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4 Seasonal and temporal variation in the effects of forest thinning on headwater stream benthic

5 organisms in coastal British Columbia

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18 **Abstract**

19 Removal of riparian trees can alter aquatic ecosystem structure and function by
20 influencing factors such as light availability, sediment input, and stream temperature.
21 Contemporary forest practices such as variable retention harvest are used to mitigate the effects
22 of clear-cut forest harvest on stream communities, but few studies have examined the effects of
23 these techniques on aquatic ecosystems. We examined the effects of variable retention harvest on
24 light, temperature, biofilm biomass and macroinvertebrate consumers in three coastal headwater
25 streams in British Columbia, Canada and compared them to three nearby reference streams with
26 unlogged riparian stands. Variable retention harvest increased light and stream temperature
27 variability. Harvested catchments had higher stream biofilm biomass in all seasons except winter
28 and higher invertebrate abundance in summer. Variable retention harvest altered invertebrate
29 community composition, largely driven by increasing Chironomidae abundance and decreasing
30 Simuliidae abundance. In conclusion, we found that variable retention harvest modified stream
31 benthic communities, but responses varied seasonally and among taxa. This is one of few studies
32 to investigate the impacts of variable retention harvest on multiple trophic levels over multiple
33 seasons and years. Understanding the cascading effects of forest harvest over multi-year time
34 scales is important for management decisions.

35

36 **Keywords:** timber harvest; variable retention; riparian zones; headwater streams; watershed;
37 biofilm

38

39 **1. Introduction**

40 Riparian zones are important ecotones that provide a number of ecosystem services. Riparian
41 vegetation stabilizes banks and limits sediment inputs, provides nutrients and energy to aquatic
42 and terrestrial organisms, supplies large wood to streams that dissipates energy and provides
43 habitat, and regulates microclimate and water temperature (Naiman and Décamps, 1997).
44 Therefore, the removal of riparian trees can profoundly modify the structure and function of
45 aquatic ecosystems (Vuori and Joensuu, 1996; Sabater et al., 2000; Studinski et al., 2012). For
46 example, clear-cutting riparian forests alters the size, location, and decomposition rate of woody
47 debris in streams (Bilby and Ward, 1991). This change can alter stream morphology and nutrient
48 input, affecting fish and other aquatic species (Fetherston et al., 1995).

49 One of the most significant impacts of removing riparian forests via logging is the change in
50 solar energy reaching the stream surface (Kiffney et al., 2004; Kaylor et al., 2017). The increase
51 in light has a multifold effect, causing an increase in water temperature and primary productivity,
52 which in turn can increase the biomass and abundance of higher trophic levels (Kiffney et al.,
53 2004; Danehy et al., 2007). For example, riparian logging has been shown to affect the
54 community structure of aquatic invertebrates (Murphy and Hall, 1981; Richardson and Danehy,
55 2007). In small headwater streams, aquatic invertebrates are ubiquitous and play a central role in
56 the functioning of stream and adjacent riparian ecosystems (Wallace and Webster, 1996).
57 Changes in invertebrate abundance and community composition can affect streams by decreasing
58 food availability for higher trophic levels and altering ecosystem functions such as nutrient
59 retention or litter decomposition (Suter and Cormier, 2014).

60 Headwater streams compose the upper portion of a watershed and can make up 70-80% of
61 network stream length (Leopold et al., 1964). Headwater streams are extremely important to

62 downstream reaches, providing cool water, sediment, nutrients, and organic matter to larger fish-
63 bearing rivers (Macdonald and Coe, 2007; Wipfli et al., 2007). Due to their small size, they are
64 more vulnerable than larger river sections to environmental perturbations such as changes in
65 forest cover and sediment inputs from logging or other human impacts (Benda et al., 2005;
66 Richardson et al., 2005). However, headwater streams are often overlooked compared to larger
67 downstream sections because of the difficulty of accessing and managing large and complex
68 stream networks (Gomi et al., 2002; Benda et al., 2005).

69 The use of vegetated riparian buffers has become standard practice for protecting water
70 quality and stream biota with the goal of mitigating anthropogenic disturbance to stream
71 ecosystems (Richardson et al., 2012). Buffer strips are shown to be effective at reducing the
72 impacts of clear-cutting on streams (Kiffney et al., 2003). However, the lack of disturbance in
73 these carefully managed buffers can create a habitat that is simplified to a degree that is
74 unnatural in the system (Swanson et al., 2011). More active management techniques such as
75 variable retention harvest are gaining traction as a way to minimize logging effects while
76 maintaining and promoting biodiversity within the cut site. Variable retention harvest is a
77 relatively new silviculture method designed to maintain structural diversity (such as snags,
78 coarse woody debris, and herb and shrub layers) and forest influence (i.e. the biophysical effects
79 of the forest on surrounding land) in a majority of the harvest site (Mitchell and Beese, 2002).
80 The variable retention method was first developed in the Pacific Northwestern United States, and
81 it is used as a harvesting and forest management technique by governmental organizations such
82 as the United States Forest Service and the Bureau of Land Management (Franklin and Donato,
83 2020). It has also been adopted in northern Europe and British Columbia, Canada: in British
84 Columbia about 29% of coastal public lands were harvested using the variable retention system

85 between 2006 and 2017 (Beese et al., 2019; Gustafsson et al., 2020). Variable retention harvest
86 creates “life-boating” habitat that maintains tree diversity in the cut site and allows some species
87 to persist after harvest, resulting in better maintenance of biodiversity compared to clear-cut
88 forests (Beese et al., 2019). However, little is known regarding the effects of this contemporary
89 land management practice on streams.

90 Studies on the effects of variable retention harvest have shown that increased forest cover
91 helps mitigate the effects of increased light on stream temperature, but this effect was highly
92 dependent on thinning intensity, stream morphology, and depth (Macdonald et al., 2003;
93 Guenther et al. 2014; Roon et al., 2021). Previous studies on commercial riparian thinning
94 showed little difference in biofilm or macroinvertebrate assemblages between unlogged and
95 thinned treatments, suggesting that selective cutting has less of an effect on streams when
96 compared to clear cutting or other harvesting strategies (Danehy et al., 2007; Wilkerson et al.,
97 2009). These studies show some potential for variable retention and other selective cutting
98 methods in mitigating the impacts of clearcutting. However, there is a need for more studies that
99 examine how the complex relationships between light, temperature, streamflow, biofilm
100 accumulation, and insect consumer abundance are altered by these harvesting methods.

101 The purpose of this study was to investigate the impacts of riparian forest harvest using
102 the variable retention method in headwater streams in British Columbia, Canada. We
103 investigated logging impacts on abiotic and biotic factors at several trophic levels in multiple
104 seasons and years to understand the cascading effects of logging and subsequent forest recovery
105 on headwater stream ecosystems. Our main research questions were as follows. What is the
106 extent to which increases in light from variable retention harvest increase water temperature,
107 biofilm biomass, and insect consumer abundance and biomass? How will these changes vary

108 seasonally and over time due to forest regrowth? How does the composition of insect consumer
109 taxa change with increased light availability? We predicted that increases in light due to reduced
110 forest cover would increase water temperature and periphyton AFDM, which would in turn
111 increase benthic invertebrate abundance and diversity of primary consumers because of
112 increased food. We expected the effects of harvest to be most pronounced in the summer because
113 of the combination of increased light and temperature and decreased streamflow, resulting in
114 more accumulation of biofilm and survival of insects. We predicted that these effects would be
115 largest immediately after harvest and then become less pronounced over time due to the growth
116 of riparian grasses and shrubs in the forest understory. We compared three streams with riparian
117 forests that were thinned using the variable retention method with three fully-forested reference
118 streams. We measured water temperature and biofilm biomass before and after logging and
119 streamflow and insect consumer abundance after logging. This study provides a more
120 comprehensive look into the multi-trophic, seasonal, and longer term effects of variable retention
121 forest harvest, which is important for management decisions.

122

123 **2. Materials and Methods**

124 **2.1 Study Site**

125 The experimental watersheds were located in the Malcolm Knapp Research Forest
126 (MKRF) near Maple Ridge, British Columbia, Canada, approximately 60 km east of Vancouver
127 (Table 1). The research forest lies within the Coastal Western Hemlock biogeoclimatic zone
128 (Feller, 1977). The dominant tree species are Western Redcedar (*Thuja plicata*), Western
129 Hemlock (*Tsuga heterophylla*), and Douglas-fir (*Pseudotsuga menziesii*). Black cottonwood
130 (*Populus trichocarpa*), paper birch (*Betula papyrifera*), red alder (*Alnus rubra*), vine maple

131 (*Acer circinatum*), and salmonberry (*Rubus spectabilis*) comprise most of the broadleaf riparian
 132 species. The forests in the experimental watershed have been greatly affected by humans and
 133 natural disturbances, including logging in the early 1900s and large fires in 1925 and 1931. The
 134 forest consists of naturally regenerated ~85 year old stands (Kiffney et al., 2003).

135 Climate in the study area is described as marine warm temperate rainy (Feller 1977.
 136 Between 1945 and 2007, average annual total precipitation (64 % falling as rain) measured at the
 137 research forest headquarters was 2879 mm, with a low of ~1700 mm in the 2002–2003 water
 138 year (1 Oct. – 30 Sept.) and a maximum of almost 3900 mm in 1996–1997. The elevation of the
 139 experimental watershed ranges from 135-610 m. These small (~ 0.5–1.5 m wetted width),
 140 generally steep headwater streams drain glacial soil underlain by igneous bedrock; all have a
 141 southerly aspect and are tributary to the Fraser River (Feller and Kimmins, 1979). Channel
 142 reaches consist mostly of step-pools, pools, and riffles. Stream substrates were a mix gravel and
 143 cobbles with some boulders in riffles and step-pools, with sand, gravel, and organic detritus
 144 dominant in pools and wetlands. East, Mirror, and Mike creeks also have small populations of
 145 coastal cutthroat trout (*Oncorhynchus clarkii clarkii*).

146

Stream	Treatment	Watershed area (ha)	Thinned area (ha)	Watershed logged (% area)	Summer base flow discharge (1 m ³ /s)	Elevation range (m)	Stream gradient (%)	Stream length logged (m)
East Creek	Reference	44.0	0	0	0.018	295-455	4	0
Mike Creek	Reference	25	0	0	0.005	240-310	8	0
Spring Creek	Reference	35	0	0	0.0097	135-500	4	0
Mirror Creek	Thinned	26.3	7.8	14.8	0.0035	250-320	5	137
Griffith Creek	Thinned	27.3	6.8	12.5	0.0049	370-525	13	283
Sidle Creek	Thinned	38.1	4.4	5.8	0.0031	405-610	19	233

147 Table 1. Physical characteristics of experimental reaches at Malcolm Knapp Research Forest in Maple Ridge, British
148 Columbia, Canada. 50% of the basal area was removed in each thinned section.

149 **2.2 Experimental Design**

150 Three streams were selected for each of the two treatments. Due to logistical
151 considerations, the selection of these streams was not completely random. East Creek, Mike
152 Creek, and Spring Creek were chosen as reference treatments where the riparian forest remained
153 unlogged. East Creek was chosen as a reference site because it is a long-term monitoring site,
154 while Mike and Spring creeks were reference streams for a related study (e.g., Kiffney et al.
155 2003). Mirror Creek, Sidle Creek, and Griffith Creek were harvested using the variable retention
156 method, where 50% of the basal area was removed within the cut block. This treatment involved
157 dispersed retention of single-spaced trees. Logging in Griffith Creek began in September 2004
158 and was completed in November of 2004. Logging in Sidle and Mirror creeks began in late 2004
159 and was completed in early 2005.

160 *2.2.1. Abiotic data collection*

161 We measured photosynthetically active radiation (PAR as $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at each stream
162 during each sample event using a hand-held LiCor light meter and quantum sensor (Model LI
163 250; LiCor, Lincoln, NB). Several PAR measurements were taken directly above the water
164 surface at each tile locations between 10:00 and 14:00 h under a range of weather conditions
165 (e.g. cloudy, partly cloudy, and sunny). Stream temperature was measured hourly with Onset
166 temperature loggers (Onset[®], Pocasset, MA). East Creek, one of the reference sites and Griffith
167 Creek, the variable retention site, had v-notch weirs where instantaneous water level was
168 recorded and converted to mean daily discharge (L/s). Because we only had discharge data from
169 East Creek through 2007 and Griffith Creek streamflow data from 2006 onward, we performed a

170 linear regression of discharge of the two streams and used the equation to predict discharge in
 171 East Creek for the last year of the study. East Creek and Griffith Creek had a strong linear
 172 relationship ($R^2 = 0.93$, $P < 0.001$).

173 *2.2.2. Biotic data collection*

174 Biofilm is a complex mixture of algae, bacteria, and detritus that accumulates on
 175 submerged substrates in freshwater ecosystems. We sampled biofilm using six unglazed ceramic
 176 tiles (112 cm³ each) placed in each stream and randomly distributed between pools (n = 3) and
 177 riffles (n = 3). Tiles were used instead of natural substrata to increase reproducibility and
 178 consistency within and between streams. A previous study found that unglazed tiles support algal
 179 and invertebrate communities similar to natural substrates (Lamberti and Resh, 1985). Tiles were
 180 secured to wire screens using cable ties and attached to the stream bottom using metal rods. We
 181 measured biofilm accumulation and insect abundance on tiles every 3-4 months from June 2004
 182 to April 2008. Due to logistical constraints, we were not able to sample all seasons in all years
 183 of the study (Table 2).

	Pre-harvest	Pre-harvest	Harvest	Post-harvest	Post-harvest	Post-harvest
Measurement	2002-2003	2003-2004	2004-2005	2005-2006	2006-2007	2007-2008
PAR	None	None	Spring, Summer	Fall, Winter, Spring	Spring	None
Temperature	Daily	Daily	Daily	Daily	Daily Until 03/29/07	None
AFDM	Fall, Winter, Spring	Summer	Fall, Winter, Spring, Summer	Fall, Spring	Winter, Spring, Summer	Winter, Spring
Invertebrates	None	None	Winter, Spring, Summer	Fall, Spring	Winter, Spring, Summer	Winter, Spring

184 Table 2. Seasons in each water when measurements were taken over the course of the study. Water year in the
 185 Northern hemisphere is 1 Oct to 30 Sept.

186 To quantify invertebrate abundance and biomass, we counted, measured, and identified
187 invertebrates on each tile using a hand-held 10× magnifying lens (Baush & Lomb). We observed
188 a range of invertebrate taxa including mayflies (Ephemeroptera: Baetidae and Heptageniidae),
189 caddisflies (Trichoptera: *Glossosoma* and *Neophylax*), blackflies (Simuliidae), stoneflies
190 (Plecoptera: Nemouridae), and chironomids (Diptera: Chironomidae). These insects primarily
191 feed on biofilm as collector-gatherers or scrapers (Merritt and Cummins, 1996). Although
192 invertebrates were likely lost when the tiles were removed, each tile was treated in the same
193 manner, therefore minimizing bias. Each individual was measured to the nearest millimeter and
194 the length of each invertebrate was converted to biomass using equations from Benke et al.
195 (1999). Insect taxa richness was measured as the number of different taxa observed on the tile.

196 After counting insects, we removed biofilm from the top surface of tiles by scraping with
197 a razor blade, scrubbing with a toothbrush, and rinsing into a collection vessel using distilled
198 water. The sample was then poured into a vial and frozen. In the laboratory, thawed samples
199 were filtered onto pre-combusted and pre-weighed glass fiber filters (Gelman type A/E) then
200 dried at 70° C overnight and weighed. Filters were ashed for 2–4 h at 550° C and weighed again
201 to calculate the ash-free dry mass (AFDM).

202 **2.3 Statistical Analyses**

203 To evaluate how thinning influenced stream temperature regimes, we used several
204 descriptors detailed in Benjamin et al. (2016) and Steel et al. (2017). These temperature metrics
205 were chosen to highlight different components of thermal regimes, magnitude and variability,
206 each of which have different ecological consequences (Steel et al., 2017). We used average
207 weekly average temperature (AWAT), maximum weekly average temperature (MWAT), and the

208 maximum weekly maximum temperature (MWMT) as measures of magnitude, and daily
209 temperature range as a measure of variability.

210 We conducted a before-after control-impact (BACI) analysis to evaluate the effects of
211 variable retention harvest on each stream temperature metric (AWAT, MWAT, MWMT, and
212 daily range) and biofilm AFDM using linear mixed effects models in the `nlme` package in R
213 (Pinheiro et al., 2021). Our fixed effects were season, before/after logging (BA), and logging
214 treatment. We included a random intercept by stream to account for variation between streams. A
215 significant BA and treatment interaction indicates a significant BACI effect. When models did
216 not meet the assumption of independent residuals, we fit autoregressive moving average
217 (ARMA) correlation structures to account for temporal autocorrelation in stream temperature.
218 Daily range and biofilm AFDM were log transformed to meet the assumption of normality. We
219 used the `emmeans` package to calculate pairwise temperature comparisons within each season
220 (Lenth, 2021). We also used linear mixed effects models on each stream temperature metric and
221 biofilm AFDM to test whether there was evidence of a decrease in the treatment effect over time
222 as riparian plants establish and grow, potentially thriving as more light reaches the surface. We
223 used treatment, water year, and season as fixed effects with a random intercept by stream. Only
224 post-logging data was used for this analysis.

225 We used a linear mixed model with treatment, season, and their interaction as fixed
226 effects, stream as a random effect, and log transformed biofilm AFDM as the response to
227 determine whether there were differences in biofilm AFDM between treatments in certain
228 seasons. This model was performed only on post-harvest data. This was done in addition to the
229 BACI analysis to determine how increases in biofilm AFDM in treatment streams compared to
230 natural variation between streams. To determine the relative importance of abiotic variables in

231 explaining variation in biofilm AFDM, we fit a linear model with log transformed AFDM as the
232 response, PAR, streamflow, and daily average stream temperature as the predictors and used the
233 forward selection procedure. We also tried maximum daily temperature in the model and found
234 no difference in the variance explained. We used Spearman's correlation test to explore the
235 relationships between PAR, stream temperature, streamflow, biofilm AFDM, and invertebrate
236 abundance and biomass. We used a Spearman's test because it is based on ranked data and does
237 not have the assumption of normality.

238 We did not collect pre-logging data for PAR and invertebrate abundance and biomass so
239 we could not perform a BACI analysis on these variables. Additionally, PAR and invertebrate
240 abundance and biomass deviated significantly from normality and could not be transformed to
241 meet parametric assumptions. We tested for differences between treatments using non-
242 parametric permutation tests. In addition to testing overall differences between treatments across
243 all seasons and years, we tested for differences between treatments within each season. We also
244 used randomized permutations to test for differences between treatments within each water year
245 (1 October – 30 September) to evaluate the effects of logging over time and to see whether
246 recovery of riparian vegetation had any effect on these responses.

247 Randomized permutation tests create the null distribution by reshuffling data, assigning
248 datapoints randomly to treatments, and calculating the test statistic for each random reshuffling
249 (Good, 2013). In our experiment, the test statistic of interest was the difference in mean values of
250 each tile between variable retention and reference streams. We repeated the randomizations
251 10,000 times, calculated the mean difference between groups for each randomization, and then
252 compared those randomized test statistics to our observed difference. The *P*-value was obtained

253 by calculating how many times our observed difference was larger than the randomized
254 difference and dividing it by the number of permutations (10,000).

255 Macroinvertebrates were identified at various taxonomic levels, so we divided them into
256 five groups: mayflies, caddisflies, stoneflies, blackflies, and chironomids. We used Analysis of
257 Similarities (ANOSIM) in the R 'vegan' package to test for differences in tile invertebrate
258 community composition between logging treatments (Oksanen et al., 2019). We created a matrix
259 of the abundances of each taxonomic group per tile and sampling date and analyzed whether
260 there were more similarities within or among treatment groups. To see which taxonomic groups
261 were driving differences in community composition, we used randomized permutations to test
262 for differences in the response of each group to the logging treatment.

263

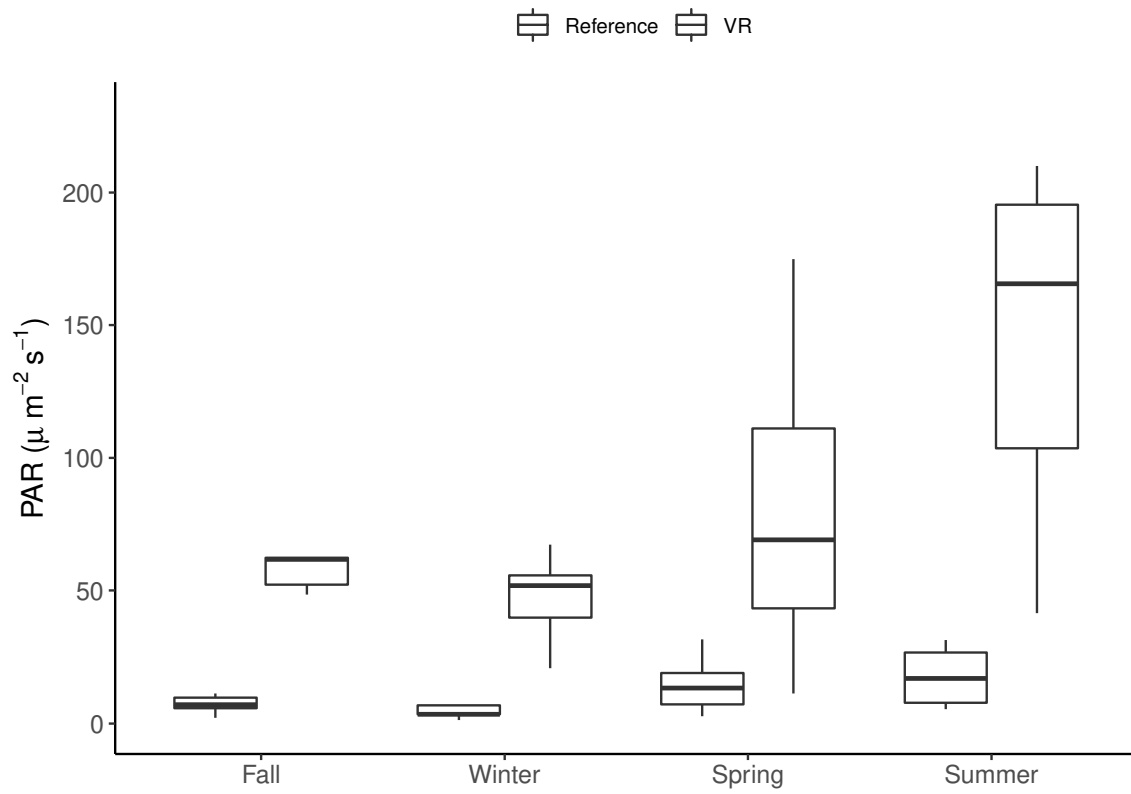
264 **3. Results**

265 **3.1. Physical Characteristics**

266 The most pronounced effect of variable retention harvest was the 10-fold higher amount
267 of light, as photosynthetically active radiation, reaching the variable retention streams ($P <$
268 0.001). PAR was 11 times higher in variable retention streams in winter, spring, and summer ($P <$
269 0.001) and 8 times higher in variable retention streams in fall ($P < 0.001$; Fig. 1). Moreover,
270 PAR was higher in variable retention streams in all and years measured (2004-2005, 2005-2006,
271 and 2006-2007; $P < 0.001$). Average weekly temperature (AWAT), average weekly maximum
272 temperature (MWAT), and maximum weekly temperature (MWMT) varied seasonally, while
273 daily temperature range did not. AWAT in the summer was $1.7\text{ }^{\circ}\text{C}$ warmer than fall ($P < 0.001$),
274 $2.11\text{ }^{\circ}\text{C}$ warmer than winter ($P < 0.001$) and $0.92\text{ }^{\circ}\text{C}$ warmer in spring ($P = 0.1$). MWMT in
275 summer was $1.5\text{ }^{\circ}\text{C}$ warmer than fall ($P < 0.01$) and $1.9\text{ }^{\circ}\text{C}$ warmer than winter ($P < 0.01$). Daily

276 temperature range had a significant treatment and BA interaction, indicating an effect of logging
277 on stream temperature variability (Fig. 2d). Pairwise contrasts show that daily temperature range
278 was higher in all seasons in treatment streams ($P < 0.01$). The statistical model indicated
279 AWAT, MWAT, and MWMT did not differ between treatments and there was no treatment and
280 BA interaction or treatment, BA, and season interaction. However, two of the streams, Griffith
281 Creek and Mirror Creek, had clear increases in all temperature metrics in the summer season
282 after logging (Fig. 2). When Sidle Creek was removed, AWAT was 1.1 °C higher, MWAT was
283 1.7 °C higher, and MWMT was 2.8 °C in Griffith and Mirror Creek in the summer compared to
284 reference. The insignificant model results indicate that the observed increases in summer water
285 temperature are comparable to between-stream and interannual variation. Additionally, stream
286 temperature did not differ by year and there was no treatment by year interaction for any of the
287 stream temperature metrics, indicating that there was no effect of vegetation recovery on stream
288 temperature over the course of the study.

289

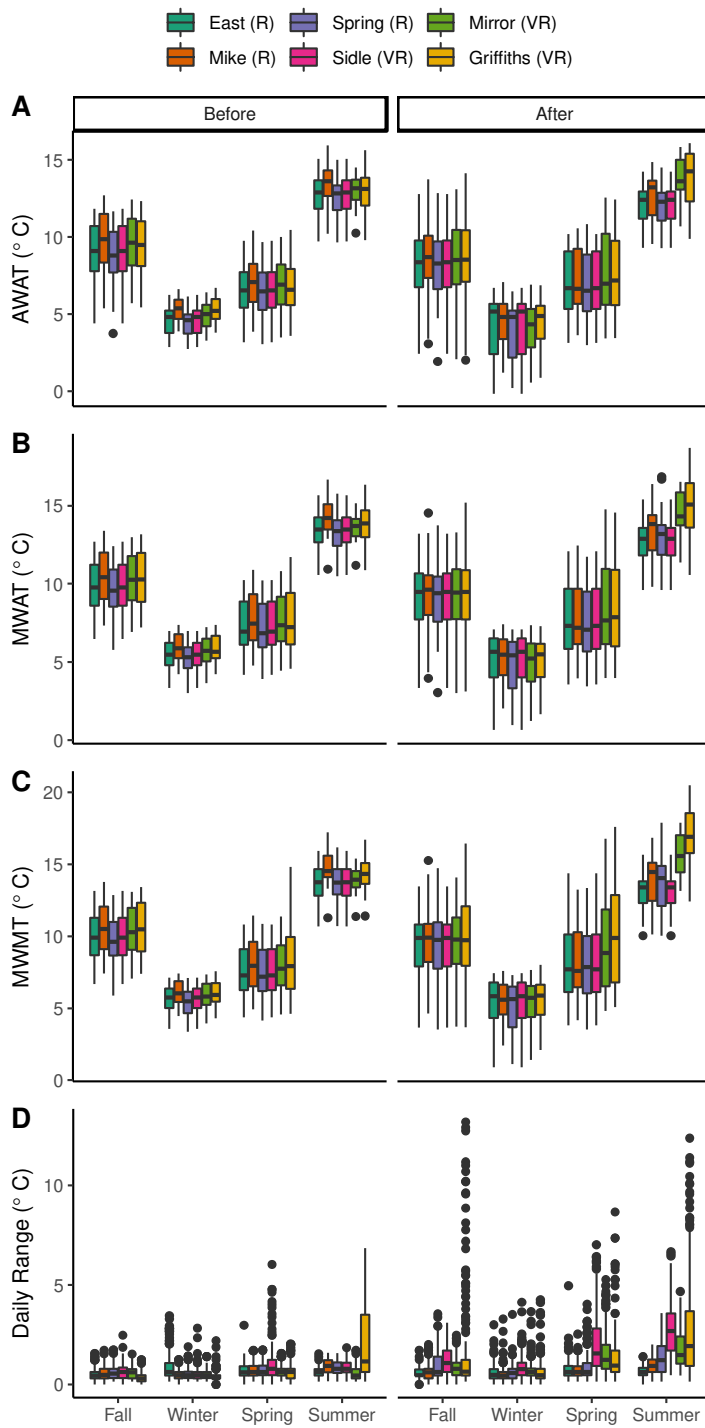


290

291 Figure 1. Photosynthetically active radiation (PAR) and timber harvest treatment by season. Includes values from all

292 post-harvest years.

293



294

295 Figure 2. Seasonal patterns of A) Average weekly temperature, B) Average weekly average temperature, C)

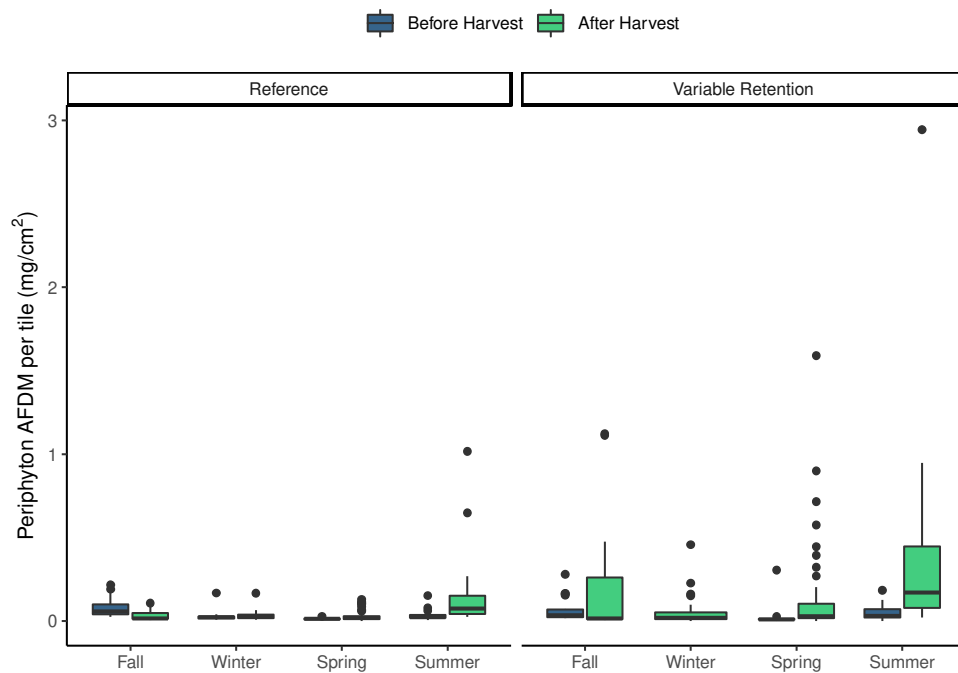
296 Maximum weekly temperature, and D) Daily temperature range for each stream. Treatments are indicated next to

297 streams in the legend (R is reference and VR is variable retention).

298 **3.2 Biological Characteristics**

299 On average, variable retention streams had three times higher biofilm AFDM than
300 reference streams. AFDM differed between seasons ($P < 0.001$) and the interaction of BA and
301 treatment was marginally non-significant ($P = 0.09$). However, post-hoc pairwise contrasts based
302 on the BACI model indicate that thinned streams had significantly higher biofilm after logging
303 ($P < 0.01$), while control streams did not (Fig. 3). The model comparing treatments using only
304 post-harvest data found no treatment effect in any season, suggesting that post-logging increases
305 in biofilm were comparable to the natural variation in biofilm biomass between streams. Biofilm
306 AFDM differed between years ($P < 0.001$), but there was no treatment and year interaction,
307 indicating that there was no effect of riparian plant recovery on biofilm biomass over time. The
308 multiple regression multiple showed that PAR, streamflow, and stream temperature were
309 important in explaining variation in biofilm biomass, explaining almost 50 % of total model
310 variation ($R^2 = 0.49$, $F_{3,149} = 49.47$, $P < 0.001$). PAR, average daily temperature, and streamflow
311 all had a positive effect on biofilm AFDM. PAR explained the most variation in biofilm AFDM
312 ($R^2 = 0.40$, $P < 0.001$), followed by average daily stream temperature ($R^2 = 0.21$, $P < 0.001$),
313 then streamflow ($R^2 = 0.03$, $P = 0.04$).

314



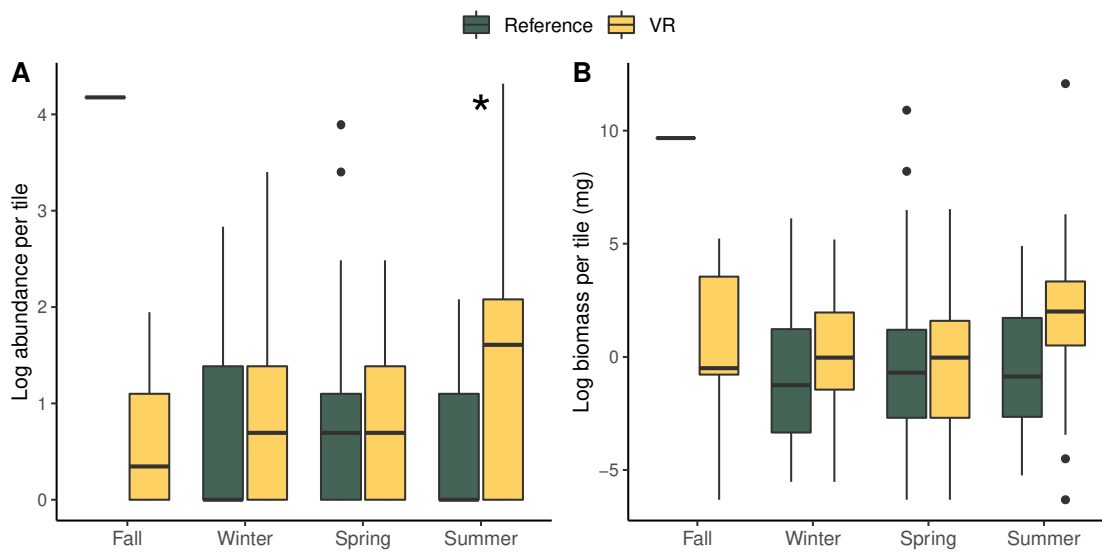
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316 Figure 3. Seasonal differences in biofilm AFDM on each tile in streams before and after logging.

317 Invertebrate abundance and biomass did not differ between treatments when pooled
 318 across seasons, but responses varied seasonally. Mean invertebrate abundance in variable
 319 retention streams was approximately three times higher in the summer ($P < 0.001$), while there
 320 were no differences in other seasons (Fig. 4a). Differences in abundance between treatments also
 321 varied by water year. Abundance was slightly higher in reference streams in the 2006-2007 water
 322 year ($P = 0.02$), but there were no treatment differences in other years (2004-2005, 2005-2006,
 323 and 2007-2008). There were no differences in average invertebrate biomass or total biomass
 324 between treatments in any seasons or years (Fig. 4b). Taxa richness also showed no response to
 325 logging when averaged over seasons and years but did show a response in some seasons and
 326 years. When data were pooled across years, mean taxa richness was 22.5 times higher in variable
 327 retention streams in the fall ($P < 0.001$). However, sample size was small in fall, and we only
 328 observed one taxon in the reference streams (Fig. 5), so this difference was only slightly over one

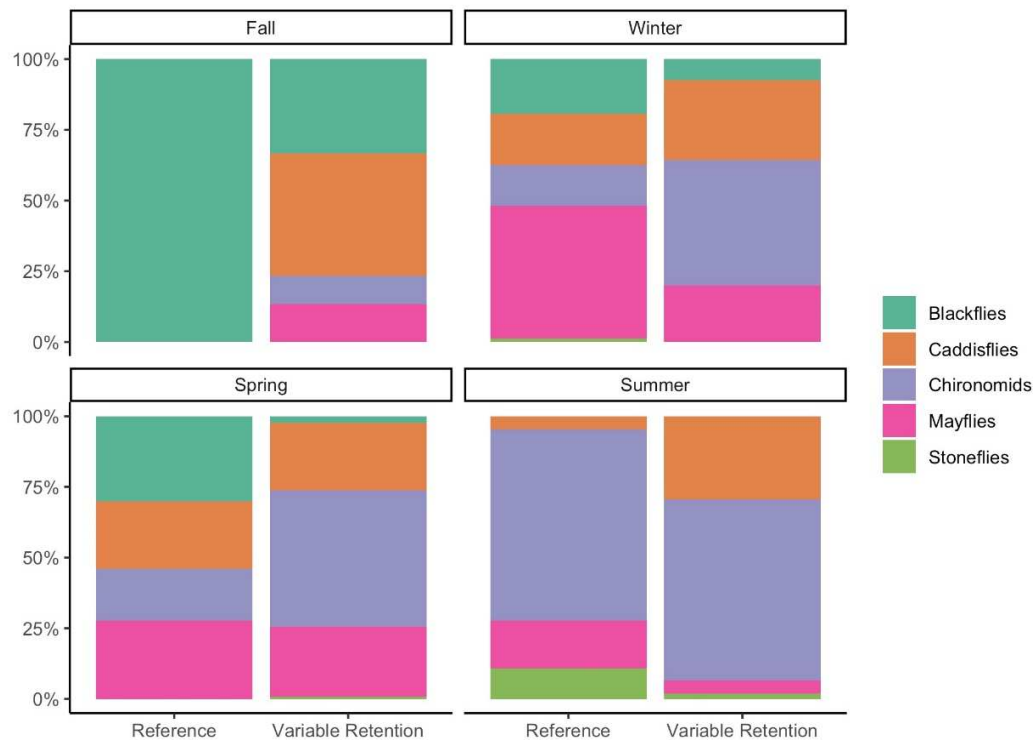
329 species per tile (1.25 in variable retention streams compared to 0.06 in reference streams). Taxa
330 richness was significantly lower in harvested streams in the 2004-2005 water year ($P = 0.01$) and
331 was higher in harvested streams in the three subsequent years (2005-2006, 2006-2007, and 2007-
332 2008), but high variability limits our inference regarding these differences ($P = 0.11$; $P = 0.056$;
333 $P = 0.11$).

334



335

336 Figure 4. Seasonal differences in A) Invertebrate abundance and B) Invertebrate biomass in reference and variable
337 retention (VR) streams. Data include all years post-logging. Stars indicate significant within-season differences
338 between treatments.

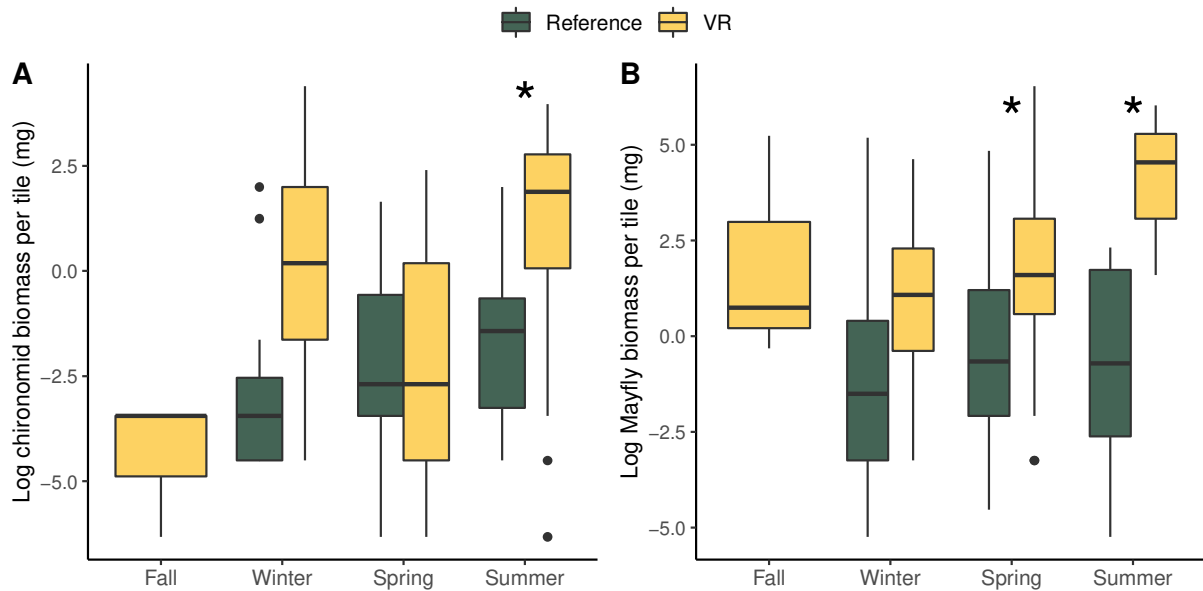


339

340 Figure 5. Seasonal percent composition of invertebrate taxa in variable retention and reference streams.

341 The results of our ANOSIM showed that invertebrate tile community composition in
 342 variable retention streams was different relative to the reference treatment ($R = 0.31$, $P = 0.001$;
 343 Fig. 6). Our analyses of individual taxa suggest that the shift in community composition was
 344 largely driven by changes in chironomid and blackfly abundance in harvested streams. In terms
 345 of taxon-level responses, Chironomid abundance ($P < 0.001$), total biomass ($P < 0.001$), and
 346 average biomass ($P < 0.001$) were higher in variable retention streams compared to reference
 347 streams (Fig. 6a). Correlation analysis showed that chironomid abundance was positively
 348 correlated with PAR ($\rho = 0.23$, $P < 0.001$) and biofilm AFDM ($\rho = 0.16$, $P < 0.001$) as well as
 349 mean ($\rho = 0.07$, $P = 0.04$) and maximum ($\rho = 0.09$, $P < 0.01$) daily stream temperature. There
 350 was no difference in mayfly abundance between treatments, but mayfly total biomass ($P < 0.001$;
 351 Fig. 6b) and average biomass ($P < 0.001$) were higher in variable retention streams. There was a

352 five-fold but marginally non-significant decrease in the abundance of blackflies in the thinned
353 treatment ($P = 0.1$; Fig. 5).



354
355 Figure 6. Seasonal differences in A) Chironomid biomass B) Mayfly biomass in reference and variable retention
356 (VR) streams. Data include all years post-logging. Stars indicate significant within-season differences between
357 treatments.

358
359 PAR was positively correlated with all of the daily stream temperature metrics, and most
360 strongly correlated with MWMT. PAR had a weak positive relationship with biofilm AFDM and
361 invertebrate abundance. Streamflow had a weak but significant positive correlation with
362 invertebrate biomass. Stream temperature was positively correlated with biofilm AFDM, with
363 maximum daily temperature and daily range having the strongest relationship with AFDM.
364 There was a positive relationship between temperature range and invertebrate biomass and a
365 weak relationship between biofilm AFDM and invertebrate abundance and biomass (Fig. 7).

378 variable retention harvest is a method that leads to smaller changes in the stream environment
379 and associated benthic communities compared to clear-cutting (Kiffney et al. 2003).

380 **4.1 Abiotic Variables**

381 The ten-fold increase in light was the direct result of the removal of riparian vegetation,
382 as solar flux reaching the stream surface is largely influenced by stream width, tree height, and
383 canopy density (Lhotka and Loewenstein, 2006). Compared to the Kiffney et al. (2003) study on
384 the effects of riparian buffer treatments, the relative increase in PAR reaching the variable
385 retention streams was smaller than clear-cut (58x) and the 10 m (16x) buffer treatment, but larger
386 than the 30 m buffer treatment (5x). This is likely because variable retention harvest involves
387 cutting trees closer to the stream edge. The increase in biofilm AFDM after logging suggests that
388 the light increase in variable retention streams had an effect on primary productivity. Primary
389 productivity is primarily limited by light in small heavily shaded forested streams (Richardson
390 and Danehy, 2007; Hill and Fanta, 2008). However, there was a relatively weak correlation
391 between PAR and biofilm AFDM, especially compared to results of previous studies on riparian
392 logging (Kiffney et al., 2003), potentially due to a smaller treatment effect in variable retention
393 streams compared to clear-cut or buffered or reduction of biofilm accrual by stream invertebrate
394 consumers.

395 The effect of variable retention harvest on stream temperature was minimal and
396 seasonally dependent. The most pronounced effect of harvest on stream thermal regimes was an
397 increase in stream temperature variability, which may be due to a reduction in the ability of this
398 habitat to regulate the microclimate (Moore et al., 2005). Increases in stream temperature
399 variability due to riparian thinning have been observed in other studies (e.g. Roon et al., 2021)
400 and can have biological consequences such as changing the emergence time of fish and other

401 organisms (Steel et al., 2012). The lack of significant BACI results for other metrics suggest the
402 temperature increases we observed in some streams and seasons (see Fig. 2) are comparable to
403 the temperature variation between streams. A previous study on one of the same treatment
404 streams, Griffith Creek, found an increase in temperature compared to reference streams
405 (Guenther et al., 2014). In our study, Griffith Creek was the variable retention site with the
406 largest change in stream temperature magnitude and variability followed by Mirror Creek, with
407 no change in Sidle Creek (Fig. 2). One possibility explaining this discrepancy in responses may
408 be due to the steepness of Sidle Creek relative to the other two streams, which may limit the
409 influence of solar heating on stream water. These among-site differences in the temperature
410 response to thinning suggests that the effects of variable retention harvest is dependent on local
411 conditions and highly variable between streams within the same treatment. These site-specific
412 effects of thinning on stream temperature regimes have been observed previously (Roon et al.,
413 2021), suggesting that evaluating the best forest management strategy must be done on a case by
414 case basis. However, variable retention harvest seems to have less of an impact on stream
415 temperature than buffer systems, as Kiffney et al. (2003) observed an 3 °C and 1.6 °C increase in
416 10 m and 30 m buffer treatments, respectively, compared to reference streams.

417 Although two of the variable retention streams had a 1.1 °C increase in average temperature in
418 the summer, none of the observed temperature increases were significant due to high variation in
419 responses between streams. This suggests that variable retention harvest has a smaller effect
420 stream temperature regimes than the buffer method.

421 In agreement with a variety of studies in larger streams, our results suggest that
422 streamflow is important in structuring headwater stream communities. Streamflow was
423 negatively associated with both water temperature and biofilm AFDM. Because we were not able

424 to measure streamflow in all streams and used data from one stream as a proxy for the others,
425 this association could be stronger than our study detected. However, we do not think streamflow
426 confounded our results for the following reasons. First, these sites were close in proximity and
427 the climate and precipitation did not differ between them. Second, the stream gradients were
428 higher in treatment streams, which would cause faster flows and thus greater scour and decrease,
429 not increase, the biofilm biomass in those streams. Because of these reasons, we believe the
430 differences in biofilm AFDM are attributable to the effects of the logging treatment.

431 **4.2 Biotic Variables**

432 Our data did not support the prediction that biofilm AFDM or stream temperature would
433 decrease over time due to the recovery of riparian plant assemblage. This is likely because the
434 time frame of our study was not long enough to observe the effects of forest recovery on stream
435 benthic communities. Because both temperature and biofilm AFDM are related to PAR, and
436 PAR is largely determined by canopy cover (Kaylor et al. 2017), the growth of underbrush that
437 likely occurred in the short term was not enough to reduce the amount of light reaching the
438 stream. However, we were unable to determine whether PAR decreased over time because of
439 limited sampling in the final years of the study. A previous study on the long-term effects of
440 clear-cut logging on streams found that it took 16 years for stream macroinvertebrates to fully
441 recover (Stone and Wallace, 1998). Future studies should explore whether the rate of stream
442 recovery is faster in forests harvested with the variable retention method than forests that are
443 clear-cut or buffered (Warren et al., 2016; Kaylor et al., 2017).

444 Stream biofilm increased after logging in all seasons, most likely due to an increase in
445 PAR reaching the stream. Results from previous studies on the effects of riparian thinning on
446 biofilm or periphyton (the autotrophic component of biofilm; Suberkropp, 1998) biomass have

447 been mixed. One study found that streams with thinned riparian reserves had higher periphyton
448 AFDM than streams with clear cut and buffer treatments (Danehy et al., 2007) while another
449 study found no difference in periphyton between thinned and reference streams (Wilkerson et al.,
450 2010). The relative increase that we observed is similar to the AFDM increase in streams with 30
451 m buffer treatments in Kiffney et al. (2003). In the summer season, variable retention streams
452 had twice the biofilm AFDM than control streams, while Kiffney et al. (2003) observed a 6-fold
453 increase in periphyton AFDM in clear-cut streams and a 3-fold increase in streams with a 30 m
454 buffer. However, there was high variation in AFDM between sites in our study.

455 Variation in the response of biofilm to logging may be caused by site and seasonal
456 variation in light, temperature, and geomorphology; limitation by consumers; differences in
457 nutrient availability; or variation in thinning intensity (Hillebrand, 2002; Roon et al., 2021).
458 Important site characteristics that may influence how logging influences stream light flux are
459 gradient, channel confinement, substrate composition, and aspect. For example, light flux to high
460 gradient, confined streams may be less affected by riparian thinning because of topographic
461 shading. Studies on the effects of riparian buffer systems have found that biofilm increases with
462 decreasing buffer widths and is strongly influenced by light (Kiffney et al., 2003; Wilkerson et
463 al., 2010). However, we speculate local site attributes can have a large influence on the relative
464 change in headwater stream light conditions associated with forest harvest.

465 We observed a seasonal increase in invertebrate abundance, which was positively
466 correlated with both stream temperature and biofilm (Fig. 6). Stream temperature increases can
467 accelerate invertebrate growth and development, which may increase productivity (Patrick et al.
468 2019). Additionally, previous studies have shown that stream invertebrates and vertebrates that
469 consume biofilm are often limited by food resources (Townsend 1981, Feminella and Hawkins,

470 1995; Quinn et al., 1997), so increased primary productivity would be expected to increase the
471 abundance of consumers that feed on stream biofilm. We did not measure the impact of logging
472 on other invertebrate functional feeding groups, but previous studies have shown that shredder
473 abundance decreases with forest loss due to reductions in leaf litter input, while other groups
474 (gathering-collectors, filtering-collectors, and predators) do not experience changes in percent
475 composition (Moraes et al., 2014; Brand and Miserendino, 2015).

476 The difference in invertebrate abundance and community composition between the
477 reference and variable retention treatment was largely driven by an increase in the absolute and
478 relative abundance of chironomids. Chironomids are the most widely distributed and abundant
479 invertebrate in freshwater systems (Pinder, 1986) and they are often used as a proxy to monitor
480 water quality due to the sensitivity of some taxa to environmental change (Rosenberg, 1992;
481 Brooks and Birks, 2004; Engels et al., 2020). Chironomids are also key sources of energy for a
482 variety of species ranging from fish to ducks to songbirds (e.g., Einarsson et al., 2004). The
483 increase in chironomid abundance and biomass in response to logging has been observed in
484 several studies (Kiffney et al., 2003; Nislow and Lowe, 2006; Martel et al., 2007). Chironomids
485 have life-history strategies that are advantageous to colonizing disturbed habitats, such as strong
486 dispersal, rapid juvenile development, short generation times, and synchronized emergence
487 (Verberk et al. 2008). Additionally, they are generalists and can live off of a variety of food
488 sources (Gurtz and Wallace, 1984). Chironomid abundance was positively correlated with
489 biofilm AFDM, suggesting that chironomids were responding to increased food resources.
490 Chironomid abundance was also positively correlated with PAR and stream temperature. It is
491 difficult to disentangle the effects of these environmental variables, but previous studies suggest

492 that light is more important than stream temperature in structuring invertebrate communities
493 (Kiffney et al. 2004).

494 We also observed a five-fold reduction in blackfly abundance in harvested streams.
495 Although blackfly abundance was highly variable between sampling events and streams, this
496 effect was consistent across seasons (Fig. 5). Blackflies play a key role in stream ecosystems as
497 filterers of suspended organic matter, making nutrients available for other aquatic invertebrate
498 species that feed on them (Ciadamidaro et al., 2016). Variable retention harvest was also
499 associated with an increased mayfly biomass. Previous studies have attributed increases in
500 mayfly biomass after logging to increased food availability (Wallace and Gurtz, 1986) or
501 increased stream temperature (Imholt et al., 2010). Increased stream temperature has also been
502 associated with accelerated emergence time, which could impact adult fecundity (Harper and
503 Peckarsky, 2006). However, we did not find an association between mayfly biomass and
504 temperature or biofilm AFDM.

505 Changes to macroinvertebrate communities can alter ecosystem function in headwater
506 streams (Cao et al., 2018). Macroinvertebrates provide a number of ecosystem services,
507 including providing food for fish and other vertebrates, retaining nutrients for the stream and
508 surrounding forest, and helping maintain healthy amounts of organic matter (Suter and Cormier,
509 2014). The dominance of chironomids and reduction of the relative abundance of other species
510 could alter nutrient transport and ecosystem function in harvested streams (Cao et al., 2018).
511 Additionally, increases in mayfly biomass and earlier emergence time could have far-reaching
512 effects, such as increased predation and reduced fitness (Harper and Peckarsky, 2006).

513 Average taxonomic richness in variable retention streams was 22.5 times higher than
514 reference streams in fall. Some studies have observed increases in macroinvertebrate species

515 richness due to logging, likely because of increased primary productivity and water temperature
516 (Stone and Wallace, 1998), while others have observed decreases (Newbold et al., 1980).
517 However, we had a small sample size in the fall and only observed one invertebrate taxa in
518 reference streams, so it is unclear whether this difference is ecologically important. It is also
519 important to note several limitations to our measure of taxa richness. First, our taxonomic
520 resolution was coarse (family to order-level), second, our tile method largely selects for biofilm
521 consumers and does not capture the diversity of other functional feeding groups, and third, we
522 were unable to use a diversity index due to the large number of tiles with zero or only one
523 individual. Therefore, this measure does not take into account the relative abundance of each
524 taxonomic group, only the number of unique taxonomic units.

525 Previous studies on the effects of riparian thinning have found no differences in
526 macroinvertebrate assemblages or abundances between reference and thinned streams (Danehy et
527 al., 2007; Wilkerson et al., 2010). These studies had higher stand retention (60%-70%) and only
528 sampled at one point in the year (late spring-early summer), both possible reasons why they
529 obtained different results. Additionally, in the Danehy et al. (2007) study, there was no logging
530 within 15 meters of the stream edge. Kreutzweiser et al. (2005) found that low-intensity selective
531 logging (29% removed) had no detectable effect on insect communities in streams, while
532 medium intensity logging (42% removed) increased invertebrate abundance. However, these
533 changes were similar in magnitude to interannual changes in the reference site over the course of
534 the five-year study. Studies on the effects of riparian buffers have found that invertebrate
535 abundance increases with decreasing buffer width, and a 30 m buffer is necessary to prevent
536 significant changes in macroinvertebrate communities (Kiffney et al., 2003; Sweeney and
537 Newbold, 2014).

538 An important caveat of our invertebrate results is because we did not have pre-logging
539 data for our invertebrate measures, we are unable to distinguish between differences due to
540 logging and underlying site variation. It is possible that observed differences are due to stream-
541 level variation in insect abundance, diversity, and/or community composition rather than the
542 effects of logging. However, because we performed BACI analyses on biofilm and stream
543 temperature, which are positively correlated with invertebrate measures, we believe it is likely
544 that these differences are attributable to logging impacts.

545 **4.3 Management Implications**

546 Our results suggest that variable retention harvest has a smaller effect on streams than
547 clear-cut harvesting. Studies have shown that clear-cut harvest results in large alterations in light,
548 temperature, primary productivity, and insect consumer abundance and diversity (Kiffney et al.
549 2003; Danehy et al. 2007; Wilkerson et al. 2010). Previous studies have found that 30 m buffer
550 sites can prevent the effects of timber harvest on streams (Kiffney et al., 2003; Sweeney and
551 Newbold, 2014). Comparing our results with previous studies on buffer width suggests that
552 variable retention harvest causes larger changes to stream abiotic and biotic factors than the 30 m
553 buffer treatment. This makes sense considering that variable retention harvest involves cutting
554 trees closer to the stream edge. However, the effects of harvest were highly variable across
555 seasons and sites, with the largest effect in summer when there is low streamflow and high light
556 levels and temperature. Important considerations for determining the best logging practice
557 include species composition and demographics, the size of the area harvested, location and size
558 of sensitive areas like wetlands, the magnitude of the impact on downstream reaches, and the
559 speed of regrowth and recovery. Variable retention harvest may be the most effective approach

560 for limiting changes to streams and forests while preserving biodiversity and promoting
561 regeneration in regions that regularly undergo natural disturbance (Martínez-Pastur et al. 2020).

562 Riparian ecosystems often undergo natural disturbances such as landslides, windthrow or
563 wildfires that create light gaps fueling stream productivity and promoting forest regeneration,
564 habitat heterogeneity, and species diversity and abundance (Kiffney et al., 2004; Kreutzweiser et
565 al., 2012; Warren et al. 2016). In the absence of natural disturbance (e.g. in a carefully managed
566 riparian buffer), habitats can become homogenized (Swanson et al., 2011). An alternative
567 approach to riparian forest management is finding a logging method that mimics natural
568 disturbance, but also maintains economic viability in the long term (Kreutzweiser et al., 2012).
569 The variable retention logging method results in many of the characteristics that promote
570 diversity in habitats recovering from natural disturbance, such as increased spatial heterogeneity
571 and light availability (Swanson et al., 2011; Beese et al., 2019; Franklin and Donato, 2020).
572 Additionally, structural retention results in higher carbon storage and sequestration compared to
573 clear cut forests (Nunery and Keeton, 2010). Future assessments of the impacts of various
574 logging practices on riparian systems should consider not only how they compare to alternative
575 management practices or unharvested reserves, but also how they compare to natural disturbance
576 events in that system and how they influence climate resiliency (Dymond et al. 2015).

577 **5. Conclusion**

578 Our study demonstrated that variable retention logging had the largest effects on PAR
579 and biofilm AFDM, which were consistently higher in harvested streams year-round. Stream
580 temperature and invertebrate abundance and richness only responded to the effects of logging
581 during specific seasons. Additionally, the invertebrate response to logging was taxa-specific,
582 with only mayflies, chironomids, and blackflies showing changes in abundance and biomass.

583 Based on the results of previous studies, variable retention harvest can have a smaller effect on
584 stream communities than clear-cut harvest and 10 m buffers and a similar effect to the use of 30
585 m buffer strips (Kiffney et al. 2003, Danehy et al., 2007). However, more direct comparisons of
586 the effects of buffer systems and variable retention harvest on stream dynamics over time are
587 needed.

588

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600 **Authorship contributions**

601 P. Kiffney: Designed the study and helped collect data. Kiffney advised on data analysis and contributed to
602 writing and editing the manuscript.

603 J. Griffith: Conducted data analysis and led manuscript preparation.

604

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