

# Long-term effects of wildfire on stream macroinvertebrates

Master Thesis

Master of Science in Biology / Ecology

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# Statement of Authorship

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Zurich, 30<sup>th</sup> June 2015

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## Abstract

Contrary to past assumptions, recent studies have shown that increasing severity and frequency of fires along with a warming climate drive shifts in vegetation from boreal forest to grassland steppe, emphasizing the need to understand the long-term response of stream ecosystems to fire. In the northwest USA, many streams fringed by conifers burned with high severity, retaining an open canopy even 10-15 years postfire. We hypothesized that the higher light availability to these streams results in increased abundance, biomass and production of macroinvertebrates relative to streams with greater canopy cover. We tested this hypothesis using a nested, multi-factor “snapshot” analysis of 12 streams along a gradient of fire history and canopy cover, and with repeated sampling, a comparison of two paired streams that both burned with high severity in 2000 but exhibit contrasting riparian recovery. Canopy cover was negatively correlated with macroinvertebrate abundance and biomass among the 12 streams. Additionally, *r*-strategist taxa such as Chironomidae and Baetidae correlated positively with light availability. In the two-stream comparison, biomass was greater in the stream with higher light availability. Secondary production of macroinvertebrates was higher in the stream with higher photoactive radiation and corresponded with chlorophyll-*a* concentration of primary producers. The results suggest that fire severity, but especially the trajectory of riparian vegetation recovery and associated canopy and light input, play an important role in mediating long-term responses of stream food webs to wildfire.

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## Introduction

Global climate change is a topic receiving increased attention over the last few decades; many studies have been dedicated to it and many models have predicted ecological effects of climate change. Dale et al. (2000) suggested that disturbances, climate change and forests interact very closely. Disturbance type and characteristics such as frequency, affected area, intensity, seasonality, and duration often depend on weather and climate in addition to site characteristics. The most common disturbances in boreal forests are increasing drought periods, insect outbreaks and wildfire. At a broad scale, drought related die-offs due to prolonged water deficits are often spatially extensive and mainly in species with limiting climatic factors (Allen et al. 2010). At a fine scale, drought induces forest defragmentation and often interacts with insect outbreaks and competition (Allen et al. 2010). Trees respond with reduced leaf function, deformed tree structure, altered regeneration patterns and even death (Dale et al. 2000, Allen et al. 2010). Warmer climates can shorten insect reproduction time, e.g., up to twofold (Berg et al. 2001), resulting in higher frequency and duration of insect outbreaks (Kurz et al. 1995). Increasing rate of herbivory and damage, and insect outbreaks can lead to tree mortality, which decreases forest carbon uptake or even increases emission from decaying dead trees, turning carbon sinks into carbon sources (Kurz et al. 2008).

The effect of fire has been extensively studied, as it is the third but perhaps most important disturbance regime, and the easiest to interfere with and manage. In the northwest USA, the frequency and intensity of wildfires have dramatically increased since 1980 (Westerling et al. 2006), causing what appears in some regions to be a vegetation shift from conifer forest to grassland steppe (Davis et al. 2013). Fire severity will likely increase with further global warming and the fire season can be up to 20 days longer in the future (Flannigan et al. 2013), thus understanding the effects of fire and developing strategies for vulnerable habitats are essential. The National Fire Plan (USDA, 2000) developed goals and strategies to reduce fuels in high-risk areas, rehabilitate fire-damaged sites and protect vulnerable communities. However, many of the action items have not been tested and their ecological consequences are uncertain. Fire size and severity is mostly related to physical and climatic variables such as wind, atmospheric humidity and temperature, fuel moisture, fuel type and topography (Turner et al. 1994). Climate change affects disturbance regimes, which

influence the global carbon cycle by deforestation. These impacts can lead to positive feedbacks to the global climate system (Dale et al. 2000, Kurz et al. 2008).

Global and human threats impacting ecosystems are greater for freshwater than terrestrial ecosystems (Dudgeon et al. 2006). Freshwater ecosystems are essential for the sustainability of the human population and present a rising challenge as only a small fraction of these ecosystems is accessible and more than half of those renewable freshwater sources are already used up (Polunin 2008). Although rivers and streams only comprise about 1% of the global freshwater availability (Polunin 2008), they are important for natural global cycles, transporting nutrients and water to the sea, as well as for human use as drinking water, irrigation, energy, harvesting source (fishery) and transportation (Allan 2007). Even though cumulative effects of human activities such as land use and management have a large impact on stream ecosystems (Dwire et al. 2003, Marcarelli et al. 2010), stream ecosystems are better studied isolated from any human impacts to better understand the ecosystem reaction to disturbances and natural variation.

Climate change can influence stream ecosystems directly through hydrological alterations, including higher frequency of winter floods, decreased summer base flows, reduced snowpack and earlier snowmelt, as well as indirectly through wildfire that leads to altered ecosystem types, reduced forest cover and increased water temperature and nutrients (Davis et al. 2013). Freshwater ecosystems are particularly vulnerable to climate change and disturbances due to the fragmented nature of habitats, the limiting dispersal abilities of inhabiting species, and climate-dependent water temperatures (Woodward et al. 2010). Owing to these specificities, streams and their streamside riparian vegetation form an ecosystem that reacts differently to disturbances than most forested terrestrial ecosystem. Due to topographic position, the proximity to surface waters and saturated soils, riparian areas form a microclimate with vegetation often better adapted to fire and drought disturbances than adjacent slope forests (Kauffmann et al. 1989, Kauffmann et al. 1990, Dwire et al. 2003).

Wildfires are a natural disturbance, which affect terrestrial and stream ecosystems through the riparian linkage (Dwire et al. 2003, Davis et al. 2013). The severity of a fire mostly depends on the amount of vegetation removed. While high-severity fires burn understory and crowns in a large area, low-severity fires burn less area and mostly understory (Malison and Baxter 2010). Stream-riparian response to wildfire can vary in time and is categorized into four stages corresponding to the time elapsed since the last disturbance event

(Minshall et al. 2004): while immediate (time of burning until a few days later) and short-term (a few days to the first year, usually at spring-runoff) effects have been shown to include pulses in light and nutrient inputs to streams, much less is known with respect to the mid-term (one to 10 years post-fire) and long-term effects (occurring decades or centuries later) of wildfires. Initially, stream-riparian ecosystems were expected to return to pre-fire conditions (Minshall et al. 2004, Goetz et al. 2007). However, subsequent research has shown that wildfire results in increased primary production, biomass and abundance of benthic invertebrates as well as altered community structure up to 5 years post-fire (Malison and Baxter 2010, Rugenski and Minshall 2014). This suggests that some ecosystems might not recover, but rather shift to a new ecosystem state with increased productivity and abundance of disturbance-adapted species (Rugenski and Minshall 2014). Wildfire can affect an ecosystem at many different organizational levels of the food web (Spencer et al. 2003, Woodward et al. 2010). After the removal of riparian vegetation by fire, light and nutrient flux, and warmer stream temperatures stimulate autotrophic productivity (Davis et al. 2013). The effects of wildfire on stream macroinvertebrate communities have been reported as shifts in communities from leaf litter shredders and grazers to generalist feeders that have high larval dispersal capability (Mihuc and Minshall 1995, Spencer et al. 2003, Vieira et al. 2004). Furthermore, macroinvertebrates may increase in abundance and biomass as a short- to mid-term post-fire response (Mihuc and Minshall 1995, Malison and Baxter 2010). This may have important consequences for aquatic vertebrates, which are strongly dependent on the available food and habitat structure. For example, Dunham et al. (2003, 2007) reported that tailed frogs and rainbow trout were able to persist in a habitat that remained changed many years post-fire, but fish species with narrow habitat requirements in degraded and fragmented habitats were more vulnerable to fire-related disturbances, in addition to the threat of invasive species and human influences. Increased insect emergence after severe fire along with habitat change may lead to an increased number of terrestrial predators such as tetragnathid spiders, bats and birds (Malison and Baxter 2010, Jackson et al. 2015). Most research of post-fire responses has focused on one species rather than interactions between species. Additionally, there is still a lack in knowledge regarding the long-term effects of wildfire.

My thesis focuses on stream macroinvertebrates because they serve as an important link between primary producers and vertebrates in stream food webs, as well as prey for terrestrial insectivores. My research was part of a broader, multi-trophic level study aiming to investigate the mid- to long-term effects of wildfire on stream ecosystems with a focus on

several trophic levels (periphyton, benthic invertebrates and fish) and trophic interactions, as well as to provide inputs for management strategies for vulnerable communities. We conducted our research in the Frank Church River of No Return Wilderness in Central Idaho, USA, 14 years after a severe, stand-removing fire, to assess the effects of wildfire without the influence of other human activities.

My research questions were:

- 1) Does photoactive radiation influence the abundance and biomass of macroinvertebrate communities?
- 2) Does potentially high primary production lead to increased secondary production of macroinvertebrates?
- 3) Does post-fire response of stream ecosystems affect the community composition of stream macroinvertebrates?

I hypothesized that high light intensity reaching the stream, after fire removed riparian vegetation, leads to increased biomass and abundance of macroinvertebrates (Malison and Baxter 2010). Through the bottom-up effect, higher levels of light availability should lead to increased primary production of periphyton and therefore increased secondary production of macroinvertebrates.



## Methods

### Study Area

The Frank Church River of No Return Wilderness is located in central Idaho, USA, and is part of the Northern Rocky Mountains (Figure 1). A wilderness in the USA is legally defined as an area that has not been modified by anthropogenic activities such as construction of roads, pipelines or agriculture (US legal). The Taylor Wilderness Research Station is located at an elevation of 3800 m a.s.l. and is only accessible by single engine airplane from Cascade (~70 air miles) or Challis or on foot, starting at the trailhead 35 miles upstream. Big Creek is a sixth-order tributary of the Middle Fork of the Salmon River with a catchment area of 1540 km<sup>2</sup>, a mean elevation of 2117 m a.s.l., and mean precipitation of ca. 400 mm, although elevation and precipitation are highly variable due to the mountainous terrain. The majority of the annual precipitation occurs as winter snow, resulting in peak flows from late spring through mid-summer as snow runoff. The streams generally remain near baseflow from late summer through autumn. Primary vegetation on forested slopes is Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*) and aspen (*Populus tremuloides*). Additionally, open areas of grass and sagebrush (*Artemisia* spp.) are common on drier slopes, in combination with bare soil and rock (20-30% of the surface area). Primary riparian vegetation consists of alder (*Alnus* sp.), dogwood (*Cornus canadensis*), chokecherry (*Prunus virginiana*), serviceberry (*Amelanchier alnifolia*), willow (*Salix* spp.), hawthorn (*Crataegus douglasii*), birch (*Betula nigra*) and mountain maple (*Acer glabrum*).

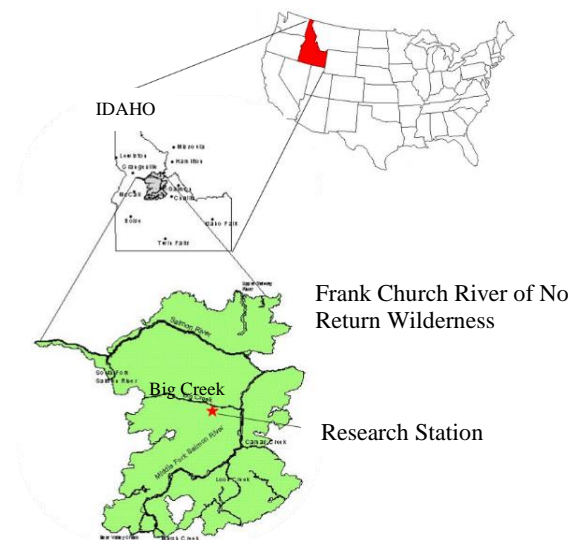
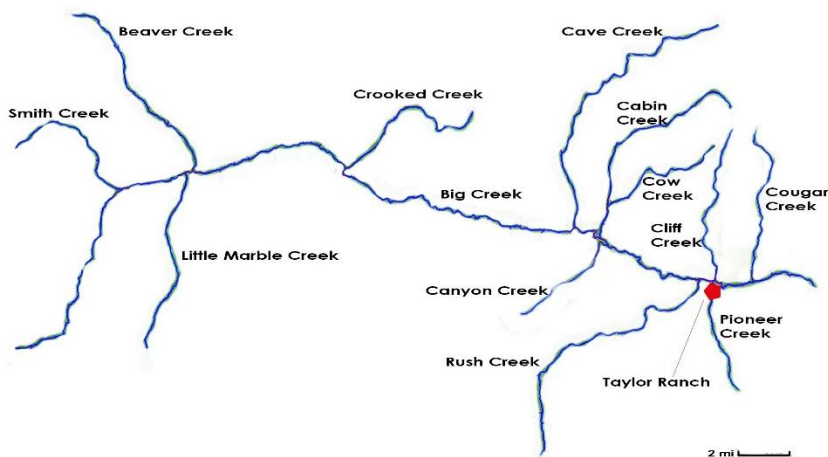


Figure 1. Location of the research station

Third order, north facing Pioneer Creek (Rugenski and Minshall 2014) and second order, south facing Cliff Creek are located at the same elevation with their confluence into Big Creek being about 100m apart (Figure 2), although on opposite sides of Big Creek. Discharge (0.3 m<sup>3</sup>/s) and slope (7-8 %) were approximately the same for both tributaries. Both streams burned severely in 2000. In a smaller fire in 2006, only Cliff Creek burned, while Pioneer Creek remained unburned. Predominant riparian vegetation at Cliff Creek is alder (*Alnus* sp.), river birch (*Betula nigra*) and willow (*Salix* spp.), whereas Pioneer Creek is

mostly bordered by alder (*Alnus* sp.), river birch (*Betula nigra*) and dogwood (*Cornus canadensis*). Aspect, riparian species and fire history results in a canopy coverage difference of 20% (90% at Pioneer Creek vs. 68% at Cliff Creek).

The Diamond Peak Fire, a particularly large, stand-replacing fire, burned a large portion of the Big Creek catchment in the year 2000. Some of the tributaries affected by the fire have been monitored annually as part of a long-term study (see Rugenski and Minshall 2014 for details) that started in 1988 examining natural variation in montane wilderness streams. Cave, Cabin, Rush, Cliff, and Pioneer Creeks had high severity burns while Cougar Creek remained unburned (Malison & Baxter, 2010) (Figure 2). Between 2005 and 2010, several smaller fires burned the riparian vegetation of some of these streams again, while others had time to recover, resulting in a gradient of light (solar radiation) intensities among these streams.



Additional to the creeks mentioned above, the basin wide study included the severely

**Figure 2.** Tributaries of Big Creek that were sampled for the basin wide study. Cliff and Pioneer Creeks at the location of Taylor Ranch were part of both basin wide and two-stream comparison studies.

burned Beaver, Canyon, Cow, Crooked Creeks and the unburned Little Marble and Smith Creeks (Table 1). The study was biased towards severely burned areas as only a few unburned Big Creek tributaries were within walking distance from the research station. Additionally, because this was a collaborative study involving three trophic levels, study streams were chosen that were large enough to have fish. Study reaches were 200m long and located in the lower part of each tributary within 300m from the Big Creek confluence to facilitate access by hiking.

*Paired-stream comparison*

We sampled Pioneer and Cliff Creeks every 14 days from June 15 until August 11, 2014. The study reaches were identical to those sampled annually for 26 years as part of the long-term monitoring program. We measured multiple environmental parameters following methods from the long-term monitoring (Davis et al. 2001). Once a month, we measured photoactive radiation (PAR) with a light meter (LI-250A, Licor), width and depth, and estimated canopy coverage with a densitometer. In addition, from June 18 until August 18, 2014, we deployed sondes (data loggers) for measuring temperature, conductivity and oxygen. Between June 18 and July 10 2014, some data of Cliff Creek are missing because the data logger was out of water, so the data were only comparable in the latter two months of the data recording.

Periphyton samples were collected by scrubbing three random rocks at each of the five sampling sites and preserving 10ml of water containing the periphyton solution in Lugol's solution (all five replicates combined) for analysis of chlorophyll-*a*. By filtering the other part of the water onto Millipore membrane filters, one for each replicate, biomass as ash free dry mass (AFDM) could be evaluated according to a standard protocol (Davis et al. 2001). For macrozoobenthos, we took five replicates from random locations within riffles every ~50m along the study reach using a Surber sampler (0.09m<sup>2</sup> area, 250µm mesh size; Aquatic Research Instruments, Hope, Idaho). To avoid sampling effects of disturbance produced by the sampling method itself, we took the samples haphazardly a number of meters up- or downstream of the transects used for the long-term monitoring study. Further, the alternating weeks between two sampling dates were used to snorkel the entire stretch for the fish study, which presents a disturbance to the stream bed, but because of the consistency was neglected in the analysis. Macroinvertebrates were preserved in 70% ethanol and transported to the lab for identification.

In the lab, we split the samples with sieves into large (>1mm) and small organisms (<1mm, >250µm). The small-fraction was usually split into halves, quarters or eighths with a splitting device, so that each subsample consisted of at least 120 individuals. For further calculations, the fraction identified was extrapolated to the whole Surber sample. Under 4X magnification, we identified invertebrates to the lowest level possible, usually genus (Adams et al. 2004) and measured their length by placing millimeter paper under the petri dish.

Means of biomass, using the mass-length regression (Benke et al. 1999), abundance and taxonomic richness were calculated for both tributaries. For the taxa *Baetis*, Elmidae larva and *Epeorus longimanus*, I established cohorts with size-frequency graphs and estimated their growth rate and secondary production (Benke et al. 1984). For the other common taxa occurring in both streams, literature derived P/B ratios (Bellmore et al. 2012) were used to estimate secondary production.

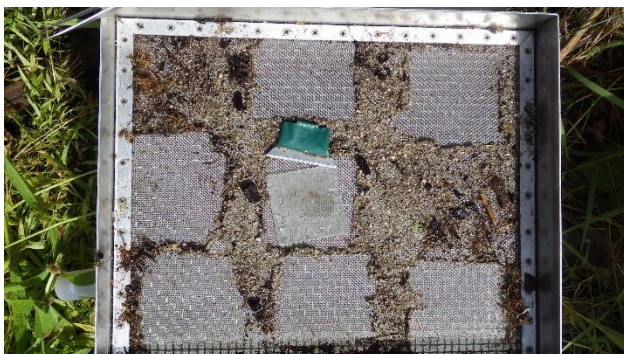
### *Basin wide study*

For the basin-wide study, we selected 12 tributaries of Big Creek (Figure 2). All were second or third order streams, and they encompassed a gradient of variable fire history, riparian canopy recovery, and light input. Rush, Smith and Canyon Creeks had relatively low canopy coverage (<40%), whereas Cliff, Cougar, Cow and Pioneer Creeks had relatively high canopy coverage (>70%). Beaver, Little Marble, Crooked, Cave and Cabin Creeks had intermediate canopy coverage (45-60%). In each stream, the study reach was 200m long and selected according to GPS coordinates from previous studies in this area (E. Davis, unpublished). Several environmental variables were measured or estimated (Table 1). We measured width and depth at three transects at a distance of 100m in between. At the same transects, we estimated relative canopy coverage with a densiometer, which were averages of four measurements (up- and downstream, river left and -right), and slope with a clinometer. Elevation was extracted from GPS. Velocity was coarsely estimated by measuring the time a small piece of wood took to float a stretch of 10m. This procedure was repeated three times and was used to calculate discharge at each respective transect. Substrate heterogeneity was evaluated for the whole study reach, approximately every 2m, measuring the b-axis and embeddedness (classes: 0 = 0%, 1 = 0-25%, 2 = 25-50%, 3 = 50-75%, 4 = 75-100% embedded) of a haphazardly picked rock at a randomly generated percentage (distance) from one bank.

Creek	Order	Elevation (m)	Coverage (%)	Discharge (m <sup>3</sup> /s)	Slope (%)	Substrate size (m)	Burn class	Time since burn (year)
Beaver		1534	56	3.5	3	0.2	Severe	14
Cabin		1229	49	1.1	3	0.1	Severe	6
Canyon		1247	28	0.1	9	0.1	Severe	14
Cave	3	1229	57	0.6	5	0.1	Low	6
Cliff	2	1214	69	0.3	7	0.2	Severe	8
Cougar	3	1184	80	0.2	9	0.1	Severe	8
Cow		1337	86	0.1	7	0.1	Severe	6
Crooked		1393	47	0.7	5	0.1	Severe	14
Little Marble		1565	53	1.8	2	0.1	Unburned	
Pioneer	3	1221	89	0.3	8	0.1	Severe	14
Rush	3	1181	25	1.7	3	0.1	Low	8
Smith		1653	36	1.7	6	0.2	Unburned	

*Table 1. Measured or estimated environmental variables for the 12 streams.*

We collected zoobenthos with a Surber sampler and combined three Surber samples, taken within a distance of 20m, into one composite sample to get a better representation of the actual assemblage of macroinvertebrates for each stream. For each stream, we took three composite samples approximately every 100m. After transferring the composite sample into a Caton sub-sampler (Figure 3), we removed subsamples for identification, following a rapid bioassessment approach developed and applied for this study (Giersch 2001, unpublished). For subsamples, we used a plastic square of 6x6 cm, scraped off the biomaterial around it and transferred the material into a small white pan for identification to family level. We estimated lengths and measured the large individuals (>10mm). This resulted in a “snap shot” analysis, in that each tributary was only sampled once at the beginning of August (all streams within two weeks).



*Figure 3. Caton with sub-sampled squares.*

*Statistical analysis*

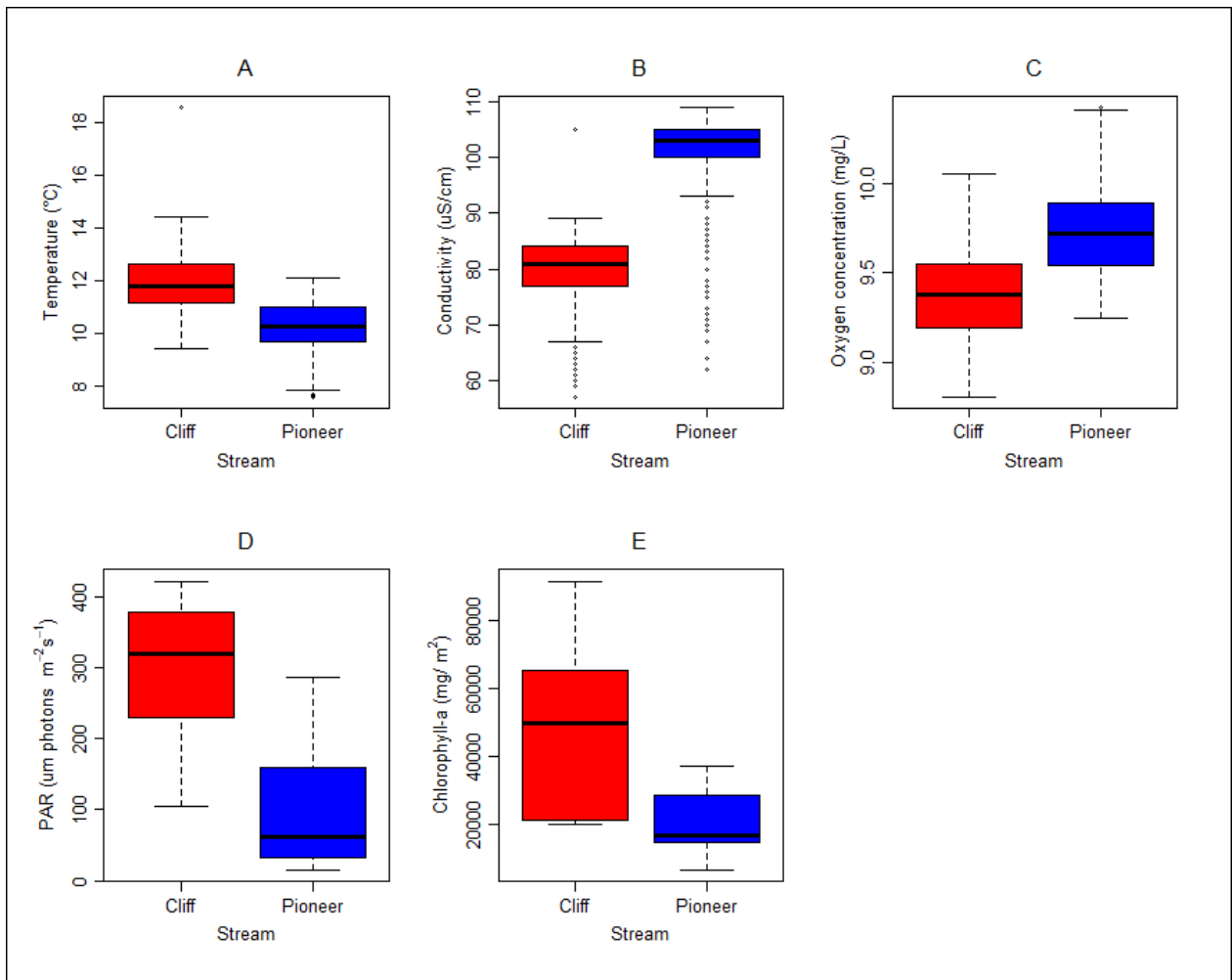
For the production study, differences between the two streams were analyzed with a two-sample t-test. To test if abundance or biomass changed over time, we performed an ANOVA. P-values <0.05 were considered significant.

To increase statistical power for the basin wide analysis, abundance and biomass were not averaged for each stream, but all samples from each of the three transects of each stream were treated as replicates (n = 36). Environmental variables, however, had to be averaged for each stream as some were point measurements taken at transects and others, such as substrate heterogeneity, involved many measurements along the entire study reach. Additionally, the composite Surber sample approach precluded analysis of macroinvertebrate responses within specific habitat types (e.g. pools vs. riffles), but this was justified by the fact that the research question was more focused at the reach-ecosystem scale than the habitat unit scale. Correlation analysis showed a strong correlation of slope, discharge, water depth and substrate embeddedness. We reasoned that more light would lead to more periphyton biomass, and that this might lead to more invertebrate biomass, but also higher biodiversity as new ecological niches might open up (Minshall 2003). Therefore, we tested the effect of canopy coverage, and other explanatory variables such as elevation, on Simpson and Shannon diversity. Because of the high number of explanatory variables, a principle component analysis (PCA) was performed, but resulted in components that did not explain much due to the mixture of variables that were all equally important. Thus, the linear models of the original environmental variables were tested individually with ANOVA. Statistical analyses and graphical data presentation were performed with R (version 3.1.1) and Microsoft Excel 2013 (Microsoft corporation, Redmond, WA, USA).

## Results

### *Paired-stream comparison*

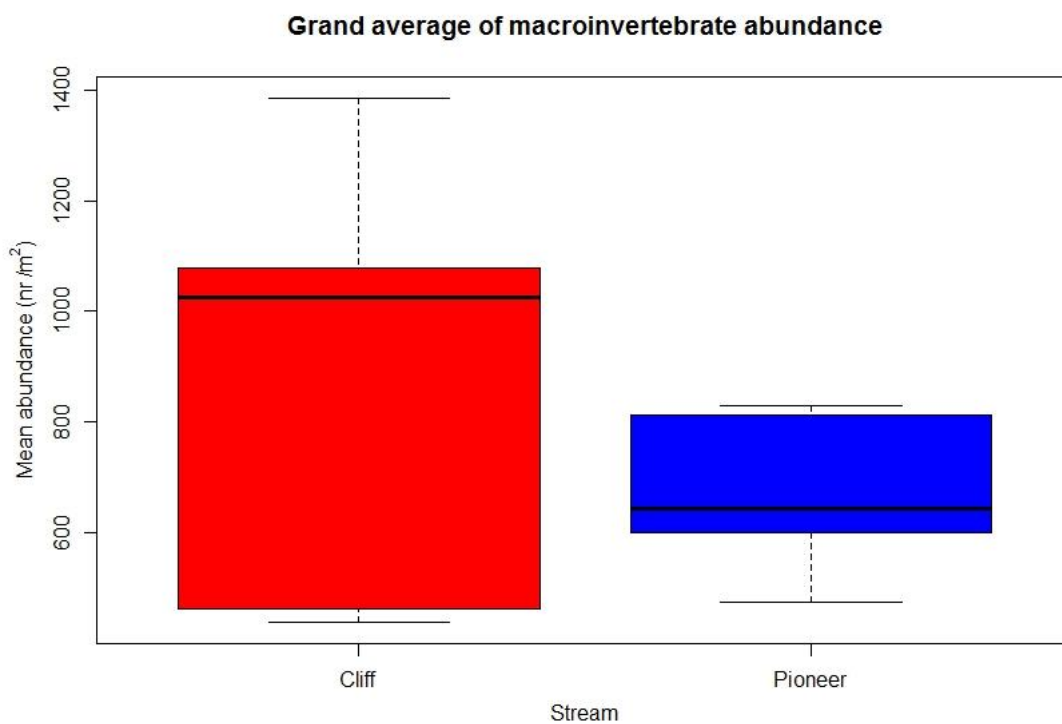
Due to the combination of a south-facing aspect and riparian vegetation, the light intensity reaching Pioneer Creek is relatively low. Photoactive radiation (Figure 4D) was about threefold higher in Cliff Creek ( $291.7 \mu\text{m photons m}^{-2}\text{s}^{-1}$ ,  $\text{SE}=12.4$ ) than in Pioneer Creek ( $101.6 \mu\text{m photons m}^{-2}\text{s}^{-1}$ ,  $\text{SE}=7.0$ ). Cliff Creek also had a higher periphyton chlorophyll-*a* concentration (Figure 4E) and AFDM than Pioneer Creek. However, the difference was only marginally significant (Cliff:  $49.8 \text{ mg/m}^2$  chlorophyll-*a*,  $6.4 \text{ g/m}^2$  AFDM; Pioneer:  $20.9 \text{ mg/m}^2$  chlorophyll-*a*,  $31.9 \text{ g/m}^2$  AFDM,  $p = 0.066$ ). Water physico-chemistry measured with the data-loggers during one month (July 15-August 18) was significantly different in the two tributaries. Water temperature (Figure 4A) was on average almost  $2^\circ\text{C}$



**Figure 4.** Water physico-chemistry and light intensity for Cliff and Pioneer Creeks, averaged between June and August 2014. A) temperature, B) conductivity, C) oxygen concentration, D), photoactive radiation, E) chlorophyll-*a*

warmer in Cliff Creek (11.9°C) than in Pioneer Creek (10.3°C,  $p < 0.001$ ), and both oxygen concentration (Figure 4C, 0.4 mg/L difference) and conductivity (Figure 4B, 21  $\mu\text{S}/\text{cm}$  difference) were higher in Pioneer Creek ( $p < 0.001$ ).

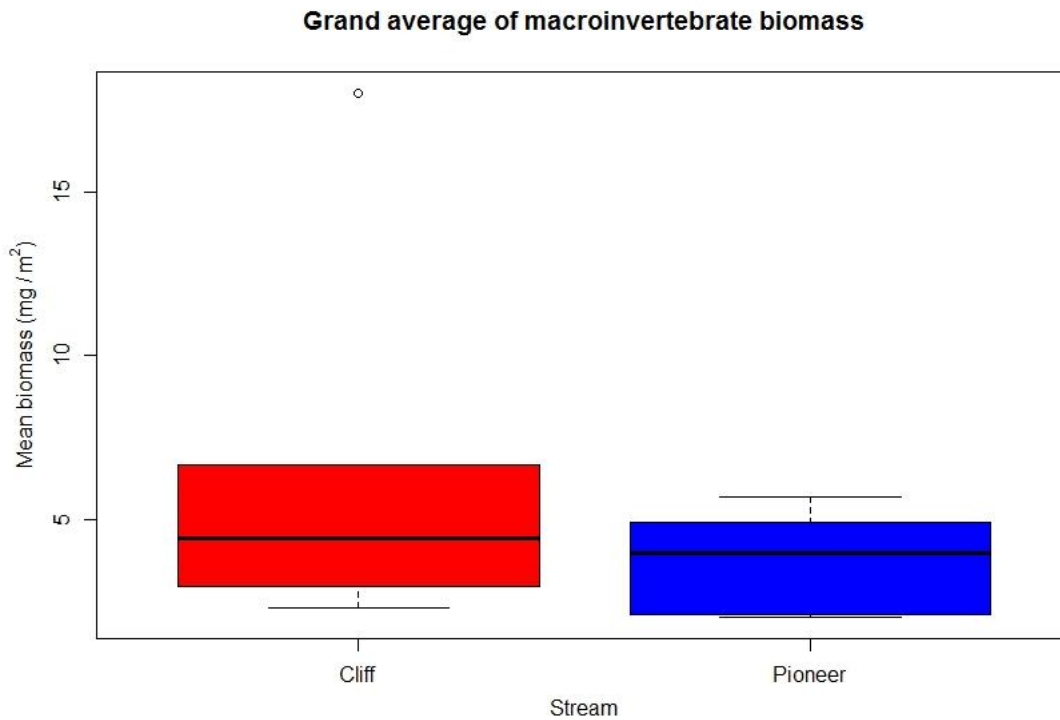
Variation in macroinvertebrate abundance was high among replicates and sampling dates. The mean abundance (Figure 5) of all samples in Cliff Creek was higher (68.7 individuals/ $\text{m}^2$ ,  $\text{sd}=138.7$ ) than the mean abundance in Pioneer Creek (60.9 individuals/ $\text{m}^2$ ), but the difference was not significant (t-test:  $t = 0.64$ ,  $\text{df} = 16$ ,  $p = 0.52$ ).



**Figure 5.** Average of abundance of all replicates and sampling dates ( $n=18$  in each stream).

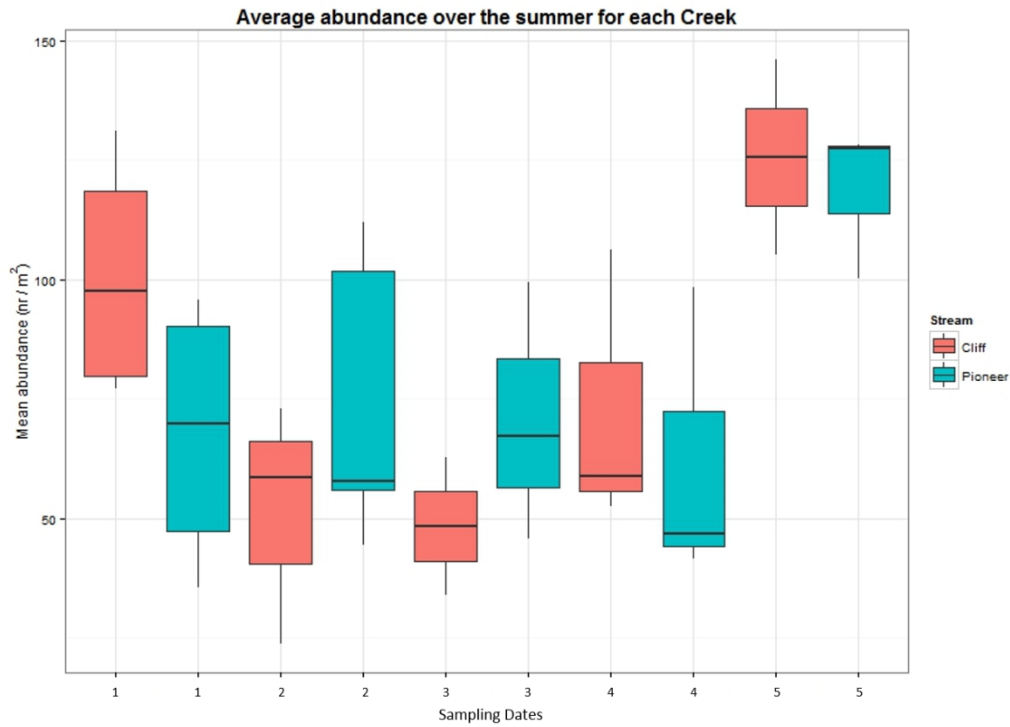
Contrary to abundance, macroinvertebrate biomass significantly differed between the two study streams (Figure 6). Even though variation was high as well, biomass in Cliff Creek (6.6  $\text{mg}/\text{m}^2$ ) was significantly higher than in Pioneer Creek (4.0  $\text{mg}/\text{m}^2$ , t-test:  $t = 2.59$ ,  $p$ -value = 0.009,  $\text{df} = 16$ ).



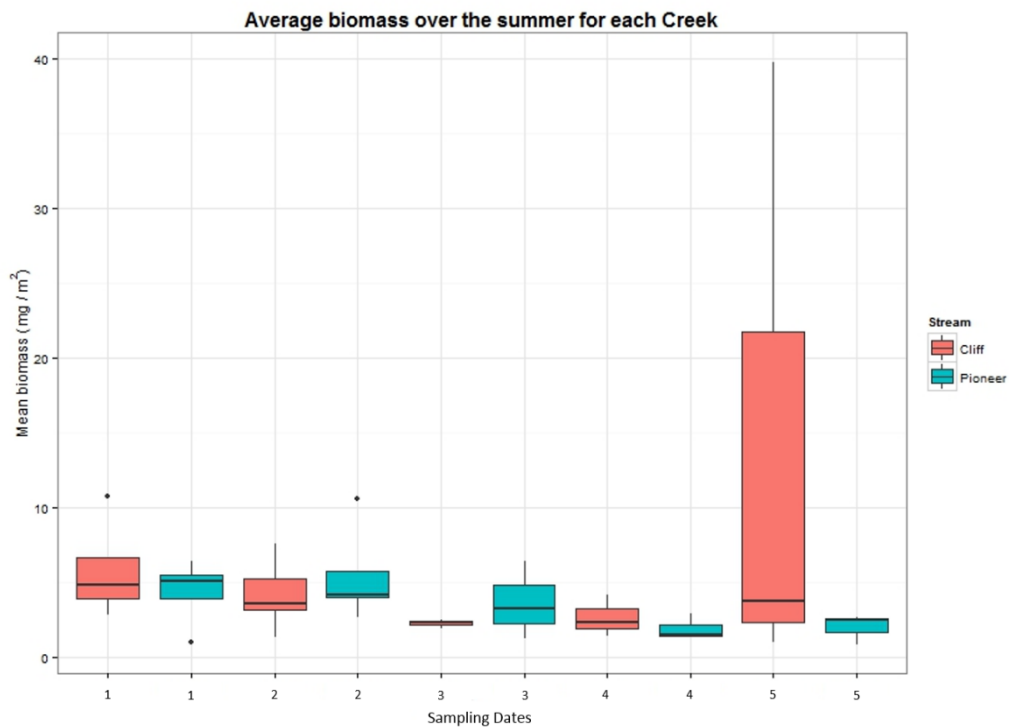


**Figure 6.** Average of biomass of all replicates and sampling dates ( $n=18$  in each stream).

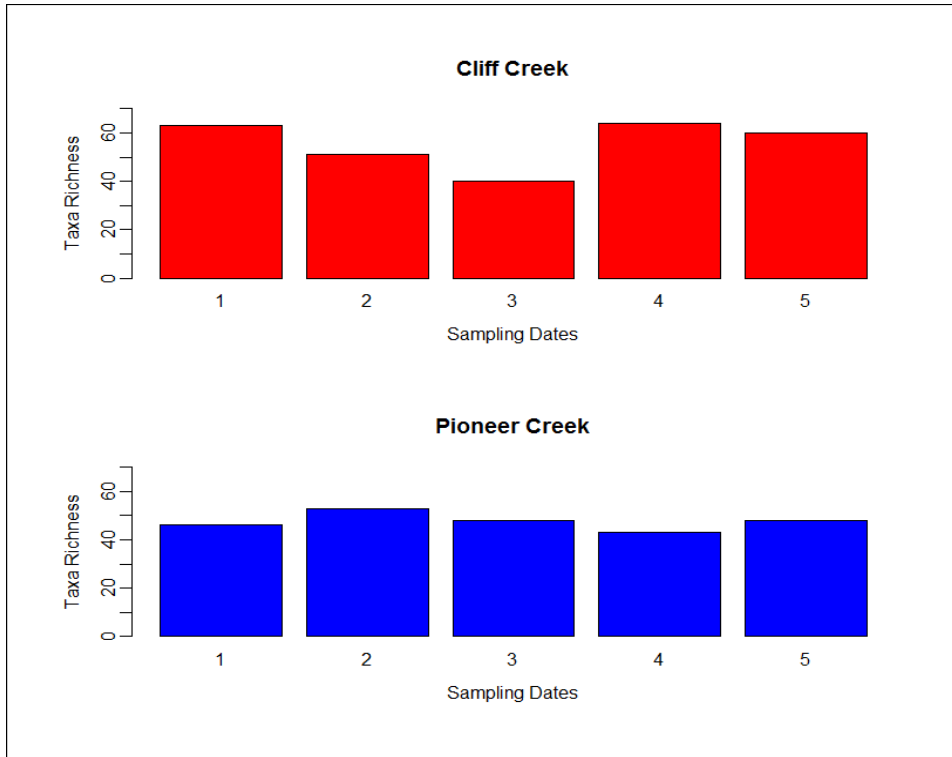
Abundance first decreased in both streams and then increased in August (Figure 7), following the increasing chlorophyll-*a* concentration (Figure in appendix). The changes in abundance between sampling dates were significant (ANOVA,  $p = 0.009$ ), but abundance did not differ among the two streams (ANOVA,  $p = 0.9$ ). The initial decrease was also detectable in biomass (Figure 8), but there was no increase afterward and the changes were not significant (ANOVA,  $p = 0.09$ ). Even though it was not obvious, the two study streams differed significantly in biomass (ANOVA,  $p = 0.01$ ).



**Figure 7.** Abundance was averaged over all replicates per sampling date, which were June 15 and 29, July 13 and 29 and August 10 (n=36).



**Figure 8.** Biomass was averaged over all replicates per sampling date, which were June 15 and 29, July 13 and 29 and August 10 (n=36).



**Figure 9.** Number of taxa per sampling date. Taxa contains different taxonomic levels such as family, genus and species.

At the end of June and beginning of July (sampling dates 2 and 3), samples from Pioneer Creek had two to eight taxa more than Cliff Creek. As expected, on all the other sampling dates, samples of Cliff Creek had up to 20 taxa more than Pioneer (Figure 9). The difference between streams, however, was not significant with a mean of 55 taxa in Cliff Creek and 47 taxa in Pioneer Creek (ANOVA,  $p=0.13$ ,  $df=1$ ). Note that taxa does not refer to species uniquely, but several taxonomic levels such as family, genus and species.

The number of common taxa inhabiting Cliff Creek was higher than in Pioneer Creek. Examining the abundance of individual species, there were some detectable patterns, especially for mayflies (Figures 10a-c). Eight out of 12 Ephemeroptera taxa decreased in abundance on the second or third sampling date and then increased again after that date. The example of *Baetis* shows that the increase in abundance occurred about a month later in Pioneer Creek than in Cliff Creek, but then exceeded the abundance of Cliff Creek. Two common *Drunella* species complement each other, as *Drunella coloradensis* was more abundant in Pioneer Creek early in summer and *Drunella doddsi* was more abundant in Cliff

Creek later in summer. Plecoptera taxa did not follow any specific pattern of decrease and increase. *Sweltsa* sp. increased earlier in Pioneer Creek whilst Perlodidae species behaved exactly the opposite. In Cliff Creek, Hydropsychidae species were absent on the third sampling date, whereas they were absent two weeks later in Pioneer Creek.

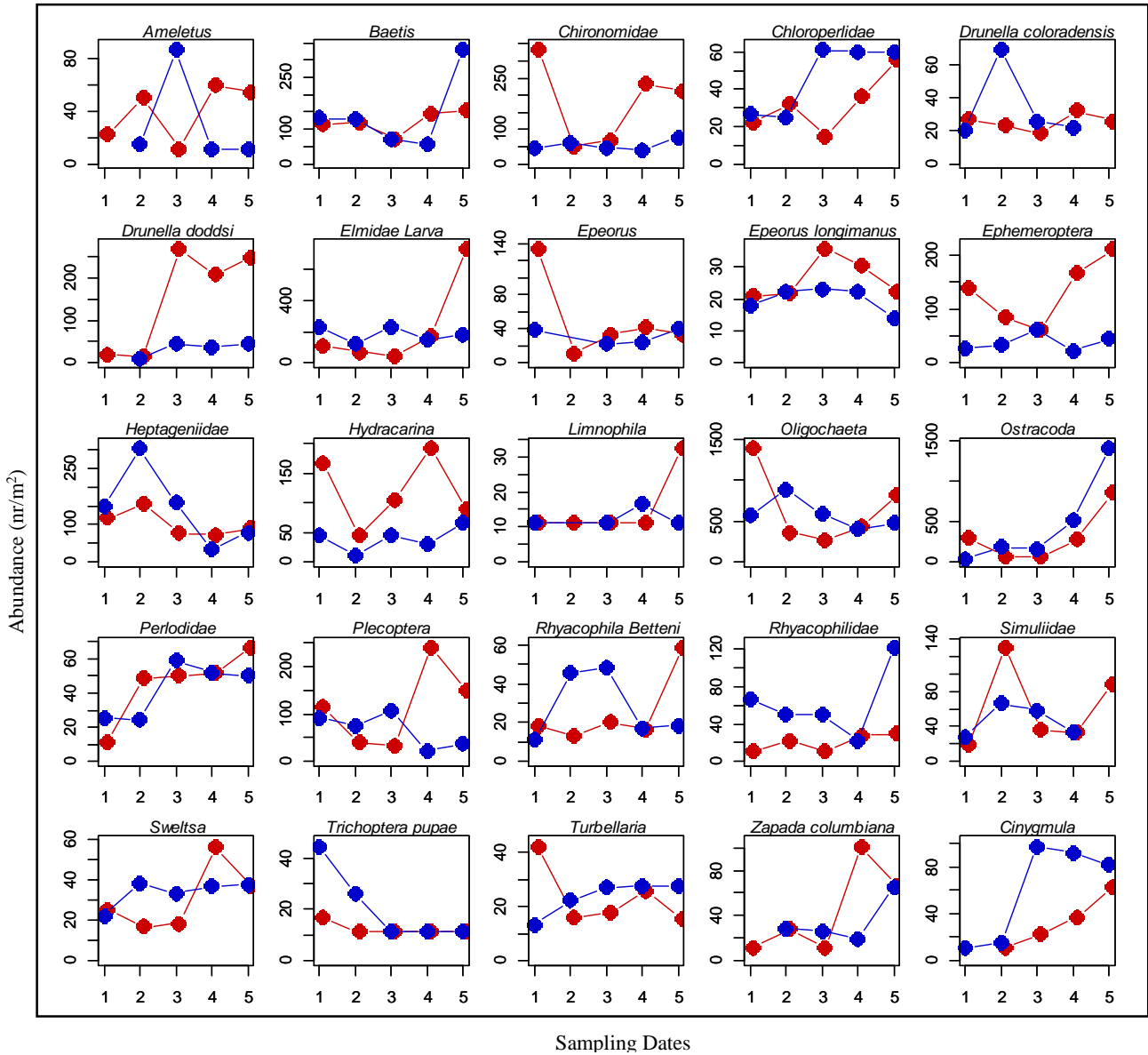
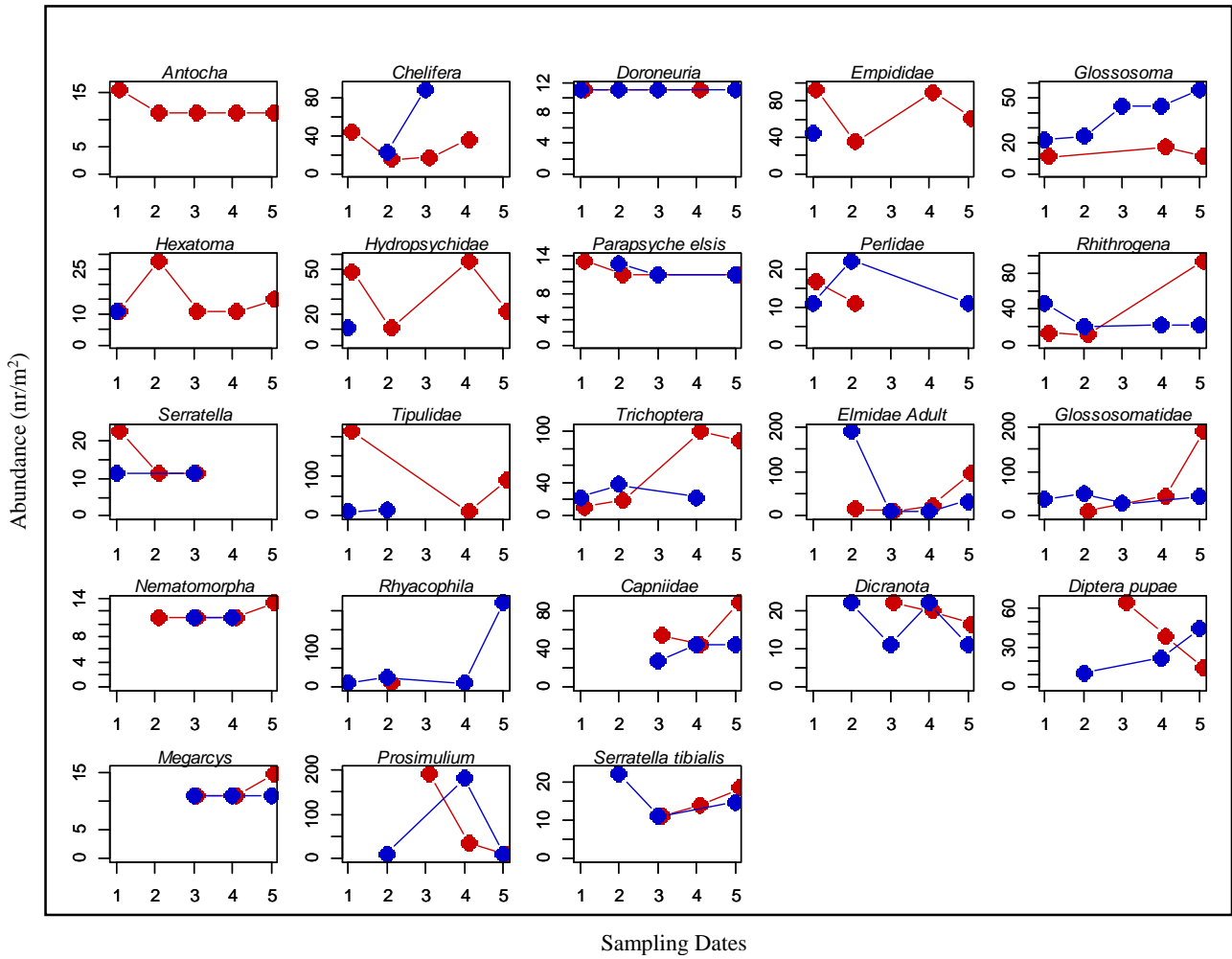
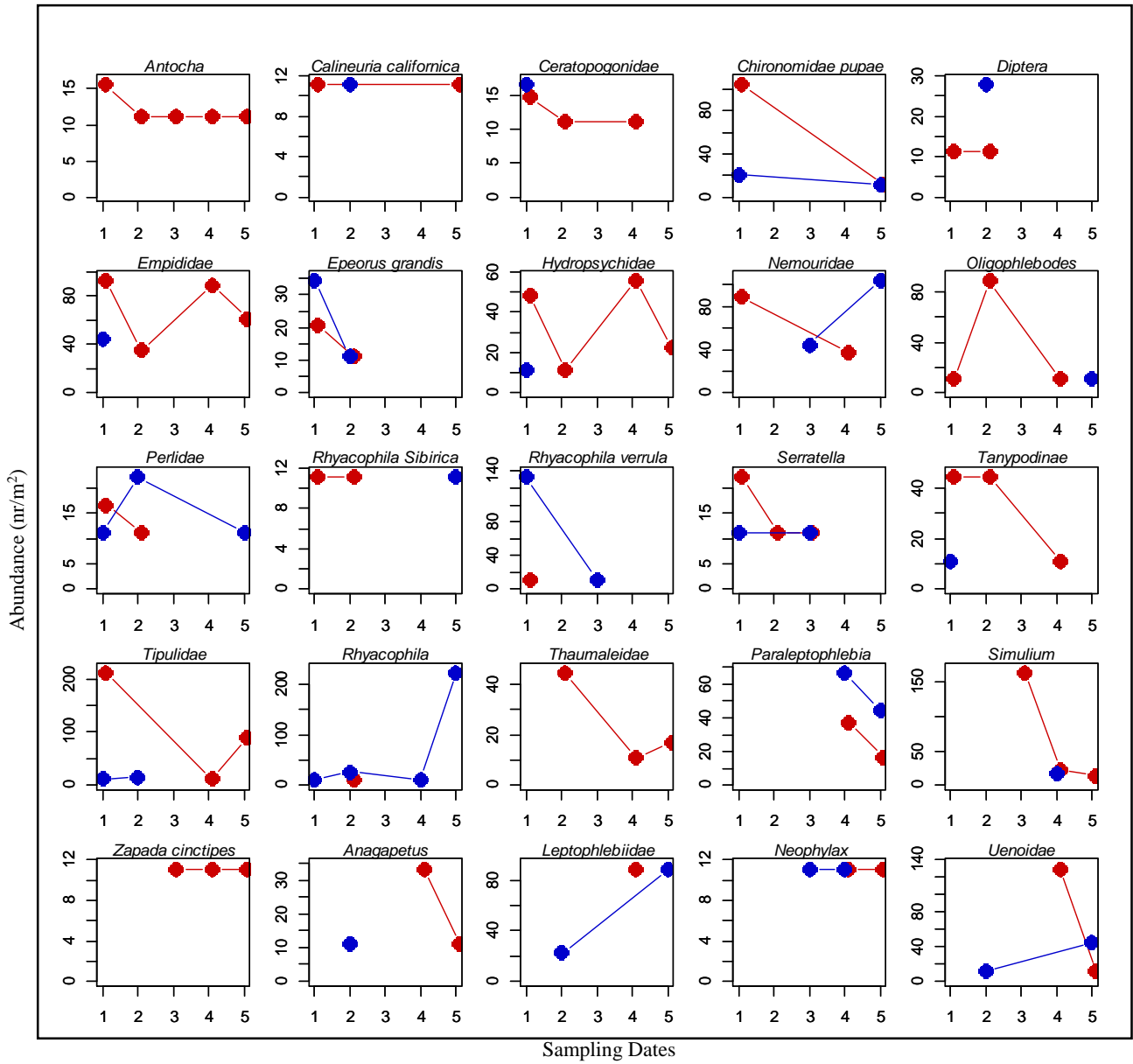


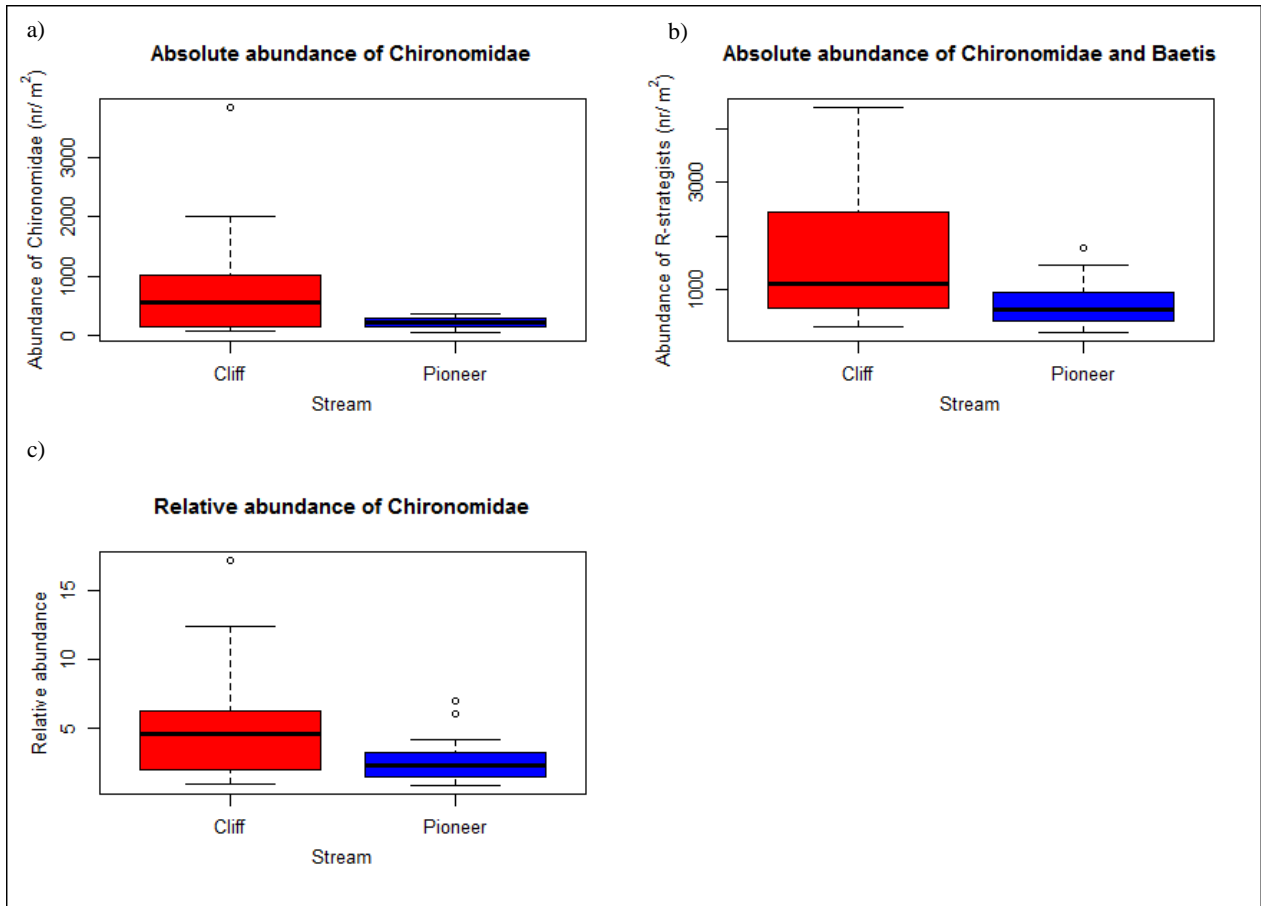
Figure 10a) Abundance of taxa that occurred frequently in both streams (9-10 times out of 10 possible). Red color represents Cliff Creek and blue color represents Pioneer Creek.



**Figure 10b)** Abundance of taxa that occurred moderately in both streams (5-8 times out of 10 possible). Red color represents Cliff Creek and blue color represents Pioneer Creek.



**Figure 10c)** Abundance of taxa that occurred sometimes in both streams (3-4 times out of 10 possible). Taxa occurring less than 3 times are not represented in any graph. Red color represents Cliff Creek and blue color represents Pioneer Creek.



**Figure 11** a) mean absolute abundance of Chironomidae in both streams, b) absolute numbers of Chironomidae and Baetis combined, and c) abundance of Chironomidae relative to all the other taxa ( $n=35$  for each graph)

Supporting my hypothesis, the absolute and relative abundance of the *r*-strategist chironomid midges were significantly higher in Cliff than Pioneer Creek (Figure 11a and 11c, *t*-test,  $p = 0.01$ ). Because baetid mayflies are *r*-strategists as well, they were expected to behave the same way, but only the combination of both *Baetis* and Chironomidae in absolute numbers differed significantly between the two streams (Figure 11b, *t*-test,  $p = 0.008$ ).

Following the pattern of chlorophyll-*a*, secondary production of macroinvertebrates was generally higher in Cliff than Pioneer Creek (Table 2). Four taxa showed a difference in production of  $\sim 100 \text{ mg}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  between the tributaries. In six out of eight taxa, average biomass in Cliff Creek exceeded that of Pioneer Creek. Calculated growth rates, however, were not consistently different between the streams. Both streams had the same number of taxa for which the growth rate was higher in one than the other stream. Hydropsychidae and Chironomidae were the two groups that form an exception, having higher production estimates in Pioneer Creek. There was no pattern among orders. Among mayflies, the annual production in *Baetis* and *Epeorus longimanus* was about  $100 \text{ mg}\cdot\text{m}^{-2}$  higher in Cliff Creek, whereas *Serratella* production was about the same in both creeks. Similarly, production in the two dipteran families was the opposite; Simuliidae was higher in Cliff Creek, while Chironomidae was higher in Pioneer Creek. For this reason, no general production estimates for families or groups were possible.

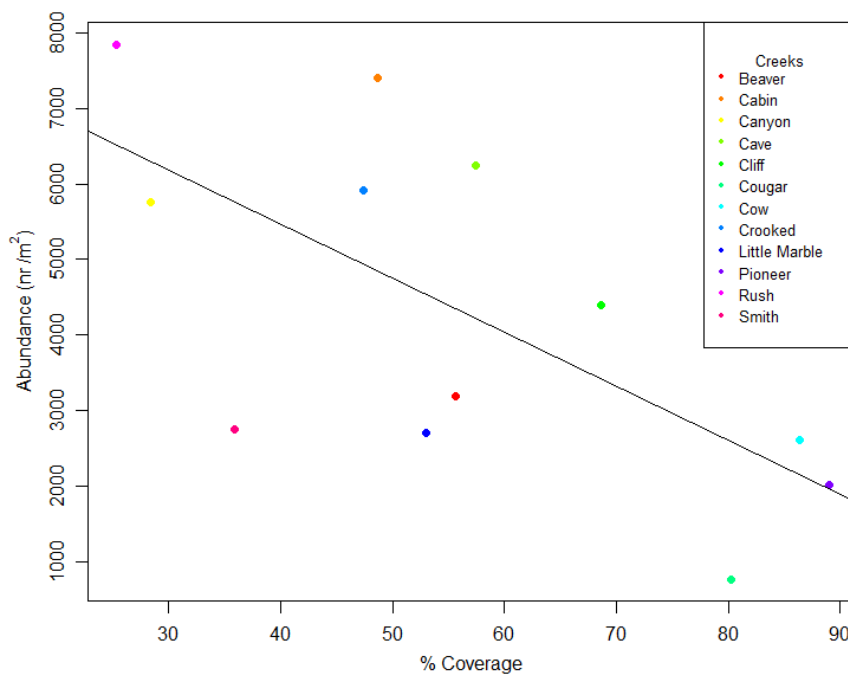
Order	Taxa	Stream	Average Biomass	Average Growth Rate	Production (mg/m <sup>2</sup> )	Annual P (mg/(m <sup>2</sup> *year))	Annual P/B
Ephemeroptera	Baetis	Cliff	10.89	1.23	13.42	174.99	16.06
		Pioneer	6.32	0.87	5.48	71.42	11.30
Ephemeroptera	Drunella coloradensis	Cliff	42.55	1.06	45.04	1174.16	27.59
		Pioneer			0.00		
Ephemeroptera	Serratella	Cliff	3.38		20.27	129.78	6.00
		Pioneer	3.34		20.02	128.19	6.00
Ephemeroptera	Epeorus longimanus	Cliff	30.71	0.51	15.61	406.93	13.25
		Pioneer	15.18	0.77	11.71	305.27	20.10
Trichoptera	Hydropsychidae	Cliff	9.56		71.70	459.11	7.50
		Pioneer	10.17		76.26	488.32	7.50
Diptera	Chironomidae	Cliff	5.08	0.30	1.51	13.09	2.57
		Pioneer	1.08	1.01	1.10	14.28	13.22
Diptera	Simuliidae	Cliff	0.45		24.58	157.39	55.00
		Pioneer	0.19		10.39	66.51	55.00
Coleoptera	Elmidae Larva	Cliff	31.08	1.29	40.01	521.55	16.78
		Pioneer	16.59	1.00	16.64	433.78	26.14

**Table 2.** Estimates of production of the most abundant taxa in Cliff and Pioneer Creeks. Blue background color indicates that the production values were calculated with literature based annual P/B values (Bellmore et al. 2012).



*Basin wide study*

Out of all the measured environmental variables, only canopy coverage (Figure 12,  $p < 0.001$ ) and slope (Figure 13,  $p = 0.03$ ) affected the abundance of macroinvertebrates across the suite of sites sampled for the basin wide comparison. Less light and steeper slope was associated with a lower number of individuals, decreasing from almost 8000 individuals/m<sup>2</sup> in Rush Creek to about 2000 individuals/m<sup>2</sup> in Pioneer Creek. However, the variation among replicates was high for some tributaries, doubling in number between the two extremes. Variation seemed to increase with the width of the tributary. Elevation (Figure 14), which was associated with water temperature and other water chemistry measures, seemed to exhibit a negative correlation with abundance, but the effect was not significant ( $p = 0.09$ ). This was mainly due to the high variation among low elevation sites and the uneven distribution of sampling sites, with only 5 between 1300m and 1700m and 7 below 1300m.



**Figure 12.** Abundance of macroinvertebrates along the shading gradient.

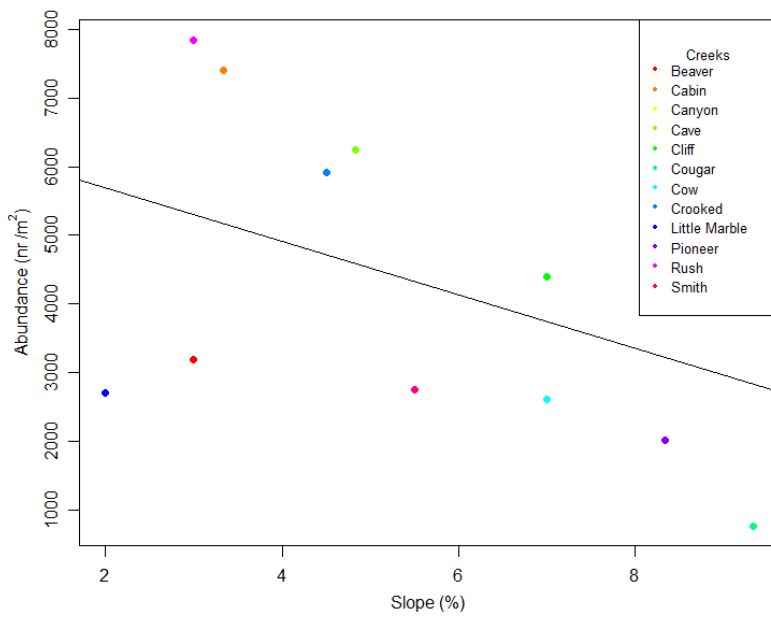


Figure 14. Abundance of macroinvertebrates in relation to stream slope.

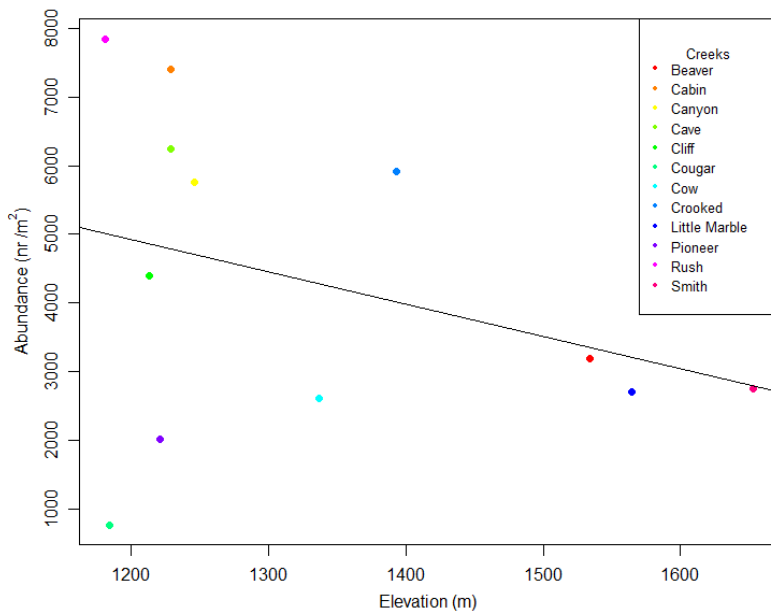
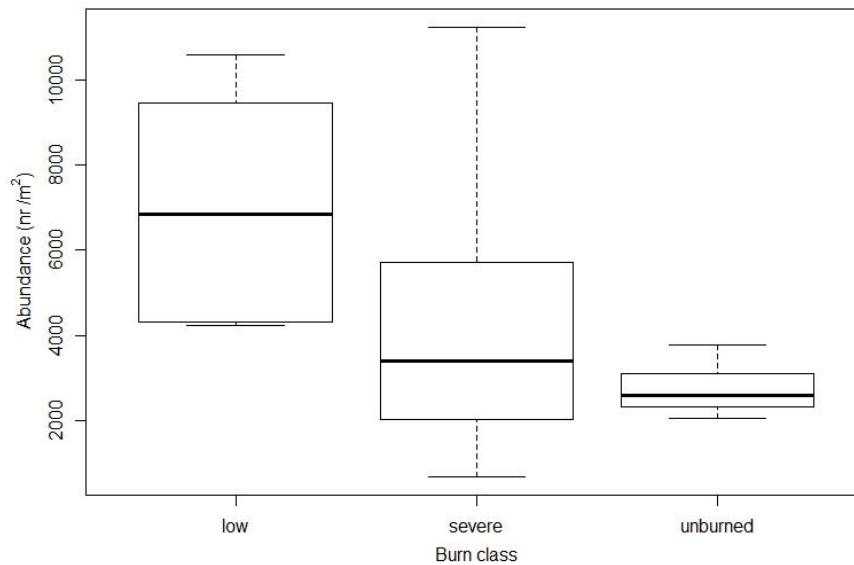


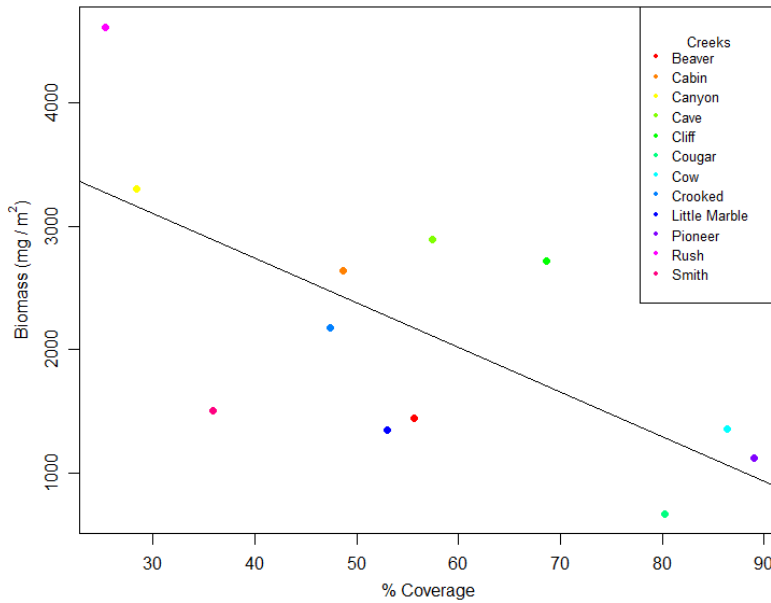
Figure 13. Abundance of macroinvertebrates along the elevational gradient.

Abundance differed significantly between burn categories (ANOVA,  $p = 0.01$ ,  $df = 2$ ). The greatest difference was contrary to my hypothesis; low severity burned streams had almost twofold higher abundance than unburned streams (Figure 15). Streams severely burned had macroinvertebrate abundances intermediate to the other two burn classes.



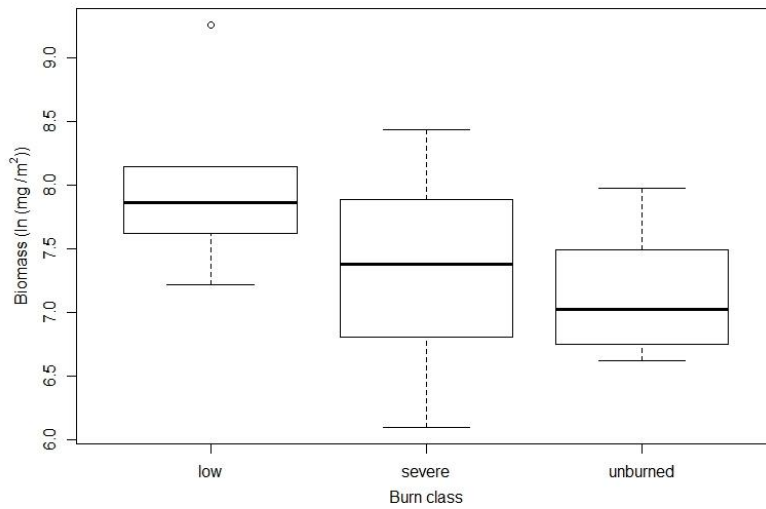
**Figure 15.** Abundance among burn categories. Two streams were unburned, two had low severity burns and eight were classified as high severity burned.

Contrary to abundance, biomass was only affected by canopy coverage ( $p=0.01$ ) but not slope or other environmental variables (Figure 16, see also Figures in Appendix).



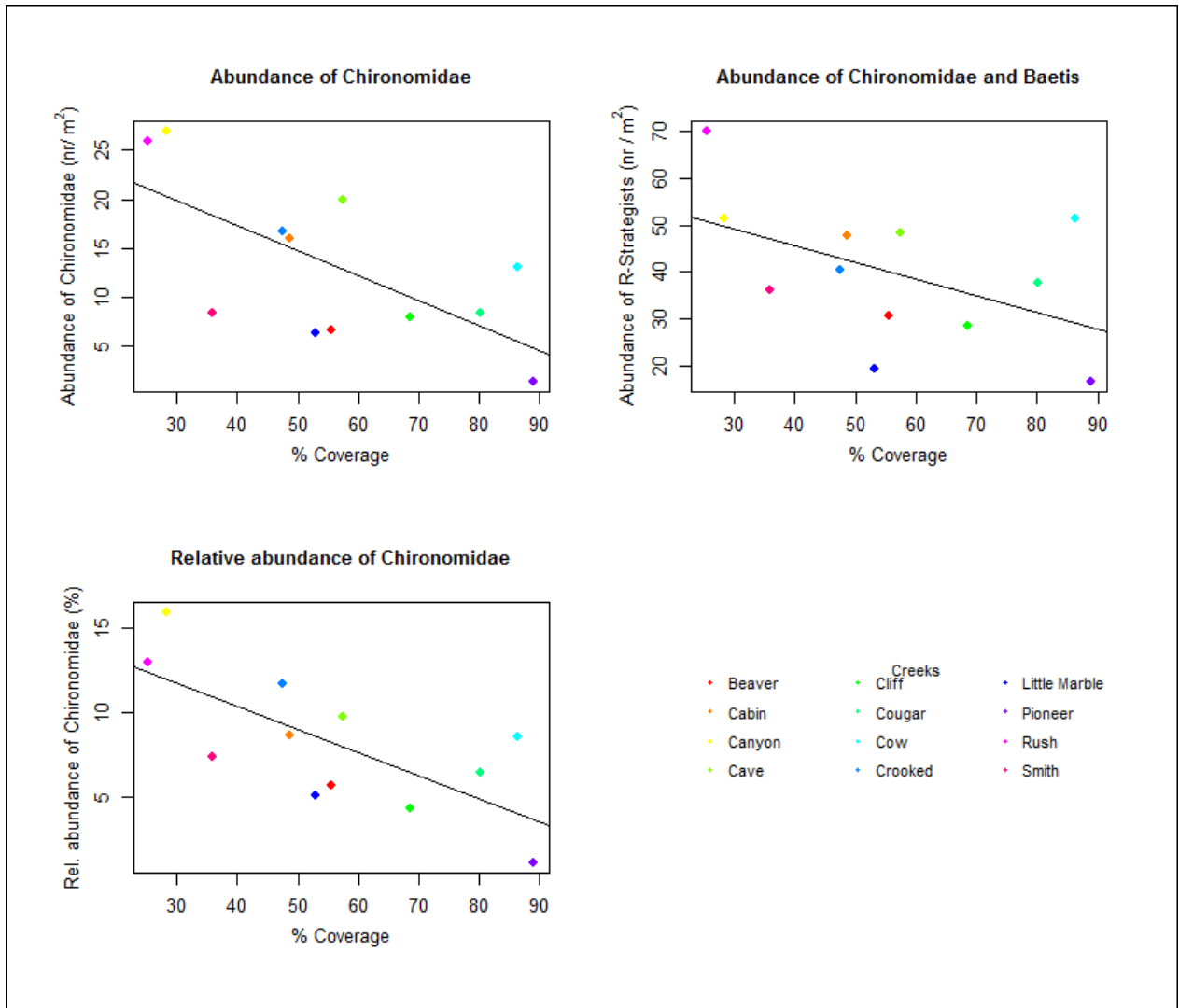
**Figure 16.** Effect of canopy coverage on macroinvertebrate biomass.

As with abundance, we observed the greatest biomass difference between low severity burns and unburned sites with biomass at low severity burned sites being almost twice as high as the biomass of unburned sites (Figure 17,  $p=0.04$ ).



**Figure 17.** Biomass difference between burn categories. Two streams were unburned, two had low severity burns and eight were classified as high severity burned.

Because wildfire and its effects on light regime represent a disturbance for streams and biotic communities, the ability to adapt to such changes is important. For this reason, we analyzed the relative and absolute abundance of Chironomidae and *Baetis*, both are R-strategists. Both absolute and relative abundances of Chironomidae (Figure 18a) and 18b)), in comparison to all the other taxa, increased positively with light availability ( $p < 0.001$ ). However, the variance was extremely high. Neither the absolute nor relative abundance of *Baetis* was affected by canopy coverage, but when combined with Chironomidae the absolute abundance of the two together was correlated with canopy coverage (Figure 18c),  $p=0.01$ ).



**Figure 18.** Effects of canopy coverage on *r*-strategists. a) absolute abundance of Chironomidae, b) abundance of Chironomidae relative to all taxa, c) absolute abundance of Chironomidae and Baetis combined.

Simpson Biodiversity Index had a range of about 0.25, but we could not detect any factor that explained the changes (see Figures in Appendix). The calculated Shannon Evenness did not differ from the distribution of the Simpson Index.

Chemical variables, such as DOC, GPP and N:P ratio, measured with data loggers in 2013 (E. Davis, unpublished) were not associated with macroinvertebrate biomass or abundance.

## Discussion

Unlike the short-term responses to wildfire, which includes light and nutrient pulses dependent on the severity of the fire, the mid- to long-term response of stream macroinvertebrate communities and their productivity appears to be mostly mediated by the trajectory of riparian canopy recovery and associated light input rather than the severity of the original burn itself.

The two-stream comparison revealed that photoactive radiation was the most important driver for macroinvertebrate biomass and production. In Cliff Creek, the insignificant positive trend between July 13 and August 11 could be found in both chlorophyll-*a* concentration and macroinvertebrate biomass. In previous studies, 2-3 times higher primary production rates were measured in Cliff Creek than in Pioneer Creek (T. Gardner, E. Davis and C. Baxter, unpublished data). This supports my hypothesis that light affects macroinvertebrate biomass and production through a bottom-up effect of the food web. In Pioneer Creek, there were no consistent patterns of change over time in all trophic levels. Rather surprising was the fact that abundance was not significantly higher in Cliff Creek than Pioneer Creek. This suggests that light intensity does not influence the number of individuals or number of offspring, but does influence growth rate and size of individuals. Data in these two streams therefore do not support my hypothesis that high light availability leads to increased abundance. A possible factor in keeping the aquatic insect abundance at a steady level could be competition or an interaction with predators. Except for *Parapsyche elsis*, which might have a different life history, most invertebrate predators, such as Rhyacophilidae, Perlodidae and Chloroperlidae, became abundant at the end of the summer, as did the number of fish in both tributaries (M. Schenk, unpublished data).

Examination of the abundance of individual taxa revealed distinct differences between invertebrate assemblages and life cycle timing of the two paired streams. *Baetis* sp. decreased in abundance two weeks later in Pioneer Creek, at the end of July instead of the beginning of the month like in Cliff Creek. The low number of individuals present at that time is likely related to an emergence event. Eleven other mayfly taxa behaved similarly in their decrease-increase due to an emergence event. This is consistent with the findings of Malison and Baxter (2010) that aquatic insect emergence from streams in this basin occurs earlier (June) in high severity burned streams in contrast to low burned or unburned streams. The contrasting appearance of the two common *Drunella* species might be due to the similar habitat and water

requirements of low alkalinity, coarse substrate and dense riparian vegetation (Magnum and Winget 1991 and Winget and Magnum 1996), which may lead to partially competitive exclusion.

Taxa of other orders behaved differently. For example, *Rhyacophila betteni* seems to have had an emergence event at date 4 in Cliff Creek as there was an increase in abundance on date 5. In Pioneer Creek, the pattern was different and peak abundances occurred on dates 2 and 3. This difference most likely was not the natural pattern, but may have been caused by variation in sampling, because it is highly unlikely that there were two emergence events within a month. There was no clear pattern detectable among Plecoptera taxa. Some increased in abundance earlier in Pioneer Creek, others behaved in the opposite way. A reason for this could be their mobility, as they are stronger than mayflies and are also able to move upstream (Delucchi et al. 1989), as well as their habitat preference for large-sized boulders (Walton et al. 1977), which were not possible to sample with the Surber sampler. A decrease in abundance could also be mistaken as emergence, when in fact it may have been due to density dependent mortality (Resh & Rosenberg 1984). In the case of *Baetis*, the abundance in Cliff Creek at date 3 was low, but the size of the individuals was large, and only after date 4 was there a clear emergence event, as two weeks later there was a large number of small individuals (see figure in Appendix).

The difference in taxa richness could be explained by the ecological niche concept. Through higher light availability and thus increased periphyton biomass, more food for invertebrates is available and new niches might open up (Abrams 1988, Milner et al. 2001, Mehler et al. 2015). The width and velocity of the stream is insignificantly greater in Cliff Creek than Pioneer Creek, but this might just be enough for new species to populate this stream. Further, a comment about identification has to be made at this point. There were two people with different levels of experience working on invertebrate identification, Matthew Schenk and myself, which may result in differences of accuracy, although, the proportion of samples identified is about the same for Cliff Creek and Pioneer Creek.

As Chironomidae are *r*-strategists, the fact that they were both absolutely and relatively more abundant in Cliff Creek is what I expected, considering that Cliff Creek burned again in 2006 and Pioneer Creek had eight years more time to recover. *Baetis*, too are *r*-strategists, but their abundance only differed significantly when combined with



Chironomidae. The reason for this might lie in their sensitivity to stressors, especially velocity and associated oxygen (Lancaster 1992, Gibbins et al. 2010).

Since the abundance of Chironomidae was higher in Cliff Creek, it is even more surprising that their production behaved contrarily. Even though the same method was used for all eight species, it is entirely possible that an error was made in the calculations of growth rates. The unusually low P/B ratios also point in that direction. The calculated annual P/B ratios are about 75-85 lower than the literature based P/B ratio, which is 88 for Chironomidae (Bellmore et al. 2012). Production usually follows biomass (Benke et al. 1997) and since this is not the case for Chironomidae because of the inverted growth rate, it is very likely that the error lies in the growth rate estimate. The fact that Hydropsychidae production was higher in Pioneer Creek might be misleading as secondary production could change throughout the year and strongly depends on the food resource available. Benke et al. (1997) found that some species of net-spinning caddisflies have higher production in summer while production is greater for other species from late summer to winter. Thus, by combining all the Hydropsychidae species into one group and only sampling a period of two months, we might have missed a lot of important information on cohorts, biomass and production. The same is probably true for Chironomidae and *Serratella*, which have a higher production in Pioneer Creek or a difference that is barely noticeable. Comparison between the eight species was not possible in this case as the production results have to be corrected with the cohort production interval (CPI, Benke et al. 1977), estimated by the mean length of larval life, which we do not know. The difference of about  $100 \text{ mg} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  in production of *Baetis*, *Epeorus longimanus*, Simuliidae and Elmidae larva could be traced to the difference in biomass in the two streams. Alternatively, the food resources available could be different in the two streams, resulting in different metabolic rates of the two populations. Potential differences of food resources could be found with a gut content analysis (Wellard Kelly et al. 2013), which will be performed later.

The results of the basin wide study strongly support my hypothesis that light positively affects macroinvertebrate abundance and biomass. Vandemyde and Wiles (2015) found experimentally that removal of canopy cover affects abundance and production of macroinvertebrates. While the short-term response of macroinvertebrates to wildfire includes a pulse in abundance and a shift to generalist feeders, dependent on fire severity (Mellon et al.

2008), a community shift during the mid-term response is more likely caused by interannual variability and other disturbances (Arkle et al. 2009). The influence of PAR on abundance was rather surprising, considered that it had no effect on abundance when only the paired streams were compared. However, the basin wide study represented just a snapshot at the end of the summer with only three replicates per stream. We expected that various light inputs reaching the stream might affect biodiversity as patches with an open canopy, among other things, have a high concentration of periphyton which leads to different habitat and ecological niches (Abrams 1988, Mehler et al. 2015). However, we could not detect any pattern of biodiversity across the 12 streams. This could be due to the limited resolution of identification, which was only to family level, each of which may have included variable numbers of species. The positive correlation of chironomid midge abundance with light is what we expected considered that they are *r*-strategists and have the ability to reproduce fast and adapt to disturbance. We expected baetid mayflies to behave the same way due to similar life history, but could not find a correlation with light intensity. In a previous study (Rugenski and Minshall 2014) analyzing pre- and post-fire conditions, the same findings were made and connected the low abundance of *Baetis* to a high discharge event in 1997, previous to the Diamond Creek Fire in 2000.

In contrast to my working hypothesis, I found that there was no correlation of burn categories or time to canopy coverage. In fact, we found that Cliff, Cougar, Cow and Pioneer Creeks had more than 60% canopy coverage eight years post fire, or 14 years in the case of Pioneer Creek, even though they burned with high severity. There are some differences in riparian tree species, which lead to variability in the time of canopy closure. Cougar, Cow and Pioneer Creeks all have a combination of alder, Douglas-fir and dogwood, whereas Beaver, Cabin, Canyon and Crooked Creeks were usually bordered with alder and either dogwood or Douglas-fir, but also with a high portion of spruce, cottonwood, hawthorn, or roses. This suggests that a certain combination of riparian species with different responses to fire disturbance is needed for a fast riparian vegetation regrowth. Dogwood is very tolerant to fire in terms of nutrients, pH, moisture and soil texture (US Forest Service 2012), which makes it a ruderal species. More importantly, they are able to bank their seeds, which may germinate because of fire (Kobziar et al. 2006). Alder, on the other hand, has a high fire tolerance due to its less flammable bark and non-resinous leaves (Kobziar et al. 2006). It is possible that with the strategy of asexual reproduction in alder and the seedling recruitment of dogwood, these two species can coexist after a high severity fire burned the overhead canopy and

understorage of riparian vegetation. Since Douglas-fir is a climax tree, it might have grown into the ecosystem during the mid-term response to fire, after the other two species were already established. This was possible because Douglas-fir has a high shade tolerance.

The tree community at Cliff Creek differs from Cougar, Cow and Pioneer Creeks, having mostly alder, birch and willow, although the year, intensity and regrowth of canopy is the same. Kaczynski et al. (2015) found that more than 70% of the birch trees and ca. 50% of willow trees resprouted in the first and second year post fire. Therefore, although having different riparian vegetation, Cliff Creek does not lag behind in terms of canopy regrowth. On the other hand, Jackson and Sullivan (2009) reported that a shift in riparian tree community can only occur after a severe fire. Thus, alternatively, post-fire riparian regrowth might be related to a combination of fire severity, riparian species and aspect associated with soil moisture.

The greatest differences in abundance and biomass by burn classes were between low severity burned and unburned sites. This is exactly the opposite of Malison and Baxter's findings (2010), where the greatest difference is between high severity and low severity sites. Although most study streams were the same, her study was conducted in 2005 and many streams have experienced another fire since then, including Cave, Cabin, Cow, Cliff, Cougar and Rush Creek. In 2014, when this study was conducted, some of these streams were grouped into other burn categories (E. Davis, unpublished data). Cave Creek was mostly burned with low and moderate severity, whereas Cougar Creek experienced high severity burns. Even though Smith Creek was unburned and had relatively low canopy coverage related to the width of the stream, abundance and biomass was lower than expected, which might be due to its high elevation and thus cold temperature and different nutrient input. In combination with Little Marble Creek, which also had below average abundance expected by the model, the difference to the low severity burned streams (Cave and Rush Creek), which were above the expected average, was quite high. Therefore, almost a decade after Malison's study, the important factor for macroinvertebrate abundance and biomass was the amount of light reaching the stream, not the severity of the original burn. Recovery of severe burned sites either regrew deciduous riparian vegetation to a density that might exceed pre-fire conditions (e.g. Pioneer Creek) due to soil moisture, or retain a more open canopy (e.g. Cliff Creek) presumably owing to repeated fire, lower soil moisture content associated with south facing aspect, or wider channels.

The results of both studies strongly indicate that biomass correlates positively with light input. Contrary to my assumption, it does not matter if increased light is available due to geomorphic factors (such as width of the stream or drainage aspect) or because a fire removed canopy coverage. The severity of the wildfire influences the stream-riparian ecosystem and induces either a shift in riparian vegetation or in-stream conditions. Severe wildfire seems to promote the *r*-strategists dogwood and alder and the climax species Douglas-fir. If these plants were not present in pre-fire riparian vegetation, streams experiencing a severe fire will not recover to their original conditions, but remain in a state of increased primary and secondary productivity, even 14 years post fire, but undergo a shift in an invertebrate community toward higher abundance of *r*-strategist Chironomidae. Such a shift in community of invertebrates has consequences for higher trophic levels as well as the terrestrial ecosystem through land-water linkages.

This raises the question whether it is better to suppress fires or let them burn in a natural way. My findings point into a direction of a strategy without any interfering fire management. Stream-riparian ecosystems and stream invertebrates in particular show no negative response to wildfire, but instead may even show persistent positive responses. In a wilderness setting, regrowth of deciduous riparian vegetation can occur quickly, such that by 14 years post fire, the largest effects on stream inverts are related to the rate and character of riparian canopy recovery rather than the severity of the original burn. In the mid- to long-term, wildfire may act as a critical mechanism to create a mosaic of stream-riparian ecosystem conditions including patches of stream habitat with high secondary productivity. This is contrasting to the common management practice of suppressing fire and keeping it out of riparian areas. However, it needs to be considered that this only applies to wilderness areas, fire in urban areas is part of another research area.

Since fire frequency and severity is known to increase with warming global climate (Westerling et al. 2006), the need for knowledge of long-term effects of fire and climate change becomes more important. Many studies have looked at individual effects of fire, increased temperature, debris flows and droughts, but there is a lack of integrative studies. Rugenski and Minshall (2014) showed that climatic factors, such as increasing temperatures, lower precipitation, reduced spring runoff and annual discharge, and fire together had a stronger influence on invertebrate communities than fire alone. To predict future ecosystem conditions and adaptability, and to develop management and conservation strategies, more

studies integrating several climatic factors and fire, including several trophic levels and land-water linkages, are needed.

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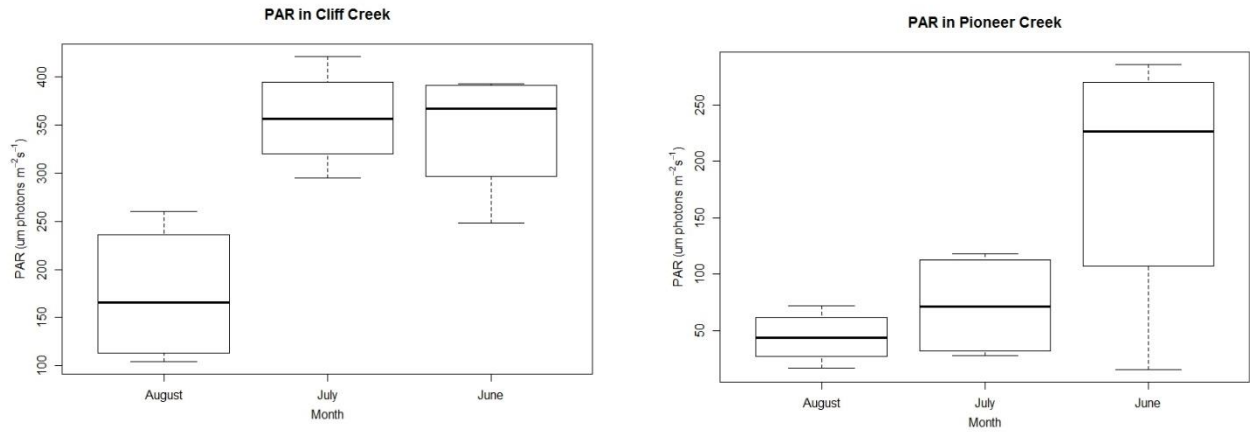
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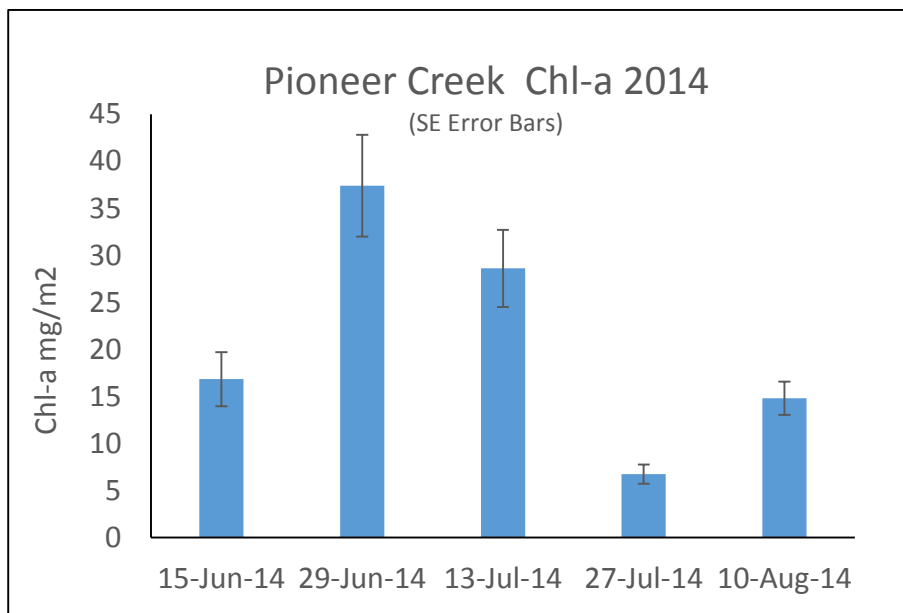
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## Appendix

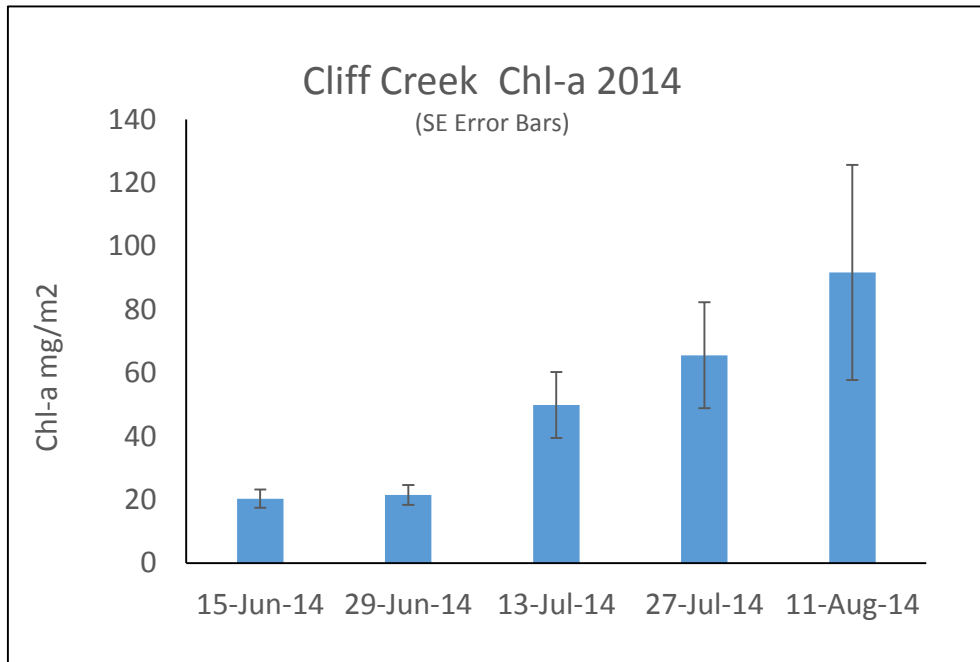
### Production



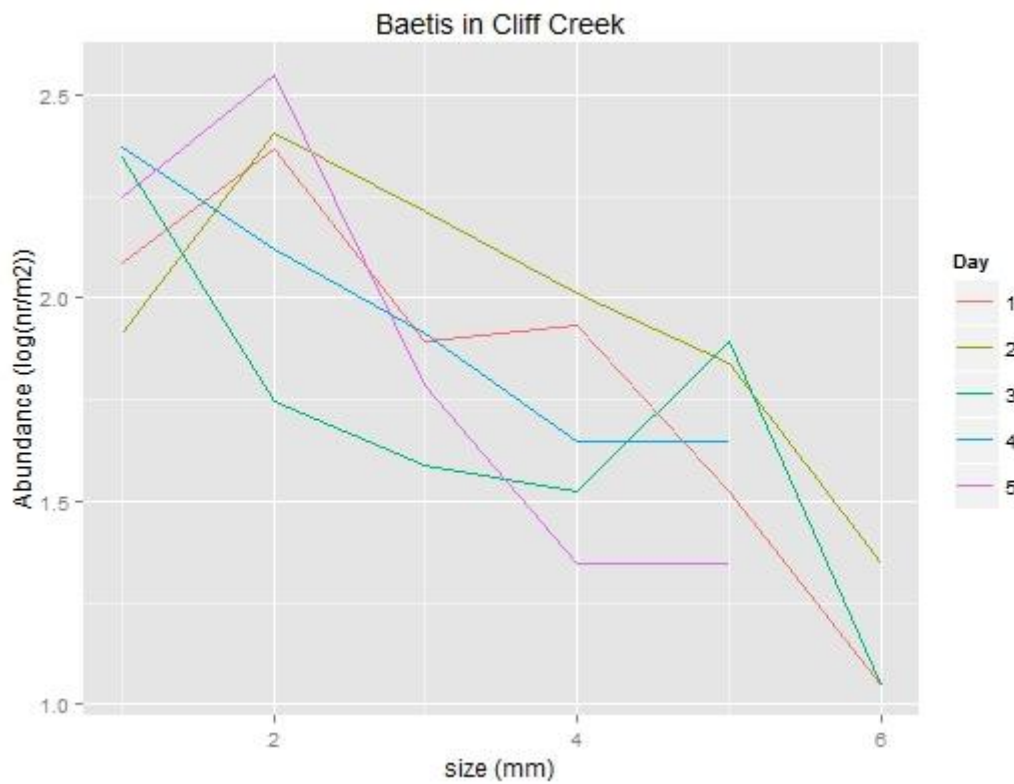
Light availability in the form of photoactive radiation for both streams over the summer.



Concentration of Chlorophyll a in Pioneer Creek over the summer.

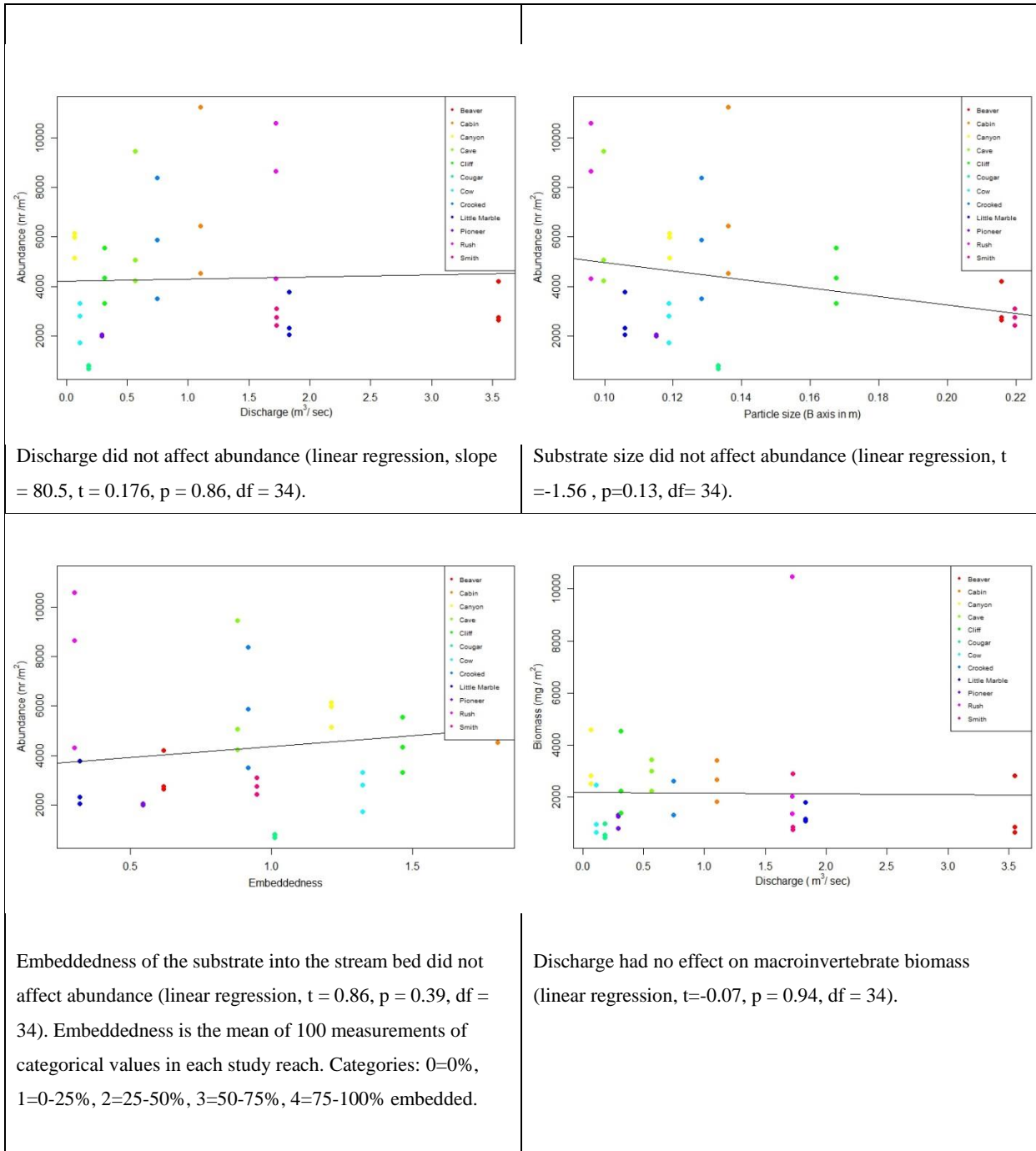


Concentration of Chlorophyll a in Cliff Creek over the summer.



Growth rate has been calculated from the difference of biomass on date 1 to date 3.

*Basin wide*

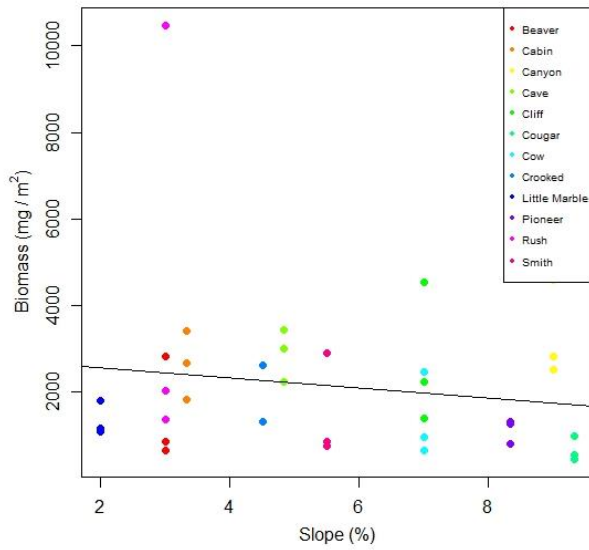


Discharge did not affect abundance (linear regression, slope = 80.5,  $t = 0.176$ ,  $p = 0.86$ ,  $df = 34$ ).

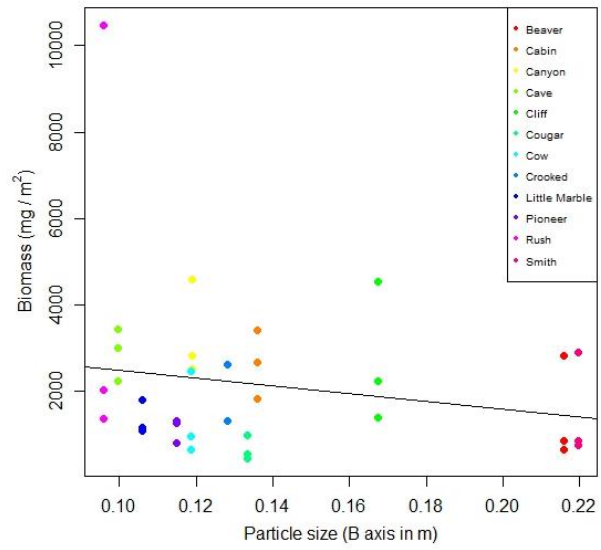
Substrate size did not affect abundance (linear regression,  $t = -1.56$ ,  $p = 0.13$ ,  $df = 34$ ).

Embeddedness of the substrate into the stream bed did not affect abundance (linear regression,  $t = 0.86$ ,  $p = 0.39$ ,  $df = 34$ ). Embeddedness is the mean of 100 measurements of categorical values in each study reach. Categories: 0=0%, 1=0-25%, 2=25-50%, 3=50-75%, 4=75-100% embedded.

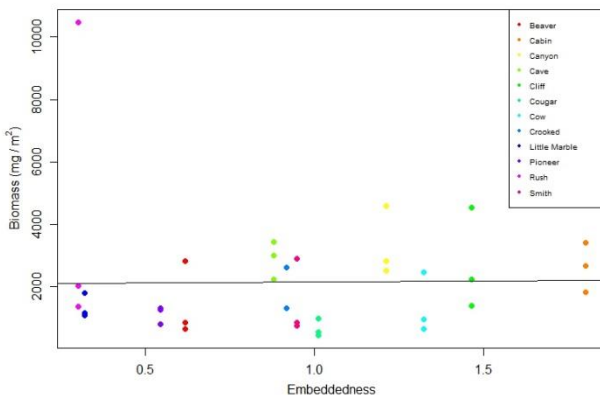
Discharge had no effect on macroinvertebrate biomass (linear regression,  $t = -0.07$ ,  $p = 0.94$ ,  $df = 34$ ).



Slope had no effect on macroinvertebrate biomass (linear regression,  $t = -0.93$ ,  $p = 0.34$ ,  $df = 34$ ).

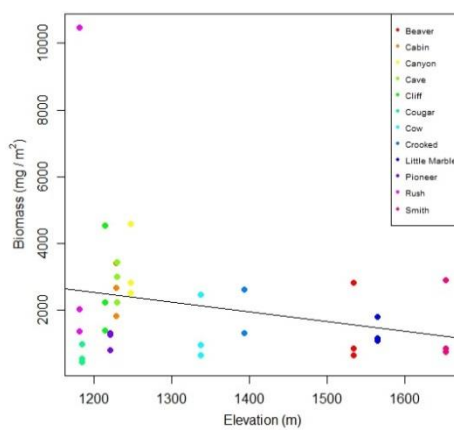


Substrate size had no effect on macroinvertebrate biomass (linear regression,  $t = -1.22$ ,  $p = 0.23$ ,  $df = 34$ ).



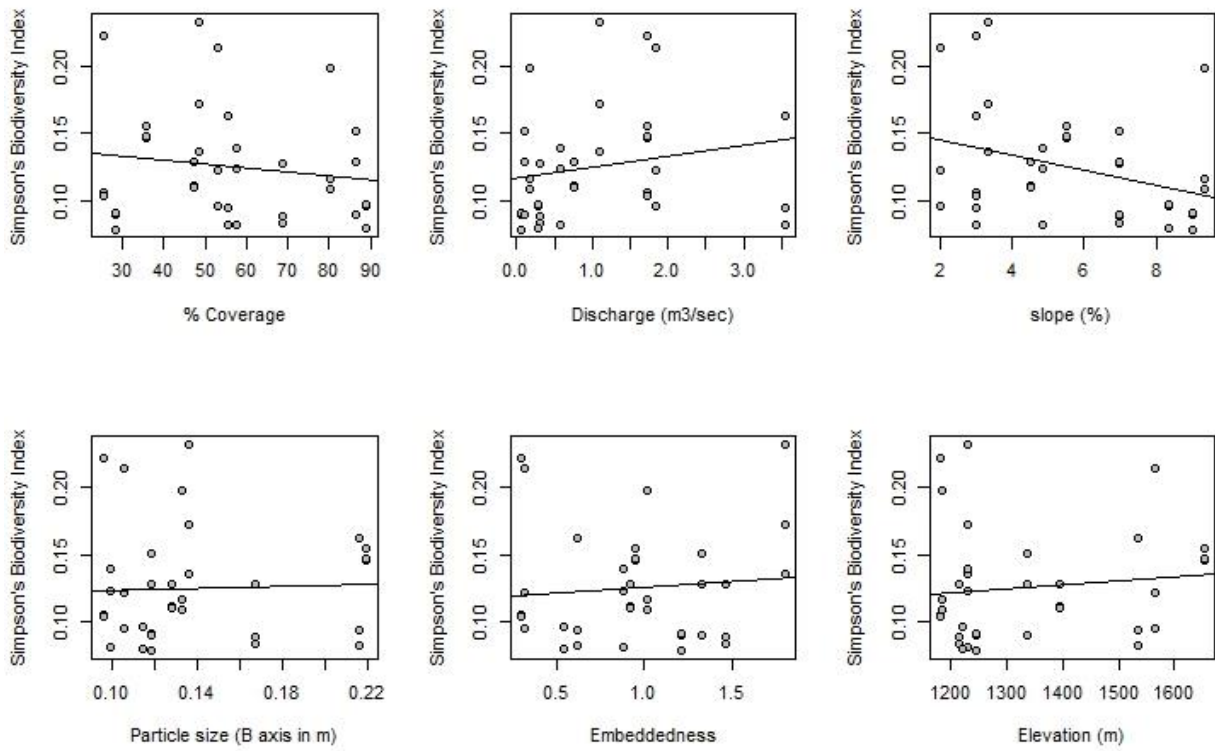
Substrate embeddedness had no effect on macroinvertebrate biomass (linear regression,  $t = 0.08$ ,  $p = 0.94$ ,  $df = 34$ ).

Embeddedness is the mean of 100 measurements of categorical values in each study reach. Categories: 0=0%, 1=0-25%, 2=25-50%, 3=50-75%, 4=75-100% embedded.



Elevation had no effect on macroinvertebrate biomass (linear regression,  $t = -1.56$ ,  $p = 0.13$ ,  $df = 34$ ).





Simpson's Biodiversity Index for all measured environmental variables. There are no colors indicating the specific tributary because there was no pattern and therefore the individual samples are not relevant.