

Biotic Response to Riparian Disturbance in Head-water Streams in British Columbia

by

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Abstract

Five forest disturbance regimes (wildfire, mountain pine beetle (MPB), commercial harvest, and two sets of references) were investigated to determine transitive effects on aquatic ecosystems in fifteen headwater streams in the southern interior of British Columbia. The particular focus for this study was aquatic macro-invertebrates and their trophic resources (forest litter, periphyton, and particulate organic matter). At each site, sampling occurred three times over the summer and fall of 2009, across a one-hundred meter reach.

Disturbances resulted in clear alterations of canopy coverage and litter loading. The two canopy consuming disturbances (fire and harvesting) showed marked decreases in their proportional canopy coverage. Litter loading in MPB was significantly greater, while fire streams' litter loading was directly related to canopy coverage, and significantly less than reference sites. Periphyton mean growth was unrelated to disturbance; however inter-stream variance was reduced in the burned systems and increased in the MPB systems. Macro-invertebrate measurements were not different across disturbances, however, abundances and biomass did exhibit different temporal interactions with the Montane Spruce disturbances. Abundances of invertebrate functional feeding groups were unrelated to their food resource, and did not differ across disturbance type. Invertebrate diversity measurements were also similar across disturbance regime.

While aquatic ecosystems were generally robust in response to riparian disturbance events in this study, we were able to uncover slight differences across disturbance regimes. The temporal and spatial findings in this paper are of particular importance as they illustrate differences between MPB and salvage logging effects.

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1 Introduction

Riparian vegetation plays an essential role in the physical and biological dynamics of streams, particularly in small first and second order headwater streams. Headwater stream environments are influenced by their riparian forests through effects on light (Kiffney et al. 2004), temperature (Moore et al. 2005), nutrient and carbon inputs (Compton et al. 2003; Cummins et al. 1989; Fisher & Likens 1973; Nakano et al. 1999) as well as habitat creation and stabilization through inputs of large wood debris (LWD) (Bilby 1984; Bilby & Likens 1980; Carlson et al. 1990; Fausch & Northcote 1992). There are also cross-ecosystem interactions via anadromous salmon carcasses enriching streams and adjacent terrestrial ecosystems, and the transfer of aquatic insects to forests through emergence, and terrestrial insects falling into streams (Helfield & Naiman 2001; Nakano & Murakami 2001).

Natural and anthropogenic disturbances (e.g., floods, debris flows, logging, dams) are a major driver of riparian/stream ecosystems (Lake 2000; Resh et al. 1988; Townsend et al. 1997) affecting biological and physical diversity in a variety of ways. The resulting effects are dependent upon the type, timing, area, intensity, duration, and frequency of the disturbance event. According to the intermediate disturbance hypothesis (Connell 1978), disturbances that are infrequent or of low intensity favour the most robust, longest-lived, and most competitively dominant species. In contrast, frequent or intense disturbances favour species that have high mobility and rapid maturity, allowing them to quickly colonize depopulated areas. Disturbances that fall in between these extremes normally exhibit higher diversity because they allow the co-existence of these two groups of traits. Regardless of the eventual interplay with diversity, the

immediate response following a disturbance event is one of lowered abundance and diversity (Connell 1978).

Recent outbreaks of the native bark boring beetle, *Dendroctonus ponderosae* Hopkins, (from here on referred to as MPB (mountain pine beetle)) have had significant effects on the forests of British Columbia (BC). Surveys indicate over 6 million hectares of BC pine forests have been infested by the MPB (Westfall & Ebata 2010). This massive infestation has received significant attention from various research fields; however, few have had an aquatic focus (Wiensczyk 2008). Furthermore, climate change may lead to warmer winters, which may increase the range of forest pests world-wide, influencing forest health, and potentially also influencing streams that drain these forests (Carroll et al. 2006). The large-scale MPB outbreak provides an opportunity to improve our understanding of this natural disturbance of riparian vegetation and ensuing effects on stream ecosystems.

Wildfires are common in the BC forests, burning on average 98,541 hectares annually (<http://bcwildfire.ca/History/average.htm>). Previous research has shown that effects of fire on streams depend largely on the magnitude of the fire and on subsequent scouring or runoff disturbances after large precipitation events or snowmelt (Gresswell 1999; Minshall 2003). Streams in Arizona displayed negligible direct effects following a massive catastrophic fire; however, the subsequent runoff events flooded the streams with suspended solids, causing heavy declines in both fish and invertebrate abundance (Rinne 1996). Scouring and increased turbidity have also been credited for the lack of predicted periphyton increases following fires

in Idaho (Minshall et al. 2001a). Intense fires, consuming all the overhead canopy, have been shown to alter the invertebrate community structure as well, driving communities towards periphyton (autochthonous) consumers rather than forest litter (allochthonous) sources (Mihuc & Minshall 2005; Spencer et al. 2003). This change in the available energy sources should lead to changes in composition of functional feeding groups, favouring the scrapers and collectors (Cummins & Klug 1979). These immediate effects seem to be short-lived as streams return to reference levels within a few years.

Much like wildfires, logging can completely eliminate riparian canopy, depending on forestry practices. Studies of the immediate effects of commercial harvest regularly report increases in the abundances of certain invertebrates. This change is credited to increased light which promotes primary production (Danehy et al. 2007; Fuchs et al. 2003; Murphy et al. 1981) and increased particulate organic matter levels from slash inputs (Hernandez et al. 2005; Kreutzweiser et al. 2005). The legacy of logging effects on streams are mixed across the literature; in some cases logging effects have been detected many decades afterward (Harding et al. 1998; Nislow & Lowe 2006), or invertebrate abundances return to reference levels ten to twenty years post harvest (Fuchs et al. 2003; Murphy & Hall 1981).

In this study we compared the early (less than 5 years) post-disturbance effects of MPB infestation, wildfire and commercial harvest on stream invertebrate food webs. We examined the relationship between invertebrate functional feeding groups and their respective food resource (forest litter, periphyton, coarse and fine particulate organic matter (CPOM and

FPOM)), and the overall abundance and diversity of these communities. We hypothesized that the riparian clearing disturbances (fire and harvest) cause immediate drops in invertebrate abundance and diversity and drive the aquatic communities toward a reliance on autochthonous food resources. We predicted that MPB influenced communities will greatly favour consumers of allochthonous materials, but will exhibit no changes in abundance or diversity. We also predicted greater spatial homogeneity in biological communities in fire and harvest streams because these disturbances have a relatively uniform (i.e., all trees are removed) effect on riparian conditions. We also expected to find greater spatial heterogeneity in MPB streams because beetles primarily effect Lodgepole pines in these mixed stands (i.e., dead pines mixed with live spruce and fir) bordering streams.

2 Methods

2.1 Site Selection and Description

Fifteen comparable low order streams (first and second orders) located across the Okanagan Valley in British Columbia (Figure 1, 2) were selected for this study, with three replicate streams for each disturbance regime (Table 1). These streams are part of a larger, long-term research project focusing on large wood debris (LWD) dynamics and their relation to forest disturbance. We sampled one-hundred-meter reaches that had been established along these streams as part of the project. These reaches were used to integrate the breadth of data from the aforementioned study. Mean annual precipitation ranges from 380 to 900 mm with mean annual temperatures of 1.6 to 9.5 °C in the lowlands, and 0.5 to 4.7 °C in the mountains. The subsurface is made up of volcanic bedrock-derived glacial deposits which are well- to moderately-well-draining (Meidinger & Pojar 1991).

Disturbance regimes (MPB, fire and forest harvest) were spread across two biogeoclimatic zones: Montane Spruce (MS) and Interior Douglas-Fir (IDF). The IDF study sites include an area within the 2003 burned Okanagan Mountain Provincial Park and undisturbed reference stands on the west slope of the Okanagan Valley. Disturbance regimes within the MS zone include MPB infestation, sites of commercial logging, and undisturbed controls. Disturbance response variables of each zone were compared to the response variables from the reference sites of their similar zone.

2.2 Spatial and Temporal Sampling

All sampling occurred over three months during the summer of 2009 (July, August and September), with allochthonous input and periphyton accumulation measured each month. Vertical allochthonous input falling into the stream was collected using 0.25 m² litter traps (0.5m x 0.5m, mesh 0.1mm) set at the approximate center of the stream and spaced at twenty-meter intervals ($N=5$). Materials blown in laterally into the stream were collected using 0.1 m² traps (0.2m x 0.5m, mesh 0.1mm) set at each side of the stream channel at forty-meter intervals ($N=3$). All material was collected within each trap each month as described by Eloise & Pozo (2005). We quantified canopy coverage at each measurement site using a convex mirror densiometer according to the methods laid out by Lemmon (1956). By counting the number of covered squares on the densiometer grind, we establish a proportion of covered sky. Water temperatures were determined using data loggers (Onset HOBO loggers) in 9 of the 15 streams, with at least one logger in each disturbance regime. Monitoring stream temperature was limited due to resource constraints. Loggers were deployed for one month to establish a relative daily average.

We haphazardly collected stream rocks from sampling stations every ten meters across the one-hundred-meter reach. Every ten meters of stream length contained a randomly selected site within it, ensuring that our random sampling would be spread out over the length of the reach (see Figure 3). A random subset of seven of these ten sites was sampled. All samples were stored at -10°C until they could be processed and measured in the lab.

Invertebrate sampling occurred monthly during the summer of 2009 (July, August and September). Organic flux and drifting invertebrates were collected using a drift net (250 μ m mesh) set in the middle of flow, capturing material for the lesser of an hour, or until the net became full. The height of the water flowing through the net and its velocity were also measured. These measurements combined with the amount of time that the net was in the stream allowed the calculation of discharge flowing through the net. We preserved all materials collected in the net in ethanol (85%) until sorting in the laboratory.

Artificial substrate trays (see Clements et al. 1989) were deployed at random along the length of the stream reach. Trays were plastic with dimensions of 10 x 10 x 5 cm and had holes throughout, allowing water, FPOM, CPOM, and invertebrates to easily move through trays. We filled all trays with similarly sized large pebble (45.8 mm average diameter) to ensure that substrate conditions were controlled. Random deployment occurred at the same sampling locations as described above (see Figure 3). A total of twenty-four trays were deployed in each stream in groups of three at each sampling location ($N=72$ per disturbance). Trays were buried in the benthos so that the substrate within the tray was flush with the substrate of the stream. Deployment of trays occurred shortly after the spring freshet. During each sampling month, one tray from each group of three was removed (8 per stream) and stored in a Ziploc bag for transport. Back in the laboratory, contents of each were thoroughly washed and scrubbed into a 250 μ m sieve, where all macro-invertebrates were removed and preserved in ethanol.

2.3 Sample Processing

Litter material collected in traps was sorted into the following categories: needles, leaves, reproductive material (seeds, flowers, and pollen cones), woody material (wood, bark, and seed cones) and other material (mostly lichen). All sorted samples were dried at 100°C for twenty-four hours and weighed to obtain the dry weight of each category. Total periphyton organic matter on each rock was measured by scrubbing and rinsing rocks, and pouring material onto a pre-ashed and pre-weighed 0.7 µm glass fiber filter. Filters were dried (at 100°C for twenty-four hours) and weighed, then ashed (at 500°C for 4 hours) and weighed again to determine ash free dry mass (AFDM). Macro-invertebrates collected in drift nets were identified to genus; individuals smaller than 4.0 mm were identified to family. Insect identifications were done using Merritt, Cummins, & Berg (2008). All other materials (e.g., leaves, needles, exuviae, POM) collected in drift nets were dried (100°C for 24 hours) and ashed (500°C for 4 hours) to determine the total content of organic flux during the sampling period.

Individuals removed from substrate trays were identified to genus (or family when <4.0 mm) and measured (body length, to the nearest 0.05mm). Individual body mass was determined by extrapolation using length-to-weight regressions (Burgherr & Meyer 1997; Meyer 1989; Sample et al. 1993; Smock 1980). All individuals from a tray were combined to determine AFDM of the total benthic invertebrate community in that tray. Functional feeding groups were determined using classifications created by Merritt, Cummins, & Berg (2008). Feeding groups include; scrapers which consume the periphyton mass covering the benthos, shredders which consume the CPOM, filterers which consume the drifting FPOM, gatherers which consume the

sedimentary FPOM, and predators which consume living animal tissue. Shannon diversity (H' , 2.1) and evenness (E' , 2.2) were calculated using the following equations.

$$H' = -\sum_{i=1}^N p_i \ln(p_i) \quad (2.1)$$

$$E' = \frac{H'}{\ln(N)} \quad (2.2)$$

N represents the total number of taxa in the sample, p_i is the proportion of taxon i out of N , and i is taxon number 1, 2, 3,.... N .

2.4 Data Analysis

We assessed mean difference across disturbance regimes between litter mass, periphyton, invertebrate abundance, invertebrate mass and diversity. Because we sampled the same streams monthly for three months, we used a nested repeated measure ANOVA. The model used was

$$y_{ijkl} = \mu + \beta_i + \alpha_j + \chi_{k(j)} + (\beta\alpha)_{ij} + (\beta\chi)_{ik(j)} + \varepsilon_{ijkl} \quad (2.3)$$

where μ is the population mean, β_i is the fixed month i ; α_j is the fixed disturbance j ; $\chi_{k(j)}$ is the random stream k nested within disturbance j ; ε is the random error at site $ijkl$. Prior to each ANOVA, tests for normality and equality of variance were conducted for each dependent variable at the disturbance level. Those found outside the bounds of the assumptions necessary for such an ANOVA were transformed accordingly. Bartlett's test for equality of variance was conducted across disturbances.

As litter inputs, periphyton biomass, and temperature can be related to the overhead canopy, Spearman correlation analyses were conducted for each biogeoclimatic zone to determine relationships among these variables. Periphyton growth can also be influenced by a number of factors, such as temperature, discharge, and scraper populations. Correlations among these variables were therefore examined. We also predicted that invertebrate feeding groups would be correlated with their dominant food source, and used Spearman correlation coefficient to examine the relationship between functional feeding group and food resources. All statistical analyses were conducted with SYSTAT 11.

Allochthonous loading was expected to be related to canopy cover; analysis of covariance was used to examine this relationship across disturbance regimes. We used an ANCOVA for this test, which was defined by the following model

$$y_{ij} = \mu + \alpha_i + \beta_0(x_{ij} - \bar{x}) + \varepsilon_{ij} \quad (2.4)$$

where μ is the population mean; α_i is the disturbance i ; x_{ij} is the canopy coverage at site ij ; ε is the random error at site ij . ANCOVA analyses were conducted using SAS 9.1.

A redundancy analysis (RDA), which incorporated environmental and invertebrate species data, was conducted to establish each disturbance's ordination through time. Environmental data included mean grain size, mean gradient, mean width, periphyton biomass, canopy coverage, and litter biomass. Species data came from 14 dominant taxa (i.e., had greater than 1000 individual counts and were found in at least 3/4 of the streams). These taxa constituted 83.3% of the total invertebrates sampled. The ordination was created using R (vegan).

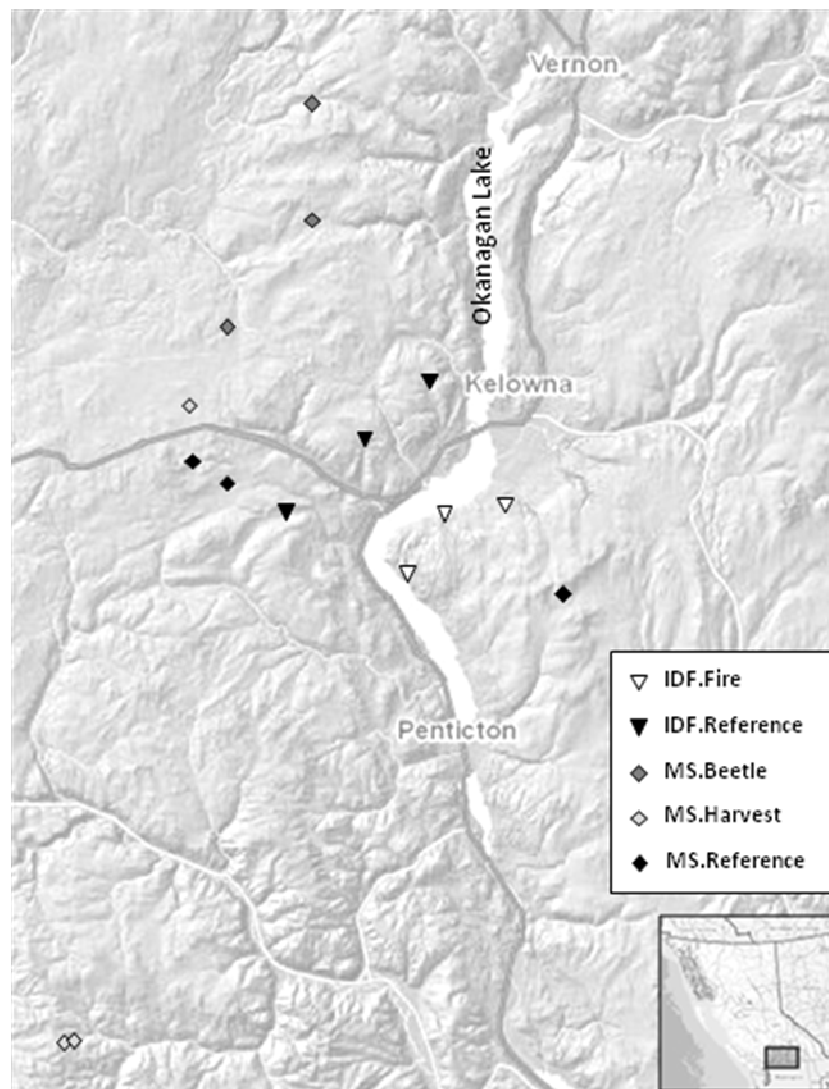


Figure 1. Map of study locations in the Okanagan Valley. Inset indicates location within British Columbia.



Figure 2. Photographs of study locations. Left; Duru #1, MS. Harvest stream, during freshet. Middle; Beak Creek, MS. Beetle stream, during freshet. Right; Pennask Creek, MS. Reference stream, during late summer low flow.

Table 1. Physical stream characteristics for all study streams. Northing and Easting in units of UTMs. Elevation and width measured in meters. Gradient measured in units of % slope. Grains are the median grain size in millimeters as measured by a gravelometer.

Stream	Treatment	Zone	Northing	Easting	Order	Elevation	Width	Gradient	Grains
Bellevue	IDF.Fire	11 U	5518365	322972	2nd	603	6.96	4.46	90
Deeper		11 U	5515649	313500	2nd	717	3.79	5.9	64
Goode		11 U	5508846	306510	1st	438	2.68	3.37	64
Greata	IDF.Reference	11 U	5519844	291274	1st	1028	2.67	2.1	22.6
Jack		11 U	5526836	303107	2nd	891	4.19	7.16	128
McDougal		11 U	5533790	312741	2nd	947	3.38	6.19	64
Beak	MS.Beetle	11 U	5558188	299098	1st	1373	2.13	6.45	128
Cotton		11 U	5574517	302106	1st	1486	2.26	7.28	32
Mellin		11 U	5547187	287384	1st	1297	1.61	3.06	90
Duru. #1	MS.Harvest	10 U	5443136	689924	1st	1714	3.12	2.23	32
Duru. #2		10 U	5442930	688921	1st	1763	2.08	10.34	32
Km 9		10 U	5534462	710633	1st	1544	1.12	4.73	5.6
Pennask	MS.Reference	10 U	5524138	714864	1st	1336	3.7	2.51	64
Trout		10 U	5527904	711057	1st	1666	2.12	2.58	16
U. Penticton		11 U	5502562	326795	1st	1605	2.81	4.43	90

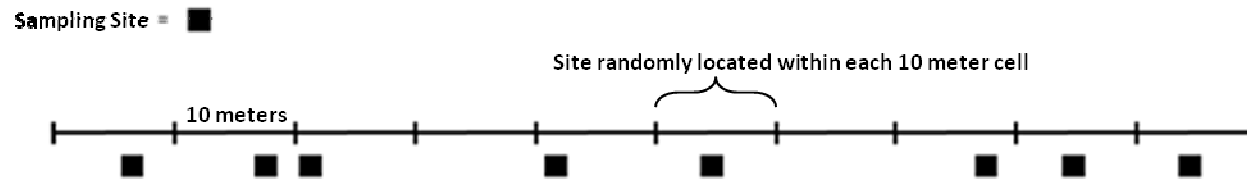


Figure 3. Diagram of randomization strategy. Whole length of line represents the designated 100 meter stream reach. Black squares represent sampling location

3 Results

3.1 Canopy

Riparian vegetation consisted of mostly large deciduous (birch and aspen) and coniferous trees. Willow and other streamside shrubs were common in the lowland IDF streams, but rare in the MS zone. Alder was also rare and only slightly more common in the IDF zone. Canopy coverage was greatest in IDF reference sites and lowest in harvest sites (Table 2). Mean canopy cover in fire and harvest streams was significantly reduced ($F = 101.0$ and 61.6 respectively, $p < 0.001$ for both), where remaining canopy was 21.8% and 15.7% of respective reference measurements. This reduced canopy cover was consistent across months for these two disturbance regimes. MPB sites were not statistically different in canopy coverage from the MS reference sites. Canopy cover increased over time in the IDF biogeoclimatic zone, where August exhibited a slightly greater coverage ($F = 4.66$, $p = 0.045$).

Canopy coverage in the harvest sites was significantly less variable than the two other MS disturbance regimes ($\chi^2 = 9.48$, $p = 0.009$), which was due to uniformly low canopy values across harvest streams. Both IDF reference and burned streams show comparably low variance across streams. There was no evidence of a correlation between canopy cover and water temperature at any site.

3.2 Allochthonous Input

Lateral traps exhibited very high variability and infiltration of bank slope material (soil and moss), and showed no difference between disturbance and reference sites ($F = 0.56$, $p = 0.582$ in IDF, and $F = 0.22$, $p = 0.806$ in MS). Due to this, only the vertical input trap data were used in the analysis. Litter inputs were greatest at MPB streams (1.77 ± 1.91 grams per month/m² [mean ± 1 SD]), while burned streams received close to an order of magnitude lower inputs (0.36 ± 0.93 grams per month/m²). Significantly less allochthonous material ($80.1\% < \text{reference}$) fell into fire disturbed streams ($F = 57.7$, $p < 0.0001$), and greater amounts ($282\% > \text{reference}$) fell in the MPB disturbance sites ($F = 4.09$, $p = 0.075$) (Table 3). A large amount of litter inputs was collected at the harvest streams, averaging 108% of the reference sites. Litter inputs were greatest during September (IDF) and August (MS) (September was dropped from MS analysis as the harvest streams were not sampled in September, $F = 8.57$ & 2.89 , $p = 0.002$ & 0.094 , respectively for month effect). The IDF streams displayed an interaction effect between disturbance and month ($F = 4.01$, $p = 0.034$), due to litter inputs increasing over time at reference streams while litter flux at burned streams was consistent across months. Litter inputs at all MS zone disturbance regimes displayed a general increasing temporal trend.

The MPB and harvest reaches within the MS zone were more variable than reference sites, (i.e., test of equality of variances, $\chi^2 = 30.5$, $p < 0.001$). The MPB disturbance sites were more variable than both the MS zone disturbance regimes and most months, (harvest variability was greater in June) (Table 3). Burned reaches were less variable than other sites ($\chi^2 = 31.6$, p

<0.001), except for August, where variance was greater than that of the IDF reference streams due to a pulse of wood matter falling into various traps during this month.

Litter material in the IDF streams was composed mostly of leaf, needle and wood detritus, while the litter in the MS zone was largely comprised of needle and wood detritus (Figure 4). These three litter categories (making up 89.1% of the total litter mass) increased over time, except at the harvest disturbance sites where needle loading was the greatest at the beginning of sampling, and decreased with time.

At both IDF and MS zones, canopy cover was strongly correlated with litter inputs; therefore we used canopy cover as a covariate in our analysis of disturbance effects. We found that differences in allochthonous input among IDF disturbance regimes were not statistically different ($F = 1.48$, $p = 0.227$) (Figure 5), meaning litter loading in the IDF zone was more related to canopy coverage than disturbance. In contrast, we found that litter inputs were significantly different among MS disturbance sites when controlling for canopy coverage ($F = 3.72$, $p = 0.028$) (Figure 6). Specifically, MPB streams had significantly greater amounts of allochthonous input compared to the MS reference streams at similar canopy coverage (Tukey's mean comparison test, $p = 0.02$). Harvest and MS reference streams remain similar in their allochthonous loading with respect to canopy cover ($p = 0.89$)

FPOM and CPOM mass captured in the drift were significantly greater during the month of May for each zone ($F = 8.629$, $p = 0.005$ in IDF, and $F = 9.973$, $p = 0.003$ in MS) (Table 4). Drift

biomass (both FPOM and CPOM) in fire streams was significantly less than reference streams ($F = 6.31$, $p = 0.087$), while MS zone disturbance regimes were no different in their POM loading ($F = 0.12$, $p = 0.887$).

3.3 Periphyton

Periphyton biomass was the highest at the IDF reference sites ($0.44 \pm 0.45 \text{ mg/cm}^2$) while the MS reference streams yielded the least amount of biomass ($0.17 \pm 0.16 \text{ mg/cm}^2$) (Table 5). Mean periphyton growth exhibited no disturbance effect for either of the biogeoclimatic zones ($F = 0.13$ & 0.90 , $p = 0.73$ & 0.45 for IDF & MS, respectively) despite the large difference between the MPB and reference disturbance regime (periphyton biomass at the MPB site was 221% of the reference mass). This is due to the large inter- and intra-stream variation at the MPB disturbance sites (Figure 7). Periphyton biomass at the MPB and harvest sites was consistently greater than reference values for all months measured; however these elevated averages can be credited to one highly productive stream in each of these disturbance regimes. There were no significant interactions between disturbance and month for either zone; however, periphyton biomass at the fire disturbance site increased about 50% each month, while periphyton biomass in other disturbance regimes was relatively constant.

Variability in periphyton standing stocks in the MS system was greatest at the MPB disturbance ($\chi^2 = 55.9$, $p < 0.001$), and this was consistent across months. This was largely due to variability across disturbance streams, not across sites, as mentioned above. A similar result was seen in

the IDF zone, as periphyton biomass in fire disturbance was less variable than other disturbance regimes ($\chi^2 = 19.2$, $p < 0.001$), due to high variability across reference streams (Figure 8).

Canopy cover was correlated with periphyton biomass at the IDF reference sites ($r = -0.46$, $p = 0.0015$). It is worth noting that all systems with an intact canopy (references and MPB streams) showed a similar negative trend between periphyton and canopy, while sites with reduced canopy (fire and harvest) showed the reverse pattern (periphyton growth increases as canopy coverage increases). There was a strong positive correlation between temperature and periphyton growth ($r = 0.58$, $p < 0.001$) (Figure 9). Stream discharge was negatively correlated to periphyton growth ($p < 0.001$), however the correlation was relatively weak ($r = -0.20$) (Figure 10).

3.4 Total Invertebrate Response

Invertebrate abundance was the greatest in the IDF reference streams (average 394 ± 285 per tray), and lowest in the MPB streams (157 ± 139 per tray) (Table 6). There was no disturbance effect on total invertebrate abundances for either the MS or IDF biogeoclimatic zones ($F = 0.17$ & 0.16 , $p = 0.71$ & 0.84 , respectively). However, there was a significant temporal difference for both IDF and MS zones ($F = 6.63$ & 10.1 , $p = 0.02$ & 0.002 , respectively), with the lowest abundance occurring in September at the IDF and July at the MS sites. Disturbance effects varied with time in the MS zone ($F = 9.1$, $p = 0.001$), where the number of individuals in the MPB streams declined over the sampling period while they increased in the other two MS

disturbance regimes. Invertebrate abundance declined in both disturbance regimes in the IDF system, though this trend was not statistically significant ($F = 0.28$, $p = 0.76$).

Spatial variability in invertebrate abundance differed across disturbances in the MS system ($\chi^2 = 18.8$, $p < 0.001$), where MPB streams were the least variable except during July where it exhibited the greatest variation (due to fluctuations in chironomids). Harvest sites were more variable than reference sites only during August. Invertebrate abundances in the fire sites exhibited lower variability ($\chi^2 = 7.2$, $p = 0.007$), with the exception of July, where measures were more variable ($\chi^2 = 5.2$, $p = 0.023$). Invertebrate variance values for abundance and biomass were in general quite high for all streams. This elevated variance was due to the occasional sample which would contain many invertebrates.

IDF reference sites also yielded the greatest invertebrate biomass with an average of 39.4 ± 35.7 mg per sampling tray, while the reference sites from the MS zone yielded the least (12.8 ± 15.3 mg, Table 6). No significant disturbance effect on mass was found in either zone ($F = 0.12$ & 0.23 , $p = 0.75$ & 0.68 for IDF & MS, respectively) (Figure 11, 12). Temporally, invertebrate biomass was the lowest in September for the IDF zone ($F = 4.26$, $p = 0.055$).

There was a significant interaction between month and disturbance ($F = 3.6$, $p = 0.037$) in the MS system; harvest streams displayed an increasing trend in invertebrate biomass over the summer, while invertebrate biomass in the other two MS disturbance regimes remained relatively constant. Invertebrate biomass in the burned system exhibited less variability across

disturbance streams ($\chi^2 = 39.5$ $p < 0.001$), and this was consistent for all months. Disturbance regimes in the MS zone did not differ in invertebrate biomass variance, except for the initial month of July within harvest sites.

Ephemeroptera, Trichoptera and Plecoptera (EPT) made up a sizable proportion of the total biomass, ranging from 63% of the total mass (in the MPB streams), to 37.5% (in the harvest streams). EPT biomass greatly resembled the overall invertebrate biomass, but no statistically significant differences were found ($F = 0.25$, $p = 0.641$ in IDF, and $F = 0.23$, $p = 0.763$ in MS). In the IDF zone, EPT biomass declined over time, where September biomass was significantly less than earlier months ($F = 12.41$, $p = 0.004$).

Distributions of individuals' weights across disturbance regimes could not be normally transformed, thus a Kruskal-Wallis ANOVA was performed. Comparing the mean weight of individual invertebrates, we observed the greatest average size in the IDF reference sites (99.9 ± 55.7 $\mu\text{g}/\text{individual}$) and the lowest average was found at the MS reference sites (56.7 ± 53.6 $\mu\text{g}/\text{individual}$). Despite the large amount of distribution overlap (Figure 13), means were significantly different ($U = 2.07 \times 10^8$, $p < 0.001$ for IDF, $H = 764.8$, $p < 0.001$ for MS). The burned streams had consistently smaller individuals than the IDF reference system during each month of this study. On average, invertebrates were larger in the harvest and MPB streams relative to reference sites during each month sampled, except July, when invertebrates were smaller in the harvest sites. There was a weak correlation between mean individual mass and abundance for each stream ($r = -0.22$, $p = 0.147$) (Figure 14).

In the IDF sites, there was no disturbance effect on the number of invertebrates in the drift ($F = 0.780$, $p = 0.442$) (Table 4) nor any differences across months ($F = 1.411$, $p = 0.302$). In the MS zone, there were significant disturbance, month and interaction effects. Drift abundance in the harvest streams was significantly greater than the reference streams ($F = 7.299$, $p = 0.070$). The lowest drift numbers in the MS were found in the month of August ($F = 3.111$, $p = 0.081$). The interaction effects ($F = 3.854$, $p = 0.035$) were a result of drift density at the MPB sites, being highest in May (13.6 ± 13.3 individuals/m³), and declining to 1.38 ± 1.5 individuals/m³ in September. In contrast, drift densities in harvest streams were lowest in May (1.15 individuals/m³) but increased to 14.2 ± 16.8 individuals/m³ in September, while reference streams had relatively consistent numbers across months, ranging only from 1.57 ± 1.58 to 3.61 ± 3.22 individuals/m³.

3.5 Community Response

Seventy different taxonomic groups were identified in collected samples (Table 7). The IDF reference sites had the greatest number of taxa, with an average of 13.4 ± 4.5 per tray, while the harvest sites had the fewest (8.5 ± 2.3 per tray) (Table 8). Mean number of invertebrate taxa was not significantly affected by disturbance in any biogeoclimatic zone ($F = 1.19$, $p = 0.435$ in IDF, and $F = 0.41$, $p = 0.680$ in MS), though all disturbance regimes tested in this study had consistently reduced mean numbers of taxa relative to reference sites across all months. Taxa richness was highest in August for both zones, though only significantly so in the IDF system ($F = 3.52$, $p = 0.08$). No interaction effects were observed.

Variability in taxon richness was significantly lower in the harvest disturbance ($\chi^2 = 4.7$ $p = 0.096$) relative to reference sites. Variation among fire sites was lower than the reference across all months, but not significantly. MPB variance remained very similar to the MS reference.

Similar to the numbers of taxa, disturbance did not have a significant effect on Shannon diversity ($F = 1.36$ & 0.49 , $p = 0.308$ & 0.631 for IDF & MS, respectively), though fire streams exhibited a trend of reduced diversity across all months. Among MS disturbance regimes, reference sites had the lowest Shannon diversity, which was in contrast to MS reference taxa richness (Table 8). Temporally, Shannon diversity was significantly lowest during the month of August ($F = 3.92$, $p = 0.049$). This is due to multiple different subgroups of Chironomidae, which appeared in most of the reference sites during this month. Temporal patterns in diversity at IDF's sites were similar to taxa richness, with August displaying the greatest Shannon diversity ($F = 4.4$, $p = 0.051$). No interaction was found in either system. Variability in diversity was significantly lower in MPB streams ($\chi^2 = 7.2$ $p = 0.026$), while fire and reference streams displayed similar degrees of variation.

Shannon evenness was not significantly affected by disturbances in either biogeoclimatic zone ($F = 0.78$, $p = 0.427$ in the IDF & $F = 0.22$, $p = 0.801$ in the MS). Invertebrate evenness in IDF was also did not vary across months, nor were there interactive effects. Evenness was lowest in August in the MS zone ($F = 11.2$, $p = 0.002$).

All functional feeding groups were represented in each stream, with the relative importance of these different feeding groups varying across time (Table 9). Predators represented the largest proportion of the invertebrate biomass in the two reference systems and in fire streams, shredders constituted the greatest portion in the MPB streams, and collector-gatherers made up the largest proportion of total abundance at the harvest disturbance sites. Unexpectedly, both reference systems exhibited a scraper:shredder biomass ratio more heavily favoring of scrapers (1.33 : 1.0 in the IDF reference, & 1.24 : 1.0 in the MS reference). The two canopy clearing disturbances (fire and harvest) also yielded unexpected results, where shredder biomass was either more abundant or equal in abundance (1.0 : 3.8 in harvest, and 1 : 1 in the burned).

Tests for correlations between the biomass of specific invertebrate feeding groups and their food resource revealed very little relationship between these variables. Biomass of scrapers lacked a significant correlation with periphyton biomass ($r = 0.036$, $p = 0.527$). The same was true for shredders, which were found to have no relationship to litter inputs ($r = -0.009$, $p = 0.895$). Invertebrate predator mass was correlated to the mass of all other feeding groups ($r = 0.375$, $p = 0.000$). Testing the correlation of filter-collector biomass to drift biomass results in a significant correlation ($p = 0.038$), however, it was a very weak negative correlation ($r = -0.114$). Therefore, filtering insect biomass was greater in locations with lesser amounts of suspended organic material.

3.6 Multivariate Analysis

The redundancy analysis for the MS zone reveals that the reference sites are centered around the origin of the array, with each month only slightly altering the ordination (Figure 15). The MPB disturbance sites are centered more towards the upper half of the array (Figure 16).

These MPB sites have a slight temporal shift in the negative direction along the x-axis.

Harvested sites tend to originate around quadrant IV of the array, shifting temporally more towards quadrant IV (Figure 17). During September, the MPB cluster of sites does not overlap with the harvest cluster of sites. Harvest sites were orientated to the position opposite of greater periphyton mass and grain size. *Paraleptophlebia* and Tanypodinae were most closely associated with sites of greater periphyton mass.

Reference sites in the IDF ordination array tend to be off-centered with respect to the origin, very slightly towards quadrant III (Figure 18). Temporality only slightly alters the shape of the point spread. Burned sites originate slightly towards quadrant I of the array, and show virtually no temporal shift (Figure 19). Fire sites were orientated to the position opposite of greater canopy and litter mass measurements. *Paraleptophlebia*, Copepoda, *Malenka*, and Ostracoda were most closely associated with sites of greater periphyton mass. *Baetis*, *Haploperla*, Chironominae, Tanypodinae, and small Plecoptera (unidentified individuals) were most closely associated with sites of greater litter mass and canopy coverage.

Table 2. Mean proportion of canopy coverage across all disturbances and months during the study. Variance values in parentheses. * is significant to $p<0.1$, ** is significant to $p<0.01$, *** is significant to $p<0.001$. Significance compared against reference.

	June	July	August	September	Total
IDF.Fire	0.152* (0.004)	0.197* (0.008)	0.225* (0.014)	0.154* (0.007)	0.182*** (0.009)
IDF.Reference	0.805 (0.005)	0.838 (0.007)	0.875 (0.007)	0.804 (0.013)	0.833 (0.009)
Total	0.413 (0.111)	0.518 (0.113)	0.550 (0.120)	0.479 (0.119)	
MS.Beetle	0.670 (0.032)	0.706 (0.022**)	0.775 (0.013)	0.663 (0.021)	0.707 (0.022)
MS.Harvest	0.131* (0.013)	0.110* (0.008)	0.099* (0.009)	0.120* (0.014)	0.115*** (0.010**)
MS.Reference	0.706 (0.018)	0.810 (0.003)	0.784 (0.016)	0.638 (0.043)	0.734 (0.024)
Total	0.482 (0.094)	0.542 (0.108)	0.553 (0.117)	0.474 (0.089)	

Table 3. Mean litter weight (grams per trap) of each litter type across all disturbances and months. Combined dry weights are in bold type. Variance values in parentheses. * is significant to p<0.1, ** is significant to p<0.01, *** is significant to p<0.001. Significance compared against reference.

	June	July	August	September	Total
IDF.Fire	0.538* (0.6208*)	0.913 (2.2333)	2.938* (53.477*)	1.686* (3.3513***)	1.462** (13.967***)
Leaf	0.035 (0.0063)	0.309 (1.1150)	0.413 (1.9980)	0.941 (1.5731)	0.406 (1.172)
Needle	0.063 (0.0088)	0.010 (0.0008)	0.010 (0.0002)	0.402 (0.9892)	0.115 (0.244)
Other	0.099 (0.0138)	0.078 (0.0097)	0.097 (0.0098)	0.050 (0.0044)	0.081 (0.009)
Reproductive	0.064 (0.0112)	0.043 (0.0052)	0.037 (0.0005)	0.033 (0.0025)	0.045 (0.005)
Woody	0.275 (0.4745)	0.472 (1.3339)	2.380 (51.863)	0.258 (0.2144)	0.812 (12.586)
IDF.Reference	2.457 (1.7552)	1.233 (2.2019)	5.510 (15.993)	18.97 (48.522)	7.327 (68.756)
Leaf	0.182 (0.0380)	0.103 (0.0322)	0.423 (0.1284)	10.206 (32.107)	2.865 (27.676)
Needle	0.779 (0.2535)	0.329 (0.0839)	3.208 (12.497)	7.912 (34.581)	3.193 (21.173)
Other	0.742 (0.2153)	0.148 (0.0285)	0.599 (0.0750)	0.341 (0.0138)	0.463 (0.129)
Reproductive	0.162 (0.0064)	0.133 (0.1296)	0.214 (0.1126)	0.306 (0.0484)	0.207 (0.073)
Woody	0.590 (0.7364)	0.518 (1.2372)	1.065 (4.4745)	0.204 (0.0483)	0.597 (1.668)
Total	1.464 (2.078)	1.062 (2.163)	4.316 (33.766)	10.946 (103.71)	
MS.Beetle	3.639 (5.6476)	8.924* (70.496***)	8.847 (88.063**)	33.039 (1805.5)	7.096* (58.150***)
Leaf	0.011 (0.0006)	0.029 (0.0034)	0.308 (0.4437)	2.820 (16.192)	0.118 (0.164)
Needle	1.827 (1.1729)	4.449 (19.881)	5.375 (61.246)	13.055 (34.150)	3.871 (28.688)
Other	0.492 (0.0933)	0.548 (0.1146)	0.566 (0.0628)	1.990 (14.722)	0.535 (0.086)
Reproductive	0.208 (0.0493)	0.784 (1.4172)	0.597 (1.5375)	1.603 (11.862)	0.524 (1.003)
Woody	1.100 (2.2385)	3.113 (11.459)	1.998 (4.0905)	13.569 (1259.8)	2.047 (6.208)
MS.Harvest	2.194 (15.725*)	2.362 (12.708*)	3.708 (80.014**)		2.723 (33.195*)
Leaf	0.017 (0.0012)	0.082 (0.0330)	0.404 (1.5270)		0.160 (0.486)
Needle	1.702 (10.682)	1.474 (5.0744)	0.601 (0.7242)		1.280 (5.552)
Other	0.070 (0.0248)	0.167 (0.1477)	0.073 (0.0023)		0.105 (0.061)
Reproductive	0.013 (0.0006)	0.043 (0.0053)	0.038 (0.0092)		0.032 (0.004)
Woody	0.389 (0.5772)	0.594 (1.1048)	2.590 (83.489)		1.144 (25.964)
MS.Reference	1.974 (5.7444)	1.646 (3.6793)	3.804 (16.106)	10.017 (192.85)	2.518 (9.306)
Leaf	0.023 (0.0062)	0.011 (0.0017)	0.058 (0.0249)	0.674 (5.8195)	0.031 (0.011)
Needle	1.092 (1.9254)	1.013 (0.9843)	1.806 (1.3224)	5.846 (37.041)	1.320 (1.462)
Other	0.286 (0.0920)	0.147 (0.0302)	0.291 (0.0762)	0.738 (4.2336)	0.241 (0.067)
Reproductive	0.107 (0.0168)	0.173 (0.0934)	0.210 (0.0354)	0.212 (0.1283)	0.166 (0.048)
Woody	0.464 (1.2628)	0.301 (0.9751)	1.437 (8.1692)	2.545 (63.059)	0.757 (3.735)
Total	2.642 (9.169)	4.266 (38.011)	5.534 (63.605)	21.925 (1129.3)	

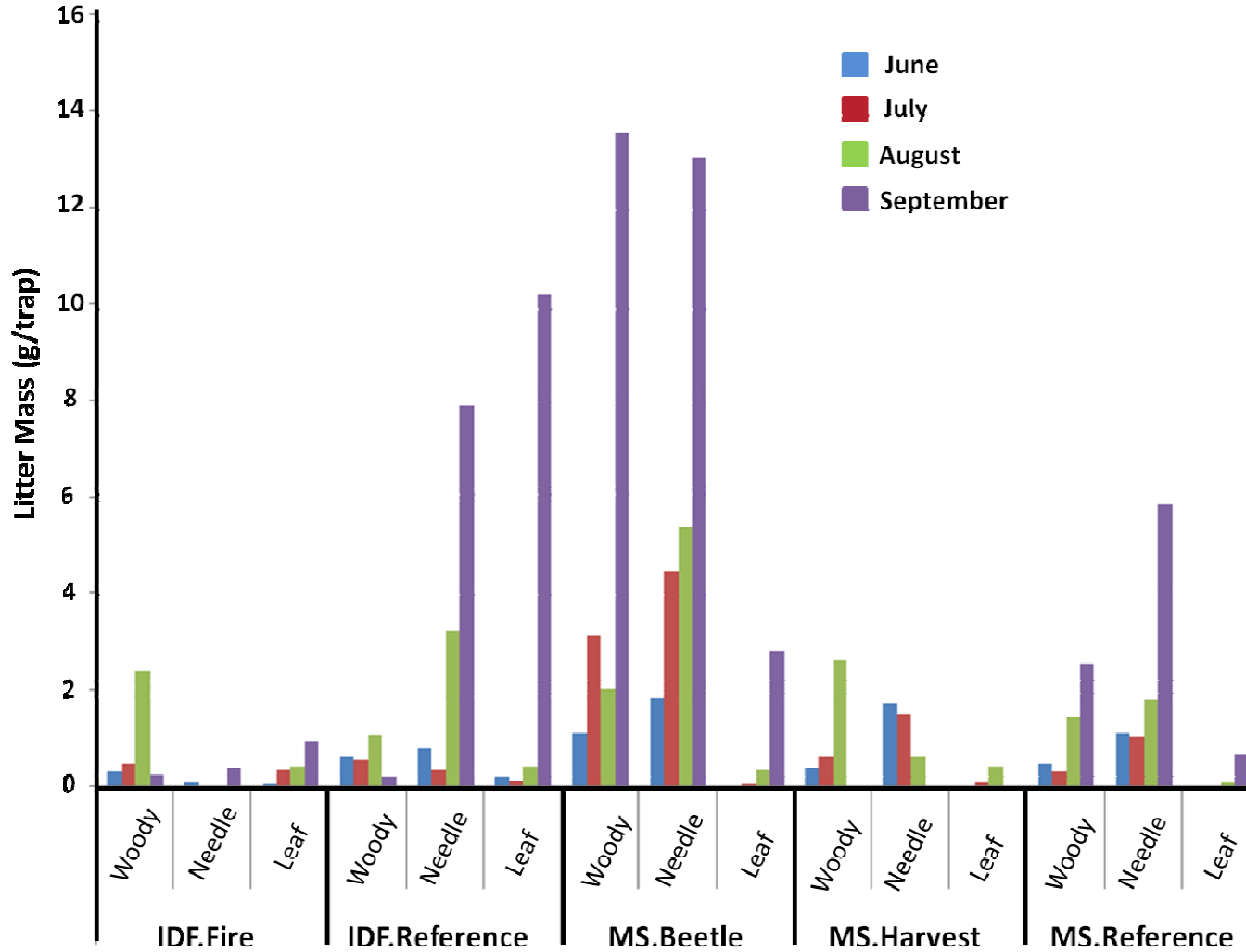


Figure 4. Bar graph of litter mass vs disturbance. Disturbances divided into each major litter category. Months represented by each colored bar.

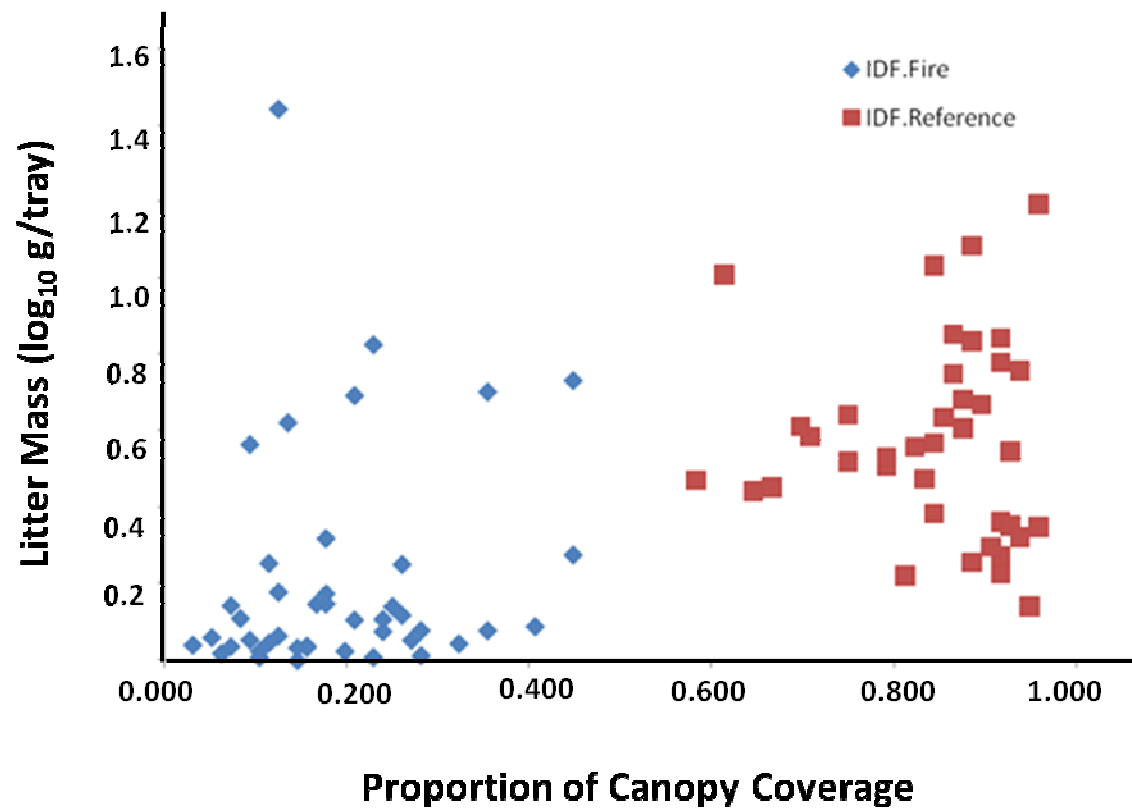


Figure 5. Bi-plot of canopy coverage and litter mass in the IDF zone. Diamonds are fire sites, and squares are IDF reference sites.

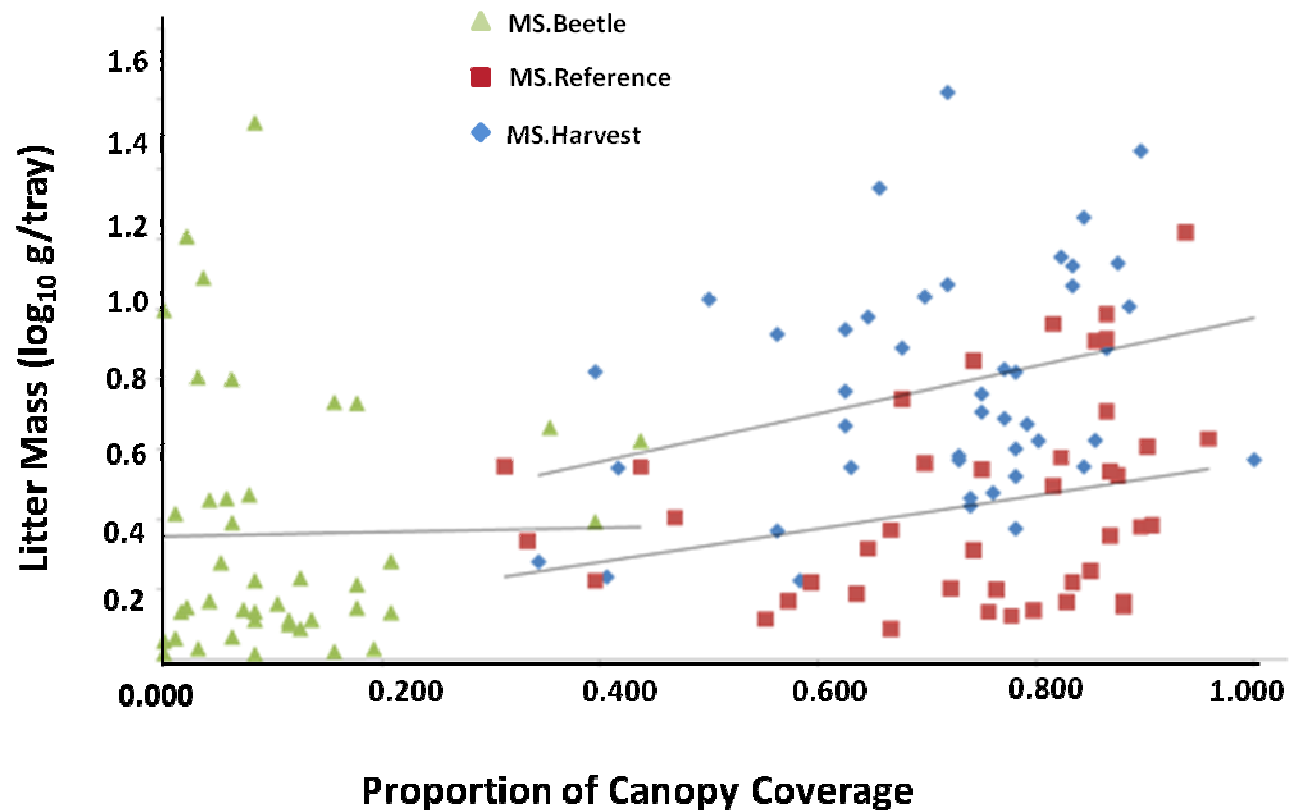


Figure 6. Bi-plot of canopy coverage and litter mass in the MS zone illustrating the ANCOVA of the disturbance effect. Diamonds are MPB sites, triangles are harvest sites, and squares are MS Reference sites. Solid lines show slope of the best fit line for each disturbance regime.

Table 4. Mean number of drift invertebrates (#/m³) and mass of CPOM/FPOM (mg/m³) across all disturbances and months. * is significant to p<0.1. Significance compared against reference. May was excluded from MS zone statistical tests due to lack of replication in the harvest disturbance.

IDF.Fire	May	July	August	Sept	Total
#/m ³	2.83 (2.06)	8.30 (26.2)	5.09 (11.0)	1.95 (1.07)	4.54 (13.9)
mg/m ³	82.9 (2595)	11.3 (181.3)	2.33 (4.39)	2.20 (3.18)	24.7* (1755)
IDF.Reference					
#/m ³	1.77 (2.57)	2.16 (0.97)	3.12 (0.85)	3.08 (4.97)	2.51 (1.82)
mg/m ³	104.3 (39.8)	7.54 (15.9)	8.87 (19.5)	46.0 (1940)	44.7 (2152)
Total					
#/m ³	2.30 (2.19)	5.85 (24.6)	4.10 (5.93)	2.40 (2.16)	
mg/m ³	93.6 (1191)	9.82 (98.9)	5.60 (22.4)	19.7 (1064)	
MS.Beetle					
#/m ³	13.6 (177.0)	7.20 (2.33)	1.46 (0.95)	1.38 (2.52)	6.77 (76.8)
mg/m ³	72.0 (5658)	5.43 (16.6)	3.49 (3.04)	44.7 (2253)	35.9 (2701)
MS.Harvest					
#/m ³	1.15	7.80 (30.9)	3.27 (3.36)	14.2 (280.7)	7.44* (73.1)
mg/m ³	68.3	25.1 (44.3)	13.8 (68.7)	14.9 (11.4)	25.1 (356.)
MS.Reference					
#/m ³	1.57 (2.51)	3.61 (10.4)	2.07 (0.21)	1.39 (0.41)	2.16 (3.30)
mg/m ³	60.4 (2556)	7.64 (23.4)	25.7 (354.2)	11.7 (5.94)	26.3 (1004)
Total					
#/m ³	6.67 (101)	6.08 (16.4)	2.24 (1.35)	5.05 (86.4)	
mg/m ³	66.5 (2772)	13.6 (113)	15.9 (231)	22.1 (621)	

Table 5. Mean biomass (milligrams per cm²) of periphyton growth across all disturbances and months during the study. Variance values in parentheses. . * is significant to p<0.1, ** is significant to p<0.01, *** is significant to p<0.001. Significance compared against reference.

	July	August	September	Total
IDF.Fire	0.206 (0.012***)	0.299 (0.026***)	0.464 (0.132)	0.323 (0.066***)
IDF.Reference	0.469 (0.322)	0.475 (0.256)	0.374 (0.070)	0.439 (0.211)
Total	0.338 (0.180)	0.384 (0.143)	0.419 (0.101)	
MS.Beetle	0.409 (0.195***)	0.364 (0.062)	0.386 (0.102**)	0.386 (0.116***)
MS.Harvest	0.233 (0.023*)	0.259 (0.022)	0.282 (0.018)	0.258 (0.021)
MS.Reference	0.140 (0.004)	0.182 (0.056)	0.202 (0.021)	0.174 (0.027)
Total	0.260 (0.084)	0.268 (0.051)	0.290 (0.051)	

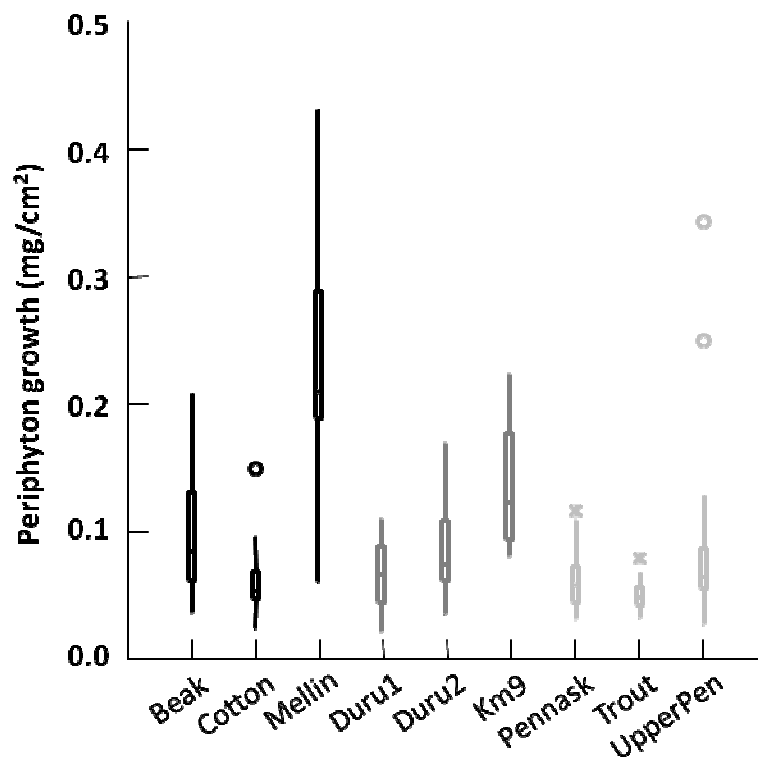


Figure 7. Box plot of periphyton growth for each stream in the MS zone. Colors represent each disturbance; black is MPB, dark gray is harvest, light gray is reference.

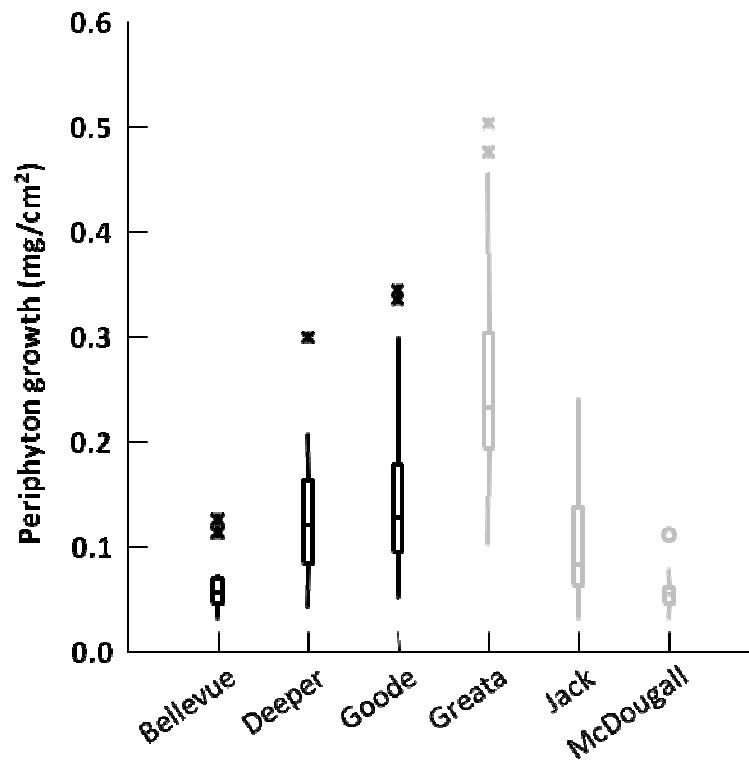


Figure 8. Box plot of periphyton growth for each stream in the IDF zone. Colors represent each disturbance; black is fire, and light gray is reference.

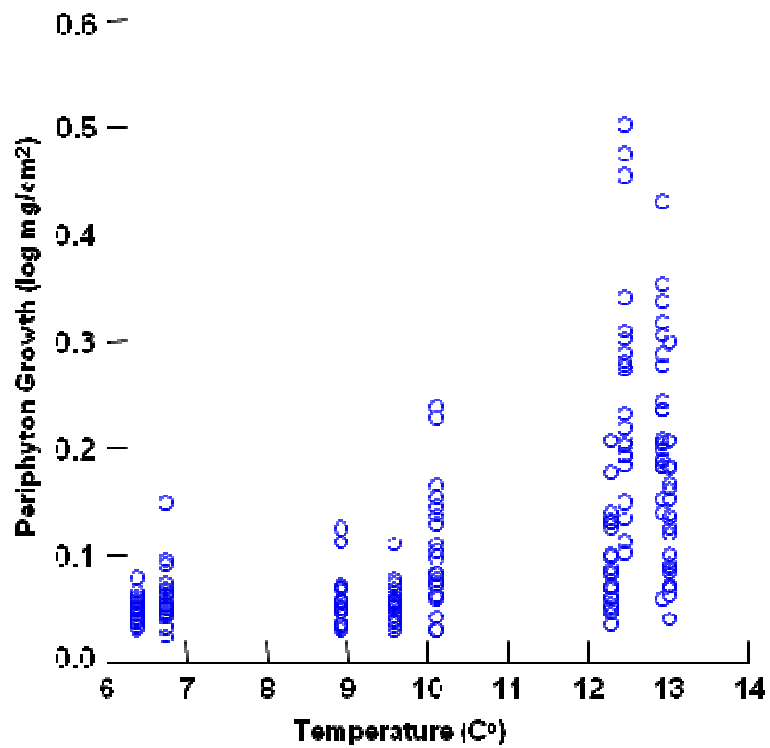


Figure 9. Bi-plot displaying the correlation between temperature and periphyton growth. Growth is measured as milligrams of AFDM per cm² of benthic surface.

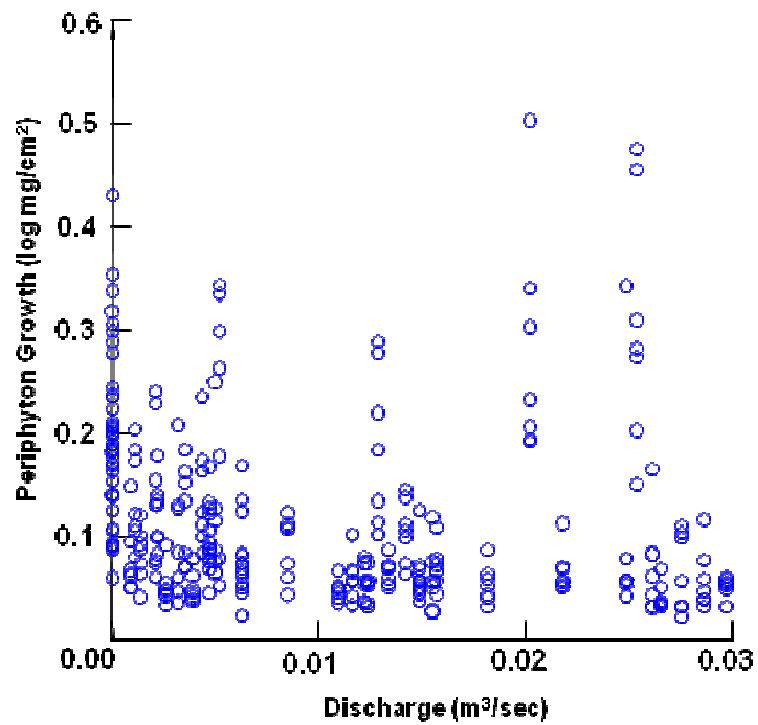


Figure 10. Bi-plot illustrating the correlation between discharge and logged periphyton growth. Growth is measured as milligrams of AFDM per cm² of benthic surface.

Table 6. Mean values of invertebrate populations across all disturbances and months, where values are expressed per sampling tray. Mass is measured in milligrams. Variance values in parentheses. * is significant to $p < 0.1$, ** is significant to $p < 0.01$, *** is significant to $p < 0.001$. Significance compared against reference.

IDF.Fire	July	August	September	Total
Numbers	348.3 (44833*)	315.3 (61179)	219.4 (14696*)	293.6 (42051**)
Numbers of EPT	50.3* (2070.3***)	123.2 (23320*)	23.7 (500.6*)	66.0 (10292)
Mass	25.2 (245.3***)	25.0 (170.5***)	23.6 (373.2)	24.6 (256.2***)
Mass of EPT	13.6 (208.0)	13.5 (105.2***)	8.2 (110.0**)	11.7 (142.7***)
IDF.Reference				
Numbers	498.3 (12287)	426.2 (67250)	261.0 (30711)	394.2 (81779)
Numbers of EPT	110.9 (10398)	104.2 (9706.7)	30.0 (1033.3)	81.0 (8129.6)
Mass	47.2 (1275.6)	51.1 (1760.2)	21.0 (412.1)	39.4 (1277.0)
Mass of EPT	27.9 (412.1)	20.7 (580.2)	4.7 (29.20)	17.7 (420.6)
Total				
Numbers	421.6 (86816)	365.7 (65557)	239.3 (22285)	
Numbers of EPT	79.9 (6936)	114.6 (16854)	26.7 (748.1)	
Mass	36.0 (855.6)	36.9 (1042.)	22.4 (384.8)	
Mass of EPT	20.6 (353.0)	16.8 (325.6)	6.5 (72.9)	
MS.Beetle				
Numbers	209.9 (34734*)	141.4 (8306.3***)	115.9* (10766***)	157.1 (19378***)
Numbers of EPT	51.9 (2202.3*)	40.3 (2479.9**)	18.2 (584.7)	37.3 (1924.0**)
Mass	14.6 (131.5)	12.8 (81.2)	16.5 (697.1)	14.6 (288.2)
Mass of EPT	9.3 (67.8)	7.8 (38.8**)	10.7 (508.9***)	9.2 (194.0*)
MS.Harvest				
Numbers	90.95 (9152.4)	328.7 (81452*)	307.7 (38175)	243.4 (53232)
Numbers of EPT	12.9 (210.7)	29.4 (718.2)	31.7 (592.6)	24.8 (565.0)
Mass	5.8 (28.4**)	16.5 (169.3)	25.4* (334.4)	16.0 (240.1)
Mass of EPT	4.1 (26.0*)	6.1 (41.1**)	7.7 (158.5)	6.0 (76.4)
MS.Reference				
Numbers	146.1 (16337)	261.9 (48878)	269.2 (75479)	226.9 (49171)
Numbers of EPT	29.6 (680.6)	32.0 (844.5)	24.8 (625.7)	28.8 (706.2)
Mass	14.2 (134.0)	10.5 (174.1)	13.8 (398.0)	12.8 (232.8)
Mass of EPT	9.2 (76.9)	7.1 (151.8)	5.4 (84.6)	7.2 (104.3)
Total				
Numbers	149.9 (22122)	244.3 (50922)	234.2 (47934)	
Numbers of EPT	31.8 (1280)	33.9 (1323)	25.1 (614.5)	
Mass	11.6 (112.3)	13.2 (143.9)	18.6 (481.7)	
Mass of EPT	7.6 (61.3)	7.0 (76.6)	7.8 (240.6)	

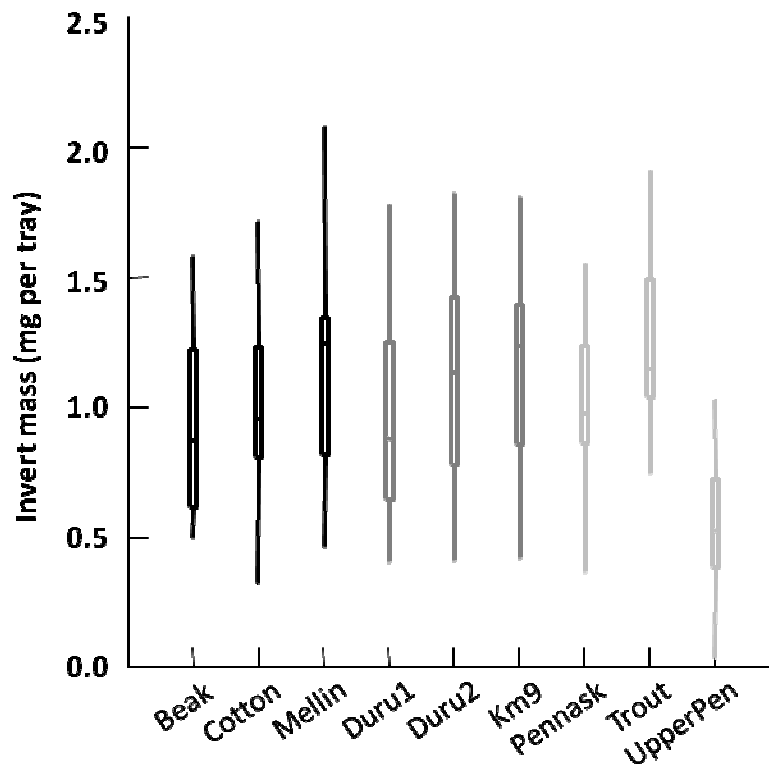


Figure 11. Box plot of invertebrate mass for each stream in the MS zone. Colors represent each disturbance; black is MPB, dark gray is harvest, light gray is reference.

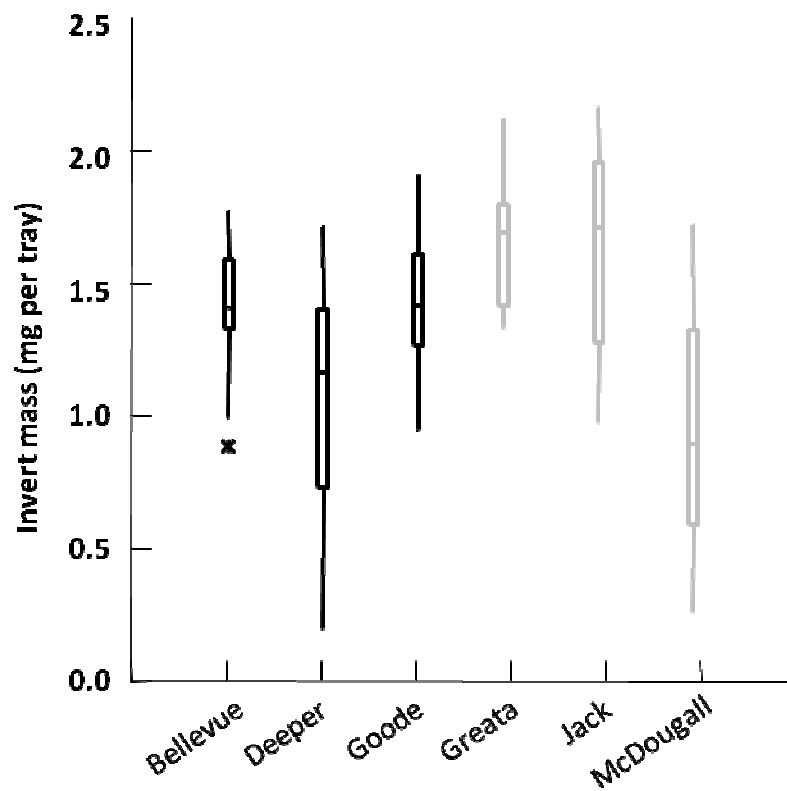


Figure 12. Box plot of invertebrate mass for each stream in the IDF zone. Colors represent each disturbance; black is fire, and light gray is reference.

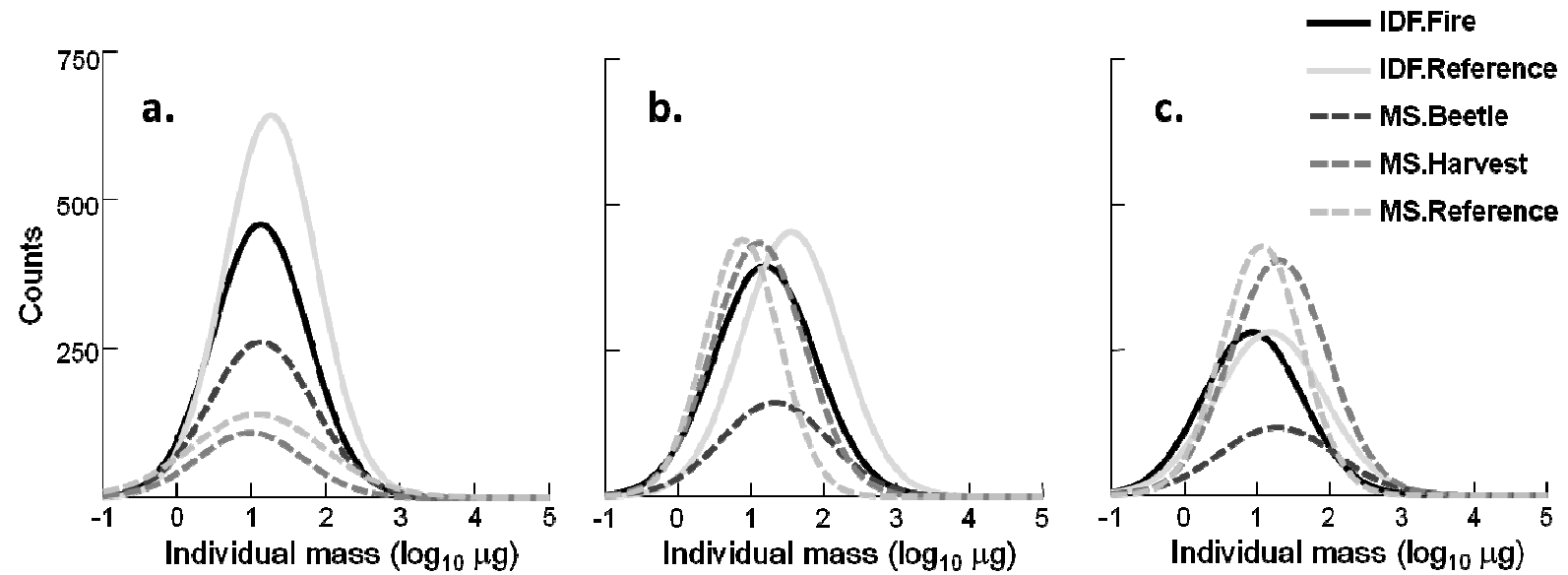


Figure 13. Distribution curves for masses of individual invertebrates. Line texture and color represent each disturbance. July is figure a., August is b., and September is c.

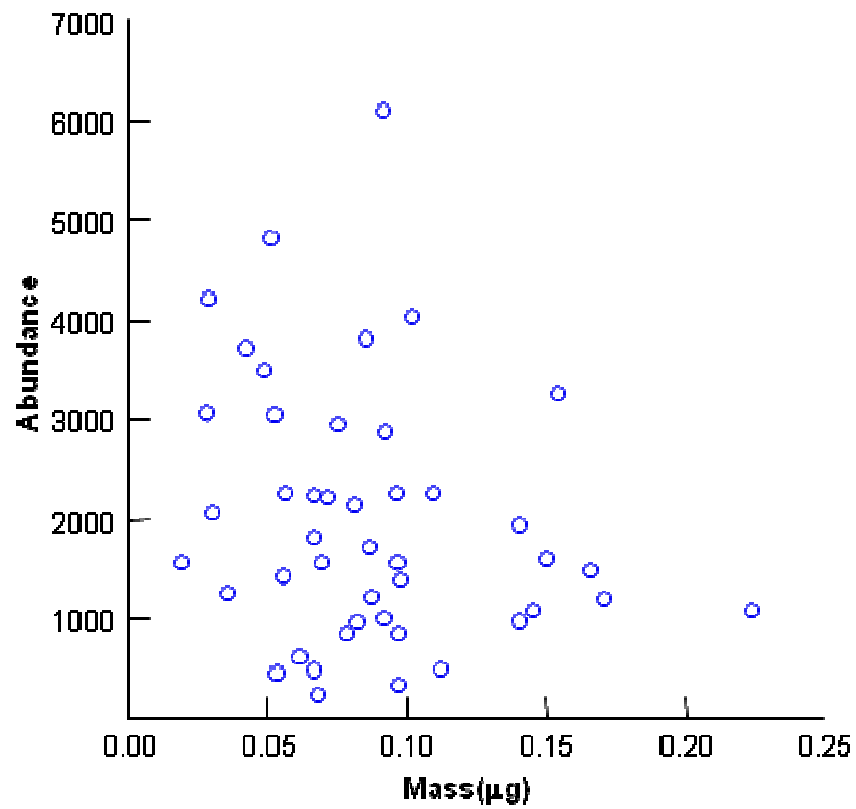


Figure 14. Bi-plot of the mean mass for each individual invertebrate vs the total stream abundance

Table 7. List of macroinvertebrate taxonomic and functional feeding groups collected during the course of this study. Filterers (F), Gatherers (G), Piercers (Pc), Predators (P), Scrapers (Sc), and Shredders (Sh).

Amphipoda	Sh	Megaloptera	
Bivalvia	F	Sialidae	P
Coleoptera		Nematoda	
Dytiscidae	P	Oligochaeta	G
<i>Heterolimnius</i>	G	Odonata	P
<i>Narpus</i>	G	Ostracoda	G
<i>Optioservus</i>	Sc	Plecoptera	
Collembola	G	<i>Alloperla</i>	P
Copepoda	F	Capniidae	Sh
Diptera		<i>Haploperla</i>	P
<i>Atrichopogon</i>	G	<i>Hesperoperla</i>	P
<i>Bezzia</i>	P	Leuctridae	Sh
Chironominae	G	<i>Malenka</i>	Sh
<i>Dicranota</i>	P	Perlodidae	P
Dixidae	G	<i>Pteronarcella</i>	Sh
Empididae	P	<i>Pteronarcys</i>	Sh
<i>Glutops</i>	P	Taeniopterygidae	Sh
<i>Hexatoma</i>	P	<i>Yoraperla</i>	Sh
<i>Liogma</i>	P	<i>Zapada</i>	Sh
<i>Maruina</i>	Sc	Prostigmata	P
Orthocladinae	G	Trichoptera	
<i>Pericoma</i>	G	<i>Arctopsyche</i>	F
Simuliidae	F	<i>Brachycentrus</i>	F
Stratiomyidae	G	<i>Dicosmoecus</i>	Sc
Tanypodinae	P	<i>Ecdysomyia</i>	G
Tanytarsini	F	<i>Ecosmoecus</i>	Sh
Thaumaleidae	Sc	<i>Glossosoma</i>	Sc
Ephemeroptera		<i>Hesperophylax</i>	Sh
<i>Ameletus</i>	Sc	<i>Homophylax</i>	Sh
<i>Baetis</i>	G	<i>Hydropsyche</i>	F
<i>Cinygmula</i>	Sc	<i>Hydroptila</i>	Pc
<i>Drunella</i>	Sc	<i>Lenarchus</i>	G
<i>Epeorus</i>	Sc	<i>Lepidostoma</i>	Sh
<i>Ephemerella</i>	G	<i>Micrasema</i>	Sh
<i>Paraleptophlebia</i>	G	<i>Parapsyche</i>	F
<i>Rhithrogena</i>	Sc	<i>Psychoglypha</i>	Sh
<i>Serratella</i>	G	<i>Rhyacophila</i>	P
Gastropoda	Sc	Uenoidae	Sc

Table 8. Mean of invertebrate taxonomic diversity across all disturbances and months, where values are expressed per sampling tray. Variance values in parentheses. * is significant to $p < 0.1$.
Significance compared against reference.

IDF.Fire	July	August	September	Total
Taxa	10.39* (14.43)	12.04 (14.56)	10.08 (11.73)	10.84 (13.93)
Diversity	1.739 (0.208)	1.738* (0.197)	1.620 (0.128)	1.698 (0.175)
Evenness	0.314 (0.010)	0.319 (0.009)	0.321 (0.007)	0.318 (0.008)
IDF.Reference				
Taxa	14.27 (18.11)	14.35 (21.50)	11.59 (18.25)	13.37 (20.30)
Diversity	2.061 (0.106)	2.171 (0.162)	1.795 (0.216)	2.004 (0.181)
Evenness	0.355 (0.002)	0.370 (0.004)	0.348 (0.011)	0.357 (0.006)
Total				
Taxa	12.2 (19.7)	13.0 (18.6)	10.8 (15.0)	
Diversity	1.89 (0.18)	1.93 (0.22)	1.70 (0.17)	
Evenness	0.33 (0.007)	0.34 (0.007)	0.33 (0.009)	
MS.Beetle				
Taxa	9.333 (4.579)	9.956 (14.04)	8.136 (4.694)	9.159 (8.106)
Diversity	1.818 (0.135)	1.783* (0.140)	1.736 (0.079)	1.780 (0.116*)
Evenness	0.368 (0.008)	0.383* (0.008)	0.401 (0.008)	0.384 (0.008)
MS.Harvest				
Taxa	7.478 (4.715)	8.826 (7.513)	9.208 (2.606*)	8.514 (5.325*)
Diversity	1.624 (0.187)	1.508 (0.226)	1.776 (0.051)	1.638 (0.161)
Evenness	0.422 (0.022)	0.291 (0.013)	0.327 (0.004)	0.346 (0.016)
MS.Reference				
Taxa	9.478 (5.715)	10.20 (13.82)	9.458 (7.041)	9.718 (8.776)
Diversity	1.842 (0.089)	1.254 (0.302)	1.694 (0.102)	1.593 (0.224)
Evenness	0.422 (0.012)	0.272 (0.024)	0.345 (0.013)	0.345 (0.020)
Total				
Taxa	8.77 (5.68)	9.67 (11.8)	8.95 (4.96)	
Diversity	1.76 (0.14)	1.51 (0.26)	1.73 (0.07)	
Evenness	0.40 (0.014)	0.31 (0.017)	0.35 (0.009)	

Table 9. Mean biomass of invertebrate feeding groups across all disturbances and months, where values are expressed per sampling tray. Values are in units of milligrams per tray. Variance values in parentheses.

IDF.Fire	July	August	September	Total
Filterer	5.33 (73.3)	5.52 (35.9)	1.04 (4.38)	3.95 (40.6)
Gatherer	5.27 (29.1)	7.18 (43.6)	2.18 (5.92)	4.87 (29.8)
Predator	5.19 (37.1)	4.37 (27.1)	11.2 (156)	6.97 (81.6)
Scraper	3.78 (69.0)	3.15 (35.7)	2.22 (56.4)	3.04 (52.4)
Shredder	3.29 (28.7)	2.61 (22.5)	3.36 (78.4)	3.09 (42.3)
IDF.Reference				
Filterer	4.08 (38.8)	13.8 (199)	1.52 (4.43)	6.25 (102)
Gatherer	12.0 (198)	15.6 (231)	9.40 (157)	12.2 (195)
Predator	18.7 (371)	10.6 (144)	7.30 (73.6)	12.3 (216)
Scraper	5.08 (62.3)	5.92 (263)	0.07 (0.07)	3.62 (107)
Shredder	5.47 (60.1)	1.28 (4.08)	1.41 (3.25)	2.77 (26.2)
Total				
Filterer	4.72 (55.6)	9.30 (124.)	1.27 (4.36)	
Gatherer	8.59 (121)	11.0 (143)	5.63 (89.8)	
Predator	11.8 (243)	7.23 (88.3)	9.37 (118)	
Scraper	4.42 (64.7)	4.41 (137)	1.19 (30.0)	
Shredder	4.36 (44.2)	2.01 (14.3)	2.43 (42.5)	
MS.Beetle				
Filterer	1.78 (4.21)	2.32 (9.03)	0.51 (1.04)	1.55 (5.24)
Gatherer	3.37 (9.58)	2.60 (6.52)	3.55 (35.5)	3.17 (16.5)
Predator	2.72 (10.0)	2.05 (3.82)	3.18 (12.6)	2.64 (8.74)
Scraper	4.25 (28.7)	4.00 (27.3)	0.46 (0.81)	2.96 (21.7)
Shredder	2.10 (30.4)	1.12 (4.29)	8.27 (526.)	3.74 (184)
MS.Harvest				
Filterer	0.60 (0.56)	2.90 (13.1)	6.26 (88.4)	3.30 (39.3)
Gatherer	0.52 (0.70)	3.78 (25.8)	7.52 (102)	3.99 (50.9)
Predator	0.73 (1.22)	3.10 (12.7)	4.89 (24.2)	2.93 (15.5)
Scraper	0.71 (1.36)	1.32 (8.42)	0.56 (0.99)	0.86 (3.56)
Shredder	2.38 (25.5)	2.57 (19.9)	4.87 (126)	3.30 (58.0)
MS.Reference				
Filterer	2.30 (15.2)	0.63 (0.52)	1.38 (1.04)	1.42 (5.77)
Gatherer	2.87 (10.2)	1.00 (4.11)	2.55 (26.1)	2.13 (13.8)
Predator	3.12 (13.4)	2.28 (8.65)	7.47 (158)	4.30 (64.3)
Scraper	4.07 (31.9)	2.49 (72.5)	0.10 (0.06)	2.19 (36.6)
Shredder	0.87 (3.17)	2.63 (60.3)	1.73 (15.5)	1.76 (26.4)
Total				
Filterer	1.56 (6.94)	1.93 (8.18)	2.78 (36.6)	
Gatherer	2.27 (8.25)	2.44 (13.0)	4.57 (58.4)	
Predator	2.20 (9.10)	2.47 (8.38)	5.23 (67.7)	
Scraper	3.03 (22.8)	2.60 (36.8)	0.37 (0.64)	
Shredder	1.79 (19.7)	2.12 (28.3)	4.86 (214)	

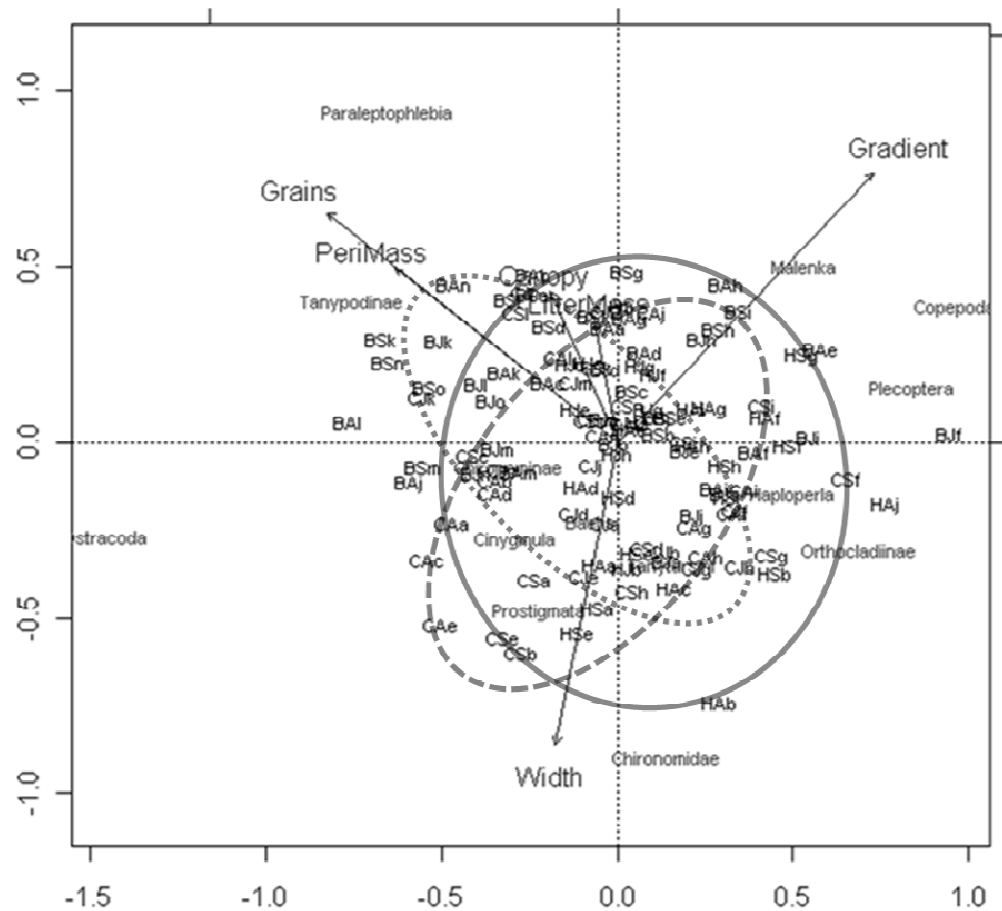


Figure 15. Correlation bi-plot from redundancy analysis of MS zone species and environmental data. Ovals delineate MS.Reference sites during each month. The dotted oval delineates July, the dashed oval delineates August, and the solid oval delineates September.

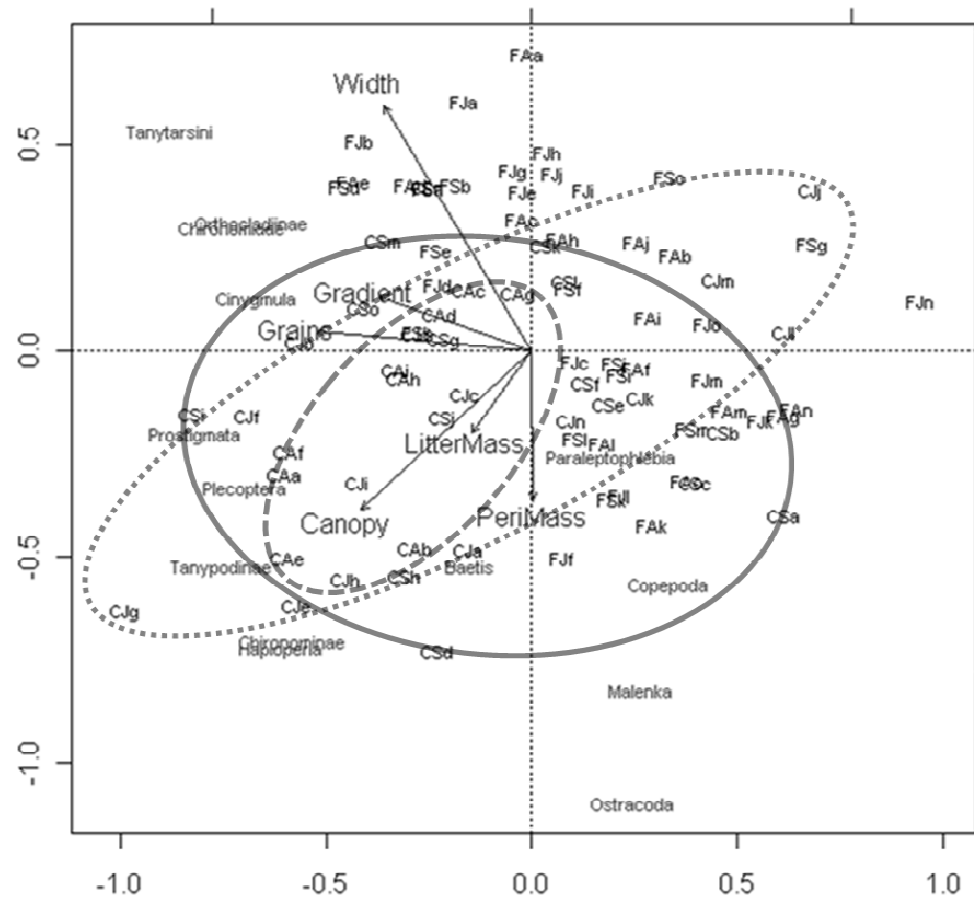


Figure 18. Correlation bi-plot from redundancy analysis of IDF zone species and environmental data. Ovals delineate IDF.Reference sites during each month. The dotted oval delineates July, the dashed oval delineates August, and the solid oval delineates September.

4 Discussion

4.1 Allochthonous Inputs

The most observable differences were the effects of riparian disturbance on canopy cover. Fire and harvest disturbances showed reduced canopy cover and litter inputs. As predicted, fire sites responded with a reduced yield of allochthonous loading. Despite having only 16% of the amount of overhead canopy coverage, harvest streams received substantial allochthonous loading as compared with reference reaches. These freshly harvested sites had a number of slash piles spread throughout their landscape, which may have allowed windblown litter to be carried to streams. This wind loading could also explain the high variability of litter inputs within the harvest streams, producing heavy loading at one site but not in adjacent sites. Heavy slash loading following commercial harvest has also been reported (Hernandez et al. 2005; Jackson et al. 2001). The fire sites experienced similarly variable inputs: locations would occasionally receive large inputs of small pieces of burnt wood. MPB streams experienced even greater variation, likely explained by the spatial distribution of dead pine trees among the living trees of the riparian areas.

Litter loading was directly related to canopy coverage. The burned and harvest disturbances received proportionally less litter mass compared to reference, such that canopy coverage was a better predictor of litter inputs than of disturbance type. This is to be expected as the canopy had shed materials directly into the vertical litter traps. Conversely, at the MPB sites, riparian disturbance condition played a significant role in litter inputs, while canopy coverage was only

of secondary importance. While it is not particularly surprising to learn that recently dead trees shed more materials than living trees, recognizing this relationship between beetle mortalities and the ecosystems below them is important. Understanding the duration, magnitude, and composition of the trophic subsidy provided by these dead trees would be important to forest and wildlife managers because it has been shown to significantly alter soil and water chemistry (Clow et al. 2011) and can support shredding invertebrates (Cummins & Klug 1979).

4.2 Autochthonous Production

Despite the significant changes in the riparian canopy and allochthonous loading, there were few noteworthy shifts in the aquatic biological communities. This lack of detected response to riparian disturbance has been commonly reported in aquatic ecology (Herlihy et al. 2005; Minshall et al. 2001a; Price et al. 2003). Though not statistically significant, the substantial rise in periphyton standing stocks in the MPB streams (221% of reference streams) should be noted. As shown by Clow et al. (2011), the soil chemistry beneath MPB killed trees contains elevated levels of NH_4^+ and NO_3^- . Their study found that water in adjacent streams contained greater concentrations of total N and P, which potentially explains our boost to periphyton production in the MPB disturbance.

Most of the significant disturbance effects were of inter- and intra-stream variance and temporal shifts. The most noticeable differences in variance were in periphyton biomass, which exhibited significantly increased variability across the MPB streams compared to the MS reference streams. As predicted, the large difference in periphyton mean biomass for the MPB

disturbance was not statistically significant because of this increased variance. The elevated variability was due to Mellin Creek, which consistently provided the greatest range of periphyton biomass while reference streams remained within a narrow low range (Figure 5). Variable nutrient leaching along the stream edge could explain this result. Also, Mellin is a slower moving stream, which experienced a very slight freshet in the spring of 2009, thus undergoing less surface scouring and allowing for a greater periphyton potential. In contrast, burned streams in the IDF were generally less variable as we predicted because of the uniform disturbance fire had on riparian canopy.

Increased variability in periphyton biomass could be explained by several factors. Periphyton biomass has been shown to be correlated to water temperature (Bothwell 1988, Figure 9) as well as nutrient rich hyporheic upwelling zones (Boulton 1993). Thus, possible hydrological differences across our chosen watersheds could be correlated to variability across streams. As shown by Richards et al. (1997), natural variability in landscape geology can mask local riparian impacts. However, we theorize that differences in hydrology should be minor or linked to disturbance effect, because streams were chosen for their compatible physical properties. Minshall et al. (2001b) proposed that widespread scouring induced by increased runoff was likely the cause of early reduction of periphyton their burn streams. Stream output during the summer of 2009 were lower than average (<http://www.wsc.ec.gc.ca/applications/H2O/index-eng.cfm>), suggesting that benthic scour was reduced. In the MPB system, variable distribution of leaching trees and new LWD would have produced a greater variety of microhabitats (Gerhard & Reich 2000), and is the probable cause of amplified intra-stream variability. The

spatially variable nature of the tree mortality in the MPB disturbance could have also produce greater variability of light penetration, leading to the increased variance that we found.

4.3 Invertebrate Response

A nearly threefold increase in the number of drifting invertebrates per cubic meter of water was found in the harvest streams compared to control streams. Larval drifting can be triggered by a number of factors: food limitations, population density, discharge, time of day (Brittain & Eikeland 1988; Hildebrand 1974; Hildrew & Townsend 1980; Matczak & Mackay 1990).

Elevated drift has been documented following both fire (Mellon et al. 2008) and forest harvest (Murphy et al. 1981). Density dependent effects (Figure 14) likely explain these results, as streams in these two studies were highly productive and generated greater invertebrate abundance in the benthos. Our measured increase in drift, however, was concurrent with no disturbance effects on allochthonous, autochthonous, CPOM, and invertebrate density.

Increased discharge has been shown to produce greater invertebrate drift (Brittain & Eikeland 1988), but this is likely to be unrelated in our study as harvest streams averaged about half the rate of discharge as MS references streams. It is possible that additional light penetration improved invertebrate growth condition via greater temperature and periphyton potential.

Increased invertebrate production would allow greater numbers to reach the point of emergence, which is supported by the numbers of pupae and new adults found during August in the harvest streams.

All Invertebrate measures (abundance, biomass, EPT, richness, diversity) in burned streams were lower than reference streams, with the exception of drift abundance. Each fire disturbance measurement was on average 77% (range of 62.4 - 89%) of the corresponding measurement in the reference. Bioenergetically speaking, reductions to the invertebrate community in fire-disturbed streams make sense considering that three indices of energy availability (litter loading, periphyton mass, and fluvial CPOM) were all reduced, providing less energy for invertebrates. Minshall et al.'s (2001a, 2001b) extensive ten year study in Idaho and Wyoming, USA produced similarly non-statistically significant results, revealing shifts in invertebrate community composition, while overall abundances remained unchanged. These shifts were credited to habitat scouring and reductions of allochthonous energy. Post fire communities in Idaho, Wyoming, and New Mexico (Vieira et al. 2004) favoured high fecundity, multi-voltine taxa such as baetid mayflies and chironomids. Both studies showed a relative increase in Chironomidae abundance following the initial three years post-burn, and an increase in *Baetis* three and five years after the burn. It was not evident that our system underwent a similar rebound as Chironomidae and *Baetis* populations were greater in reference streams. However, our sampling was conducted five years post-fire, and it is conceivable that this recovery occurred and then dissipated prior to sampling. The most abundant taxon in our burned streams was early instar ephemereleid mayflies. These small instars unfortunately lacked distinguishing features to facilitate more specific identification. Ephemereleids are uni-voltine gatherers/scapers with generalized mouthparts, and are perhaps slightly better competitors for the five years post-burn environment. Vieira et al. (2004) and

Minshall et al. (1997) documented elevated abundances of ephemereids alongside increases of chironomids and baetids.

As predicted streams in the burned disturbance regime were significantly more homogenized in invertebrate abundance and biomass compared to IDF reference streams. The uniformly depleted canopy and the increased uniformity in periphyton biomass created a more even distribution of resources. This, combined with the possibility of greater uniformity in the habitat through scouring of fines and channel reshaping (Burton 2005; Dunham et al. 2007) would result in homogenization of habitat and resources. These conditions would generate the significantly less patchy distribution of invertebrates. Most of the previous research on stream response to fire have focused on temporal effects (Minshall et al. 1997; Pilliod et al. 2008; Richards & Minshall 1992; Rinne 1996; Vieira et al. 2004), and these results indicate that annual instability of invertebrate communities following a fire is highly dependent on burn severity and local precipitation. We would theorize that both temporal and spatial variation depends heavily upon the amount of post-disturbance scour through the stream channel.

The MPB infested systems experienced shifts in their spatial variance with respect to community composition. EPT abundance and biomass measures were more spatially variable than those in MS reference sites. This could be attributed to the high spatially variable litter loading and periphyton growth found in these streams, thus creating patchy resource distribution. Mean invertebrate diversity for the MPB disturbance was greater (non-significantly) than that of the MS reference sites. This too could be explained by the increases

of both periphyton and litter loading in MPB streams. Through the lessening of resource limitation, a greater variety of taxa could spread throughout the stream.

Little is known about the temporal dynamics of MPB outbreaks on stream food webs, especially since most data examining effects of this disturbance come from the early years after the attack. As infested trees change from the red kill stage (needles still attached to dead trees) into the grey kill stage (bare, needle-less trees), we anticipate a reduction in invertebrate populations as litter inputs stop and leachable nutrients associated with infested trees will have washed out, leaving fewer available to primary producers and higher trophic levels. Because some trees are unaffected by MPB (spruce, fir), temperature and light levels may remain largely unchanged (dependent upon relative abundance of pines), thus limiting growth potential of periphyton, and further exacerbate the limitations to consumers because of the reductions in allochthonous inputs.

Most invertebrate measures showed a temporal effect or an interaction between time and disturbance. Total invertebrate abundance, EPT abundance, total invertebrate biomass, EPT biomass, taxon diversity, total number of taxa, and individual invertebrate biomass were lowest during September in the IDF system, likely a response to insect emergence. Both IDF systems exhibited similar reductions in invertebrate populations, except for fire biomass measurements. Invertebrate biomass had dropped quite dramatically during September in IDF reference streams, being 44.5% and 41.1% of the mass of the previous two months, respectively. Biomass was more temporally constant in fire streams, as they were 93.7% and 94.4% of values

observed in previous months, respectively. This consistency in biomass is due to the increase of large semi-voltine taxa (*Pteronarcella*, *Rhyacophila*, and Elmidae (life-span uncertain) in fire disturbed streams. This result is confounding however, as in general, these relatively large semi-voltine species generally require stable and undisturbed habitat (Whiles & Wallace 1995).

Temporal responses to disturbance regimes in the MS streams were more complex, displaying different trends across disturbances. MPB streams exhibited a decreasing trend of total abundance, EPT abundance and diversity over the sampling period, while evenness scores and EPT mass increased. This suggests that the more abundant taxonomic groups were exiting the reach (drift or emergence), and thus evening out the invertebrate community with larger EPT taxa (mostly the shredder *Hesperophylax*). Invertebrate communities in the harvest disturbance, in contrast, increased in abundance, biomass, and numbers of taxa with reductions in evenness scores, indicating that the additional invertebrates were from a few taxonomic groups. The reference streams had yet a different temporal response, where total abundance increased while EPT abundance, total and EPT biomass, diversity and evenness decreased over the course of the summer. This response indicates that the large EPT individuals emerged or emigrated out of the reaches, while relatively smaller individuals belonging to only a few taxa (mostly chironomids), increased in numbers. The success of an individual insect to the point of emergence can be related to a number of factors, which vary widely depending upon the behaviour, habit, life strategy, and trophic requirements which can be influenced by local environment (Richards et al. 1997).

Ordination analysis of all environmental variables and the most prevalent invertebrate taxa reveals that sites within each disturbance regime shared many commonalities with their respective reference sites. The ordination analysis was conducted to provide additional evidence to support the results of my ANOVAs, and the lack of significant differences in the ANOVAs was also evident in the RDA. Harvest and fire disturbances were orientated opposite of larger canopy and litter values. The temporal interaction effect upon invertebrate abundances with the MPB and harvest disturbances was also seen in the RDA where MPB and harvest cluster of sites showed no overlap during the month of September. These results help illustrate the biologically meaningful distinction between the MPB and harvest disturbed aquatic environments.

4.4 Conclusion

Our results suggest these systems were robust and resilient to this magnitude of fire, mountain pine beetles and logging. Each disturbance exhibited a clear riparian effect (e.g., litter flux, canopy cover), yet this effect did not elicit measureable impacts on stream food webs. All disturbed systems maintained an overall primary consumer community relatively similar with their respective references. However, this study was temporally and potentially spatially limited. Moreover, we sampled five years following these disturbance events, and thus may have missed short-term ecological changes. It is our recommendation that similar studies are conducted that collect data before (if possible), and at regular intervals following riparian disturbances (e.g., Kiffney & Richardson 2010).

Our fire sites received reduced allochthonous and autochthonous energy, a reduction in all invertebrate metrics, and increased invertebrate drift relative to reference sites. The intense fire in 2003 potentially produced more detrimental effects to our study systems during the initial years following the event, and results shown in this body of work are mostly probably taken during ecosystem recovery.

Direct comparisons of large fire and commercial harvesting are difficult. While the riparian effects of a commercial harvest are similar to the fire disturbance at the local reach scale, the proportion of disturbed area at the watershed scale will not be the same. Forestry practises in BC allow for small patchwork cut-blocks to be removed from a watershed, which are not similar in area to a large wildfire. MPB effects on British Columbia forests are occurring at a large spatial scale, the full effects of this infestation to the stream environment have yet to be observed as trees are still in their red kill stage. After beetle-killed riparian stands have leached all their nutrients and litter mass, we speculate that streams will suffer a reduction in biotic production. This study provides an initial examination of the effects of MPB on aquatic biological communities... Additional research should be carried out as the medium to long term effects of this massive disturbance are not yet fully understood. This is particularly important in the Okanagan Valley as the current infestation is projected to worsen until 2013 (Walton 2010).

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