be accompanied by losses of sensitive taxa (Stone & Wallace, 1998; Danehy et al., 2007). Although we did not observe a statistical change in mean EPT densities, we did see a decrease of EPTs and of richness at GS3, a clearcut watershed with variable buffers, where percent shade had the greatest reduction. This was synchronous with the post-harvest increase in densities of two tribes of chironomid, which are short lived and able to respond quickly following disturbances. Other taxa have differing response windows; we observed an interesting shift of dominant stonefly taxa, which are long-lived. *Yoraperla,* which was generally the most abundant shredder at all sites, decreased at a clearcut watershed with variable buffers, while *Zapada,* which tend to be more tolerant to disturbances (Cole et al., 2003; Poff et al., 2006), increased. Other researchers have noted shifts in functional feeding groups after harvest (Hawkins et al., 1982) including increased or decreased

shredders (Stone & Wallace, 1998). As Richardson and Béraud (2014) and Lunn et al. (2017) point out, post-harvest responses are not consistent across studies, but tend to be associated with specifics of harvest, including the existing community composition, and whether there was increased detritus and slash (Haggerty et al., 2004), increased deposition of fine sediment (Kreutzweiser & Capell, 2001; Stednick, 2008) or greater algal densities (Murphy et al., 1981).

A criticism of most watershed studies is that the inference is only applicable to these specific watersheds. Indeed, the expense and time commitment limited the sample size and the taxonomic resolution of chironomids that could be studied. Our relatively small sample size, the high natural variability in year-to-year macroinvertebrate densities, and small differences in responses influenced our ability to detect treatment effects in the repeated measures analysis, which is not surprising. However, the results from the analysis of community composition and permutation analyses corroborated our interpretation that changes in macroinvertebrate density and community structure occurred where variable buffers were minimal, as reflected by changes in percent shade.

To characterize the "representativeness" of the Trask Basin, along with two other watershed studies conducted in western Oregon (Hinkle Creek and Alsea Watershed study), Bax (2008) evaluated the similarity of the watershed conditions in multivariate space. In his study, the total population of forested basins in western Oregon was defined in GIS and climate and landscape variables for each basin were used to estimate similarity to the study basins. The Trask and Hinkle paired watershed studies were found to be similar to and representative of 66% of the basins examined (2796 out of 5528). The remaining 44% of the forested areas that were not well represented by the basins basically defined the scope of nonstatistical inference which these intensively studied basins afford. Nonetheless extrapolation of results from studies at Trask and Hinkle seem plausible to a large portion of forested basins in western Oregon.

In conclusion, forest management practices around small streams in Oregon (Groom et al., 2017; Hatten et al., 2018) and broadly (Daoust et al., 2019) have changed over the past 60 years. Continuing evaluation of current harvest practices is essential if unintended consequences are to be identified and minimized. The streams through second-growth forests may have a legacy of primarily resilient species, given the spatial extent and magnitude of prior disturbances. Yet, the varied macroinvertebrate dynamics across our study sites were a measure of the responsiveness of stream invertebrates to changes in riparian resources and physical conditions. Our findings concur with those of Gerth et al. (2022) and show that where riparian buffers were retained along headwater streams, minimal shifts in macroinvertebrate densities and composition occurred. This suggests that small buffers may be key to maintenance of diverse stream invertebrate communities in headwaters and across basin networks.

CRediT authorship contribution statement

Sherri L. Johnson: Conceptualization, Methodology, Investigation, Data curation, Supervision, Project administration, Funding acquisition, Writing. **Judith L. Li:** Conceptualization, Methodology, Project administration, Writing. **Janel Sobota:** Methodology, Investigation, Data curation, Formal analysis. **Linda R. Ashkenas:** Conceptualization, Methodology, Investigation, Data curation, Project administration, Writing. **Amanda M. Pollock:** Formal analysis, Review & editing. **Mark A. Meleason:** Formal analysis, Review & editing. **Lisa Ganio:** Formal analysis, Review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119999.

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