



Influence of wildfire and harvesting on aquatic and terrestrial invertebrate drift patterns in boreal headwater streams

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Abstract Forested headwater streams are strongly connected to their surrounding riparian areas via the transfer of energy subsidies that underpin instream food webs and, therefore, are highly sensitive to riparian disturbances that influence allochthonous inputs. We compared terrestrial and aquatic invertebrates found in drift across headwater streams in boreal forested catchments with wildfire, harvest with minimum 30-m riparian buffers, and reference catchment histories. Fire-disturbed streams contained significantly greater aquatic invertebrate abundance and biomass compared to reference and harvested streams, but no significant trends were seen for terrestrial invertebrate abundance or biomass. Furthermore, fire-disturbed streams supported distinct drifting invertebrate communities compared to reference and harvested sites, driven by high abundances of the mayfly

Baetis and caddisfly *Dolophilodes*. Aquatic invertebrate drift communities were compositionally dissimilar between fire and harvested sites, but not reference sites and no trends were found for terrestrial invertebrate drift samples. Subtle but detectable differences in drifting invertebrate community metrics, structure, and biomass suggest that the effects of wildfire persist well beyond a decade post-fire in boreal headwater streams. Forest management that emulates natural fire disturbance, including streamside disturbance, may be important for promoting the observed patterns detected in our fire-disturbed catchments.

Keywords Aquatic macroinvertebrate communities · Terrestrial macroinvertebrate input · Forest watersheds · Catchment disturbance

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Introduction

Headwater streams are abundant in river networks in forested catchments, typically making up 70–80% of their overall spatial extent (Sidle et al., 2000; Meyer & Wallace, 2001; Gomi et al., 2002). They serve as a source of water supply, biodiversity, and organic material to larger order streams and rivers (Wipfli & Gregovich, 2002; Meyer et al., 2007; Richardson & Danehy, 2007; Bateman et al., 2016). Headwater streams are tightly interconnected to the adjacent landscape, specifically riparian forests, by the transfer

of energy subsidies across these boundaries (Kaushik & Hynes, 1971; Likens & Bormann, 1974; Wallace et al., 1997; Baxter et al., 2005). Riparian forests supply critical energy subsidies to stream ecosystems in the form of leaf litter and terrestrial invertebrates (Piccolo & Wipfli, 2002; Allan et al., 2003) that underpin aquatic food webs (Wallace et al., 1999; Abelho, 2001; Nakano & Murakami, 2001). These allochthonous inputs of organic material are the primary source of energy in forested headwater streams (Vannote et al., 1980; Pozo et al., 1997; Finlay, 2001) because the canopy cover limits light availability causing low primary production, and supports microbial, macroinvertebrate, and fish communities (Webster et al., 1992). At the reach scale, riparian forests also provide flood mitigation, sediment retention, instream thermoregulation, and instream habitat formation from allochthonous large instream wood and leaf material (Sweeney, 1993; Moore & Richardson, 2003; Richardson et al., 2010; Jyväsjärvi et al., 2014).

Due to the small size of headwater streams and their interconnectedness to the surrounding catchment, instream biotic communities can be sensitive to catchment disturbance such as wildfire and harvesting (Stout et al., 1993; Kreutzweiser et al., 2008, 2009; Houser et al., 2006). In forested watersheds, harvesting and wildfire have been linked to numerous impacts within headwater streams. For example, both wildfire and harvest-induced changes in riparian forest vegetation composition can influence aquatic habitat availability, biodiversity, ground stability, sediment and nutrient retention, riparian canopy shading, and can alter the quantity and quality of allochthonous subsidies such as leaf litter and large wood (Prepas et al., 2003; Fortino et al., 2004; Richardson et al., 2012; Kreutzweiser et al., 2012; Webster et al., 2015; Musetta-Lambert et al., 2017). Instream consequences from altered riparian vegetation communities from both natural (e.g., wildfire) and harvesting disturbances include changes in the function (i.e., organic matter decomposition processes) and structure (i.e., richness, community composition) of macroinvertebrate communities in headwater streams and riparian forests (Minshall, 2003; Jackson et al., 2012; Musetta-Lambert et al., 2017). The persistence of these effects depends on the location, frequency, and severity of the wildfire (Minshall, 2003) and extent of the harvesting (Kreutzweiser et al., 2009). In addition, the magnitude

of the responses of macroinvertebrate communities to disturbances such as wildfire are known to vary significantly due to post-disturbance events such as increased high seasonal stream flows and flooding related to snowmelt and seasonal precipitation events and drought (Verkaik et al., 2013, 2015; Bixby et al., 2015), and habitat conditions such as decreased canopy cover, altered woody input dynamics, and burn status (Verkaik et al., 2013; Vaz et al., 2014; Bixby et al., 2015). However, studies on the effects of wildfire and harvesting on macroinvertebrate communities have typically focussed on the immediate or short-term impacts (Mellon et al., 2008), while longer term and large-scale studies are rare, particularly in the boreal forest, and in other ecosystems have shown consequences for diversity and abundance that can be highly variable (Bess et al., 2002; Lepori & Hjerdt, 2006; Verkaik et al., 2015).

Modern forest management practices have progressed over the past several decades to minimize negative impacts on streams and rivers through the implementation of Best Management Practices (BMPs) such as riparian buffers, consisting of fixed-width “ribbons” of preserved older-growth forest around water bodies (Buttle, 2002; Sibley & Gordon, 2010). While the application of riparian buffers can be conveniently applied to minimize changes in water quality and aquatic habitats resulting from harvesting, it may be misaligned as an ecologically relevant management strategy in ecosystems that have evolved under periodic natural disturbances such as fire (the dominant disturbance agent in boreal forests), which can trigger forest succession in riparian forests and result in increased riparian habitat complexity (Pettit & Naiman, 2007; Moore & Richardson, 2012; Braithwaite & Mallik, 2012). Riparian forests can experience a loss of structural and functional heterogeneity without stand-replacing disturbances such as wildfire, and this can result in only a subset of the natural range of biodiversity than would otherwise exist, lowering their resistance and reliance during unexpected disturbances, potentially leading to catastrophic regime shifts (Drever et al., 2006; Sibley et al., 2012). One of the major goals of modern forestry management is to emulate natural disturbance (END) patterns and landscape conditions to ensure long-term ecological functioning (Kreutzweiser et al., 2012). If the goal of forest management is to follow this ecological perspective, then systematic riparian no-harvest

buffers may not be the most appropriate management strategy in the boreal, where riparian forests have evolved with fire and insect outbreaks (Sibley & Gordon, 2010; Naylor et al., 2012; Sibley et al., 2012). An option to achieve END management objectives involves incorporating harvesting patterns within riparian zones to mimic natural riparian disturbance patterns; however, this would require careful implementation and an extensive understanding of how natural and harvesting disturbances impact riparian–stream interactions (Moore & Richardson, 2012; Sibley et al., 2012).

While ecologists have previously studied the effects of forest disturbance on riparian–stream ecological linkages, there is a weak understanding of the long-term effects of disturbance on terrestrial invertebrate subsidies and instream invertebrate communities in boreal headwater catchments. The supply of terrestrial invertebrates to streams and drifting invertebrates instream can account for a significant portion of the energy demands of secondary consumers such as fish (Wipfli, 1997; Nakano et al., 1999). Aquatic macroinvertebrates use drifting as a means of surveying and colonizing new stream habitat, or to feed or evade predators, but also will passively drift due to accidental dislodgement from substrata (Waters, 1972; Williams & Hynes, 1976; Allan & Castillo, 2007; Principe & del Carmen Corigliano, 2006). Characterizing drifting aquatic invertebrates can be an effective way of assessing secondary production and aquatic invertebrate population dynamics in streams (Anholt, 1995; Brittain & Eikeland, 1988; Wipfli & Gregovich, 2002), as drift concentration is positively related to overall benthic density (Walton et al., 1977; Shearer et al., 2003; Kennedy et al., 2014). Invertebrate drift has also been shown to be a sensitive indicator of both wildfire (Minshall 2003; Mellon et al., 2008) and harvesting (Hoover et al., 2007) effects on stream invertebrate communities, albeit not previously tested in boreal forest catchments.

Previous studies have investigated terrestrial invertebrate input and benthic macroinvertebrate patterns in streams of varying sizes, temporal and spatial scales, and disturbance histories; however, few have studied these patterns in wildfire or harvesting-disturbed headwater streams of boreal forests (Kreutzweiser et al., 2008; Lidman et al., 2017; Musetta-Lambert et al., 2017). Furthermore, while previous studies have investigated patterns in benthic macroinvertebrate

community structure after fire and harvesting, few have studied drifting macroinvertebrate patterns (Mellon et al., 2008). We previously identified that fire-disturbed riparian forests had greater vegetative richness and contributed significantly greater and compositionally distinct leaf litter subsidies to streams than undisturbed riparian forests (Musetta-Lambert et al., 2017). This finding was coupled with significantly greater abundances and a unique community of shredder invertebrates in streams bordered by fire-disturbed compared to undisturbed riparian forests. We now examine terrestrial and aquatic invertebrate drift patterns in the same experimental setting across the summer months. We hypothesized that the denser, early successional riparian forests in fire-disturbed riparian areas would supply increased numbers and biomass of terrestrial invertebrates to streams compared to reference and harvested (with riparian buffers) catchments. We further hypothesized that the trends we detected in benthic invertebrate communities (greater abundance, unique shredder communities in fire-disturbed streams) would be reflected in invertebrate drift patterns. Furthermore, we hypothesized that these trends would be observed across all summer months, a period coinciding with peak invertebrate productivity and variability in hatch time in the short northern Ontario summer season. These temporal trends were addressed throughout the results and discussion, but were not the main objective of the study. Characterizing invertebrate drift trends in streams of naturally disturbed catchments will provide targets and benchmarks for riparian management strategies designed to emulate wildfire disturbance patterns. We compare terrestrial and aquatic invertebrate drift biomass and patterns in boreal headwater streams within catchments with fire, harvesting (with minimum 30 m buffers), and reference (minimally disturbed) histories. We then explain our results in the context of adapting END management principles for riparian management strategies in boreal forest catchments.

Methods

Study site characteristics

The study was conducted in Canada's Boreal Shield ecozone, approximately 75 km inland from the

northeastern shore of Lake Superior in the White River Forest Management Area (Fig. 1). The forest in this region is classified as boreal mixed-woods and is dominated with black and white spruce (*Picea mariana* Mill. and *P. glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marshall), and trembling aspen (*Populus tremuloides* Michx.). The dominant woody vegetation in the riparian forests are speckled alder (*Alnus incana* ssp. *rugosa* (Du Roi) Clausen), red osier dogwood (*Cornus sericea* L.), chokecherry (*Prunus virginiana* L.), and mountain maple (*Acer spicatum* Lam.) (Muto et al., 2009; Musetta-Lambert et al., 2017).

The geologic foundation of the region is Precambrian granite bedrock with humo-ferric podzol soil and, to a lesser extent, brunisols over Precambrian bedrock with frequent rocky outcrops (Gunn &

Pitblado, 2004; Kreutzweiser et al., 2009). Total elevation change in the study area is ~ 180 m. The area receives an annual average of 1000 mm of precipitation via rain and snow (Wawa, Ontario meteorological station, Environment & Climate Change Canada, 2017). Snow and ice-covered bodies of water persist from November to May, and the average annual air temperature is 1.7°C, with daily mean temperatures ranging from − 14.8 to 14.9°C. The study sites contained no linear disturbance features other than logging and mining roads, and trapper-line trails.

We focussed on headwater (low-order) streams with a similar ratio between approximate stream margin area and water volume (Minshall et al., 1989). The study catchments have histories of (1) harvesting (conventional clearcut harvesting 7–17 years prior to study initiation) with slope-

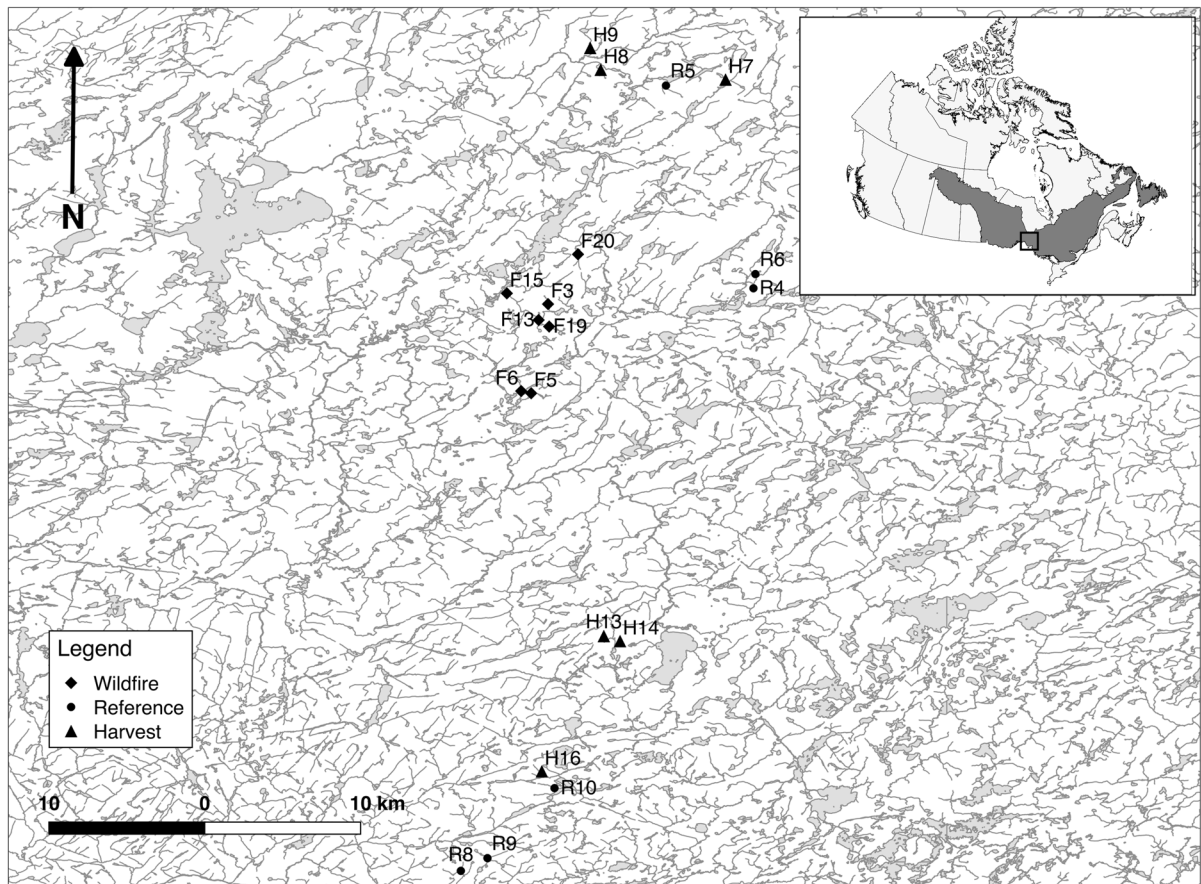


Fig. 1 A map of all study sites (6 harvest; 7 fire; 6 reference) within the White River Forest Management Area (latitude: 48°21'5", longitude: 85°20'46"), found 75 km from the

northwest shore of Lake Superior (see box in inset Canada map) in Canada's Eastern Boreal Shield ecozone

dependent, minimum 30-m riparian buffers, (2) wild-fire (burned 12 years prior to study initiation), and (3) reference (minimally disturbed, i.e., no fire or harvesting for at least 40 years). Within these disturbance types, our study sites consist of 50-m stream reaches established in 19 headwater catchments (6 harvest; 7 fire; 6 reference). Reaches within wildfire-disturbed catchments were bordered by riparian forests that had experienced fire intrusion. The total area of harvested catchments ranged from 43 to 401 ha (mean = 330 ha), fire catchments ranged from 131 to 777 ha (mean = 350 ha), and reference catchments ranged from 45 to 787 ha (mean = 356 ha) (For full site details see Table 1, Musetta-Lambert et al., 2017). Reach characteristics were primarily measured in 2010 and included bankful widths, stream depth, canopy openness, calculated in WinSCANOPY® software (Régent Instruments Inc., Quebec City, QC.) using digital hemispherical pictures taken with a fisheye lens (WinSCANOPY® O-Mount with a 185° SuperFisheye lens (5.6 mm, F/5.6), Régent Instruments Inc., Quebec City, QC.) attached to Canon® EOS 50D digital camera, and stream gradient was measured by clinometer over the 50-m reach. Prior to analyses of terrestrial invertebrate entering drift and aquatic invertebrate drift communities, we used 1-way ANOVAs to compare all reach-scale measurements (i.e., canopy openness, average water depth, average bankful width, and stream gradient) and no significant differences were detected.

Invertebrate communities: terrestrial and aquatic drift

We quantified terrestrial and aquatic invertebrate drift patterns at all streams ($n = 19$) simultaneously over three 24-h periods in late June, July, and August of 2014. The summer months were studied to account for peak invertebrate productivity and variability in hatch time during the short northern Ontario summer season. In each stream, we anchored wire-framed drift nets (47 cm × 32 cm, 363 µm mesh size) to rebar, secured into the substrate under the stream thalweg, and sampling the entirety of the water column. This method allows sampling of aquatic macroinvertebrates in drift and terrestrial invertebrates that contribute to the instream energy subsidies available for secondary consumers. The rebar poles used to secure each drift net were set up at our study streams 7 days

prior to our first sampling session to minimize substrate disturbance during sampling. After the 24-h period was over, drift samples were collected and preserved in 80% ethanol. In the laboratory, macroinvertebrates were primarily identified to the family or genus level and separated by terrestrial and aquatic life-stage except for Oligochaeta. To measure invertebrate biomass (mg 100 m⁻³), samples were separated by terrestrial or aquatic life-stage and grouped at the order level prior to being placed in a drying oven for 24 h at 60°C and immediately weighed (mg). To standardize drift density (# 100 m⁻³) and biomass (mg 100 m⁻³), drift abundance was divided by 24-h discharge for each sample site. Hereafter, we refer to drift density as total abundance. For this calculation, water velocity was measured at the time of net installation (0 h) and retrieval (24 h) at three points across the net opening to calculate the volume of water flowing through the drift. Discharge (m³ h⁻¹) was calculated by multiplying the cross-sectional area of the net by average water velocity (Gordon et al., 2004).

Statistical analyses

All univariate statistical analyses were performed in R (Version 3.4.1, R Development Core Team, Vienna, Austria 2017) and all multivariate statistical analyses were performed using PRIMER v6 (Primer-e Ltd., Plymouth, United Kingdom) software with the PERMANOVA (Primer-e Ltd., Plymouth, UK) add-on (Anderson, 2001, 2005; Clarke & Gorley, 2006). All macroinvertebrate data analyzed during this study are included within the article or supplementary information files. A $\log(x + 1)$ transformation was applied to univariate data during analyses to meet the assumption of normality. We used a fourth-root transformation for community abundance matrices to downweigh the highly abundant taxa and uncover detectable patterns associated with rare taxa (Clarke & Warwick, 2001). Additionally, multivariate statistical analyses are based on Bray–Curtis similarity matrices.

Linear mixed-effects models were used to investigate differences between disturbances in aquatic invertebrate drift communities including taxa richness (total # of taxa per sample), total EPT (Ephemeroptera, Plecoptera, Trichoptera), and mean abundance (# 100 m⁻³) and in aquatic invertebrate drift communities including using mean taxa richness, mean

Table 1 Results of linear mixed-effects model testing differences terrestrial and aquatic invertebrate drift abundance and mass-related metrics across disturbance type (references $n = 6$; harvest $n = 6$; fire $n = 7$) and time (June, July, August)

	<i>df</i>	<i>F</i>	<i>P</i>	Pairwise
Aquatic invertebrates				
Abundance				
Time	2, 28	8.74	0.001	Jun > Aug**, Jul > Aug**
Disturbance	1, 14	4.68	0.027	Fire > Ref*
Time*disturbance	4, 28	2.52	0.064	
Taxa richness				
Time	2, 31	10.89	< 0.001	Jun > Aug**, Jul > Aug**
Disturbance	2, 16	2.34	0.129	
Time*disturbance	4, 31	1.95	0.127	
Total EPT				
Time	2, 29	8.04	0.002	Jun > Aug**, Jul > Aug**
Disturbance	2, 15	0.72	0.501	
Time*disturbance	4, 29	2.19	0.096	
Total chironomidae				
Time	2, 29	10.37	< 0.001	Jun > Aug**, Jul > Aug**
Disturbance	2, 15	4.70	0.026	Fire > Ref*, Fire > Harv*
Time*disturbance	4, 29	2.73	0.048	
Biomass				
Time	2, 32	6.23	0.005	Jun > Aug**, Jul > Aug**
Disturbance	2, 16	4.72	0.025	Fire > Harv*, Fire > Ref*
Time*disturbance	4, 32	0.37	0.831	
Terrestrial invertebrate				
Abundance				
Time	2, 32	3.82	0.033	Jun > Aug*, Jul > Aug*
Disturbance	2, 16	0.75	0.489	
Time*disturbance	4, 32	2.46	0.065	
Taxa richness				
Time	2, 32	10.2	<0.001	Jun > Aug**, Jul > Aug*
Disturbance	2, 16	0.11	0.896	
Time*disturbance	4, 32	1.07	0.389	
Biomass				
Time	2, 32	2.05	0.152	
Disturbance	2, 16	0.43	0.658	
Time*disturbance	4, 32	2.05	0.113	

Site was treated as a random factor nested within disturbance type. Significance testing for metrics was estimated using the Kenward–Roger approximate *F* test approach. Tukey's HSD post hoc tests were used to test significant differences when a significant main effect existed. Significant *P* values presented in bold. Significant pairwise comparisons denoted as **P* < 0.05 and ***P* < 0.01

abundance, total Chironomidae, the percentage of functional feeding groups (shredders, scrapers, predators, filter-feeders, collector-gatherers), and total counts of each functional feeding group. We followed Merritt & Cummins (2014) to classify the functional feeding groups of all invertebrates. Furthermore, we tested for a disturbance effect on mean aquatic and terrestrially derived invertebrate biomass. The linear mixed-effects models included time (3 levels: June, July, and August) and disturbance type (3 levels: Fire,

Reference, and Harvest) as fixed factors and site ($n = 19$ levels) as a random factor nested in disturbance type. The mixed-effects model allowed for variation associated with the random factor, site, to be accounted for when fitting the model, allowing for interpretation of the fixed effects. We included an additional fixed factor, source (2 levels: terrestrial & aquatic), in an expanded linear mixed-model to test if there were significant differences between overall aquatic and terrestrial invertebrate community metrics

(abundance, taxa richness, and biomass) within disturbance types. Linear mixed-effects models were run in the *lme4* package (Bates et al., 2017) using the *anova* function in the *lmerTest* package (Kuznetsova et al., 2016) as a means of estimating the significance of main effects over and above the effect of the random variable, site, based on the Kenward–Rogers approximate *F* test approach. Any significant main effects ($p < 0.05$) were investigated using Tukey's HSD post hoc tests within the *lsmeans* package (Lenth, 2016).

We used non-metric multidimensional scaling (NMDS) to visualize overall patterns in terrestrial invertebrate subsidy and aquatic invertebrate drift community structure between the forest disturbance types. All NMDS plots had a stress level < 0.2 , permitting 2-dimensional interpretation of community composition grouping. A two-way permutational analysis of variance (PERMANOVA) design with time and disturbance type as fixed factors was used to investigate differences in abundance data. Significance tests for the PERMANOVA model were based on 999 permutations of transformed data. Similarity percentage (SIMPER) analyses were used to identify the taxa that contributed the most to observed significant differences between forest disturbances (Clarke & Warwick, 2001). Finally, we used Indicator analysis (IndVal in R package *indicspecies*) on the community abundance and biomass matrices to identify which taxa were significant indicators of each forest condition type and combinations of conditions. Indicator analysis gives an IndVal.g value measuring the degree of association between a specific taxon and forest condition type ranging from no association (i.e., 0) to complete association (i.e., 1) (Cáceres, 2013).

Results

The linear mixed-effects model detected a significant effect of disturbance on the total abundance of aquatic macroinvertebrates in drift, supported by a greater total abundance in fire-disturbed streams than reference streams (Table 1). Additionally, there was a significantly greater abundance of total Chironomidae in harvest-disturbed streams compared to reference and fire-disturbed streams (Table 1). There was no disturbance effect detected among taxa richness, total EPT (Table 1; means (\pm SE) available in Online

Resource 1, Table S1). Percent predators were significantly greater in fire-disturbed streams than in reference streams (Table 2), but no significant disturbance effect was detected among other functional feeding group abundance values (means (\pm SE) available in Online Resource 1, Table S2 and Table S3). A significant time effect was seen for all aquatic macroinvertebrate metrics. There was no significant effect of disturbance type on any of the terrestrial invertebrate community metrics (Table 1; means (\pm SE) available in Online Resource 1, Table S4).

Total aquatic invertebrate drift biomass was significantly different among disturbances ($P = 0.0050$), with significantly greater biomass ($\text{mg } 100 \text{ m}^{-3}$) at fire sites compared to reference ($P = 0.044$) and harvested sites ($P = 0.021$). Aquatic drift biomass was also different across time ($P = 0.025$), with significantly greater drift biomass in June compared to August (Table 1; Fig. 2). No significant differences were detected for terrestrial invertebrate biomass across disturbances or time ($P = 0.15$) (Table 1; Fig. 2). The ratio of terrestrial to aquatic invertebrate biomass was not significantly different across time ($P = 0.40$) or disturbance ($P = 0.25$) (significance tests in Online Resource 1, Table S5).

Overall, there was significantly greater abundance of aquatic macroinvertebrates than terrestrial invertebrates in drift samples within fire (Disturbance X Source interaction: $F = 4.84$, $P = 0.0011$; Tukey's HSD tests for Disturbance x Source, fire-aquatic vs. fire-terrestrial Ab: $P < 0.001$) and reference (Tukey's HSD tests for Disturbance X Source, reference-aquatic vs. reference-terrestrial Ab: $P = 0.021$) sites. In addition, there was a significantly greater taxa richness of aquatic macroinvertebrates than terrestrial invertebrates in drift samples (Source effect: $F = 82.048$, $P = < 0.001$; Fig. 3). There was significantly greater biomass of aquatic macroinvertebrates compared to terrestrial invertebrate drift samples (Disturbance X Source interaction: $F = 3.49$, $P = 0.035$) at fire-disturbed sites (Tukey's HSD tests for Disturbance X Source, fire-aquatic vs. fire-terrestrial: $P = 0.0050$), but not within harvested or reference sites.

Our PERMANOVA model detected a significant disturbance effect ($P = 0.016$) and time effect ($P = 0.0010$) on invertebrate drift community composition; however, the trends were not clear in our NMDS ordination plots (Online Resource 1,

Table 2 Results of linear mixed-effects model testing differences in terrestrial and aquatic invertebrate drift functional feeding group metrics across disturbance type (references $n = 6$; harvest $n = 6$; fire $n = 7$) and time (June, July, August)

Metric	Source	<i>df</i>	<i>F</i>	<i>P</i>	Pairwise
% shredders	Time	2, 31	2.96	0.065	
	Disturbance	2, 16	0.14	0.869	
	Time*disturbance	4, 31	0.21	0.931	
% predators	Time	2, 32	0.51	0.608	
	Disturbance	2, 16	3.73	0.047	Fire > Ref*
	Time*disturbance	4, 32	2.44	0.067	
% collector–gatherers	Time	2, 30	2.65	0.087	
	Disturbance	2, 15	1.02	0.383	
	Time*disturbance	4, 30	1.69	0.178	
% scrapers	Time	2, 32	1.89	0.168	
	Disturbance	2, 16	0.005	0.995	
	Time*disturbance	4, 32	0.38	0.822	
% filter-feeders	Time	2, 32	10.21	< 0.001	Jun > Aug**, Jul > Aug*
	Disturbance	2, 16	0.11	0.896	
	Time*disturbance	4, 32	1.07	0.389	
Shredders	Time	2, 28	11.07	< 0.001	Jun > Aug*, Jul > Aug**
	Disturbance	2, 15	1.35	0.288	
	Time*disturbance	4, 28	1.59	0.206	
Predators	Time	2, 30	4.13	0.026	July > Aug*
	Disturbance	2, 15	2.85	0.089	
	Time*disturbance	4, 30	1	0.423	
Collector–gatherers	Time	2, 28	3.37	0.049	Jul > Aug*
	Disturbance	2, 15	0.68	0.524	
	Time*disturbance	4, 29	2.65	0.054	
Scrapers	Time	2, 32	0.36	0.703	
	Disturbance	2, 16	0.94	0.410	
	Time*disturbance	4, 32	0.68	0.608	
Filter-feeders	Time	2, 32	9.81	< 0.001	Jun > Jul*, Jun > Aug**
	Disturbance	2, 16	0.22	0.808	
	Time*disturbance	4, 32	0.19	0.941	

Site was treated as a random factor nested within disturbance type. Significance testing for metrics was estimated using the Kenward–Roger approximate *F* test approach. Tukey's HSD post hoc tests were used to test significant differences when a significant main effect existed. Significant *P* values presented in bold. Significant pairwise comparisons denoted as * $P < 0.05$ and ** $P < 0.01$

Figure S1). Further pairwise testing found that aquatic drift communities in fire-disturbed streams significantly differed from those in streams within harvested ($P = 0.044$) and reference catchments ($P = 0.027$) (Table 3). Aquatic macroinvertebrate drift communities also significantly differed between August, and June (June–August: $P = 0.001$) and July (July–August: $P = 0.001$). There were no significant effects of disturbance, time, or the disturbance x time interaction

on community composition of terrestrial invertebrate entering drift (Table 3). SIMPER analyses identified Chironomidae as the highest contributor to dissimilarity in drift between fire, and references and harvested sites, with greater abundances at fire sites than references sites, but lower overall abundances at fire than harvested sites (Table 4). The mayfly genus *Baetis* and caddisfly *Dolophilodes* were consistently high contributors to the dissimilarity between

Fig. 2 Instream invertebrate biomass subsidies derived from aquatic (a) and terrestrial (b) sources separated by disturbance and time. In each case, the lower and upper limits of the box indicate the 25th and 75th percentile (inter-quartile range; IQR) and the bar represents the median. Whiskers indicate the range for the most extreme value within 1.5 times the IQR and disconnected dots represent most extreme outlier outside 1.5 times the IQR

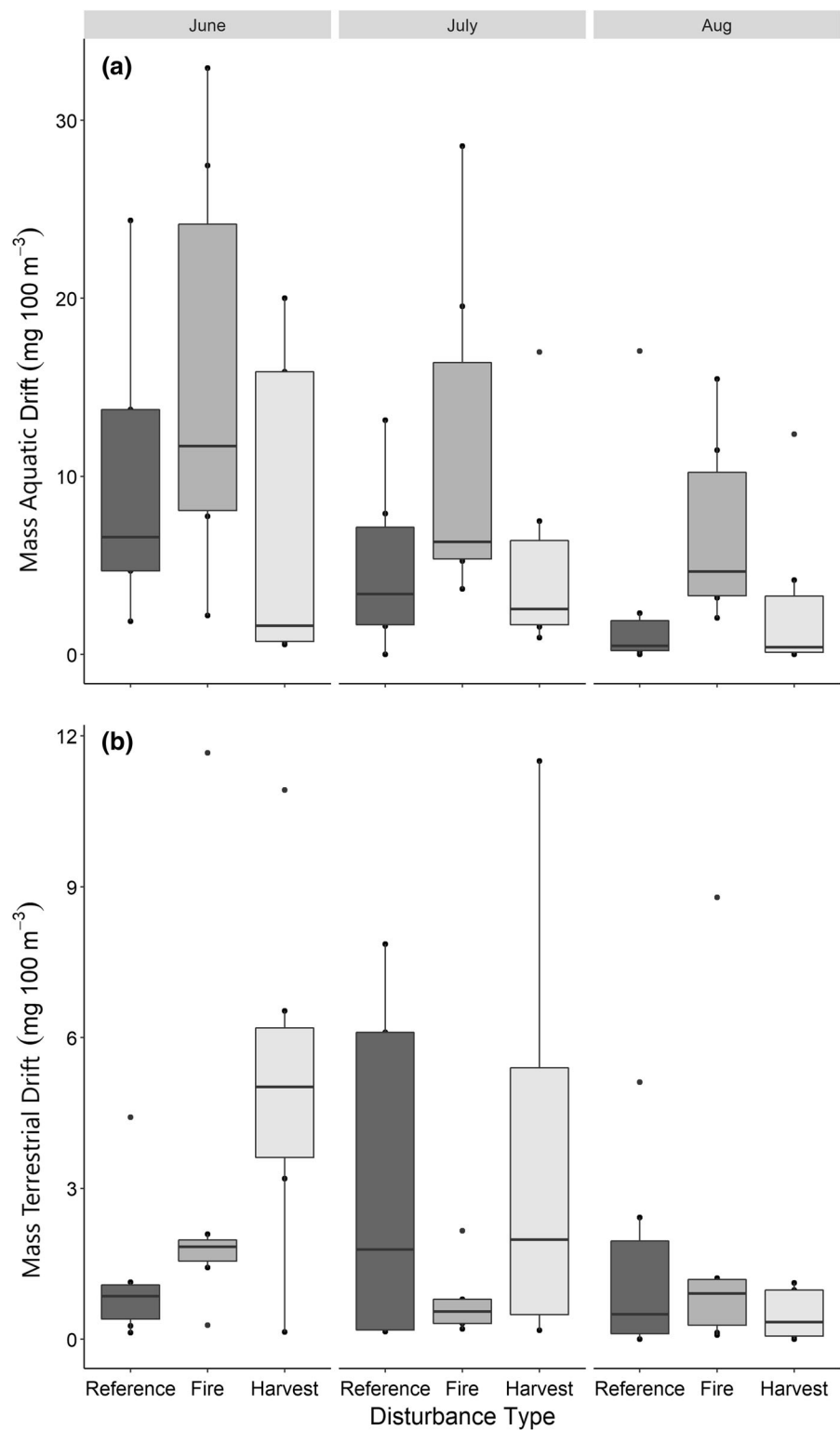


Fig. 3 Abundance (**a**: # of organisms 100 m^{-3}) and taxa richness (**b**: # of taxa 100 m^{-3}) derived from aquatic and terrestrial sources separated by disturbance and pooled over time. In each case, the lower and upper limits of the box indicate the 25th and 75th percentile (inter-quartile range; IQR) and the bar represents the median. Whiskers indicate the range for the most extreme value within 1.5 times the IQR and disconnected dots represent most extreme outlier outside 1.5 times the IQR

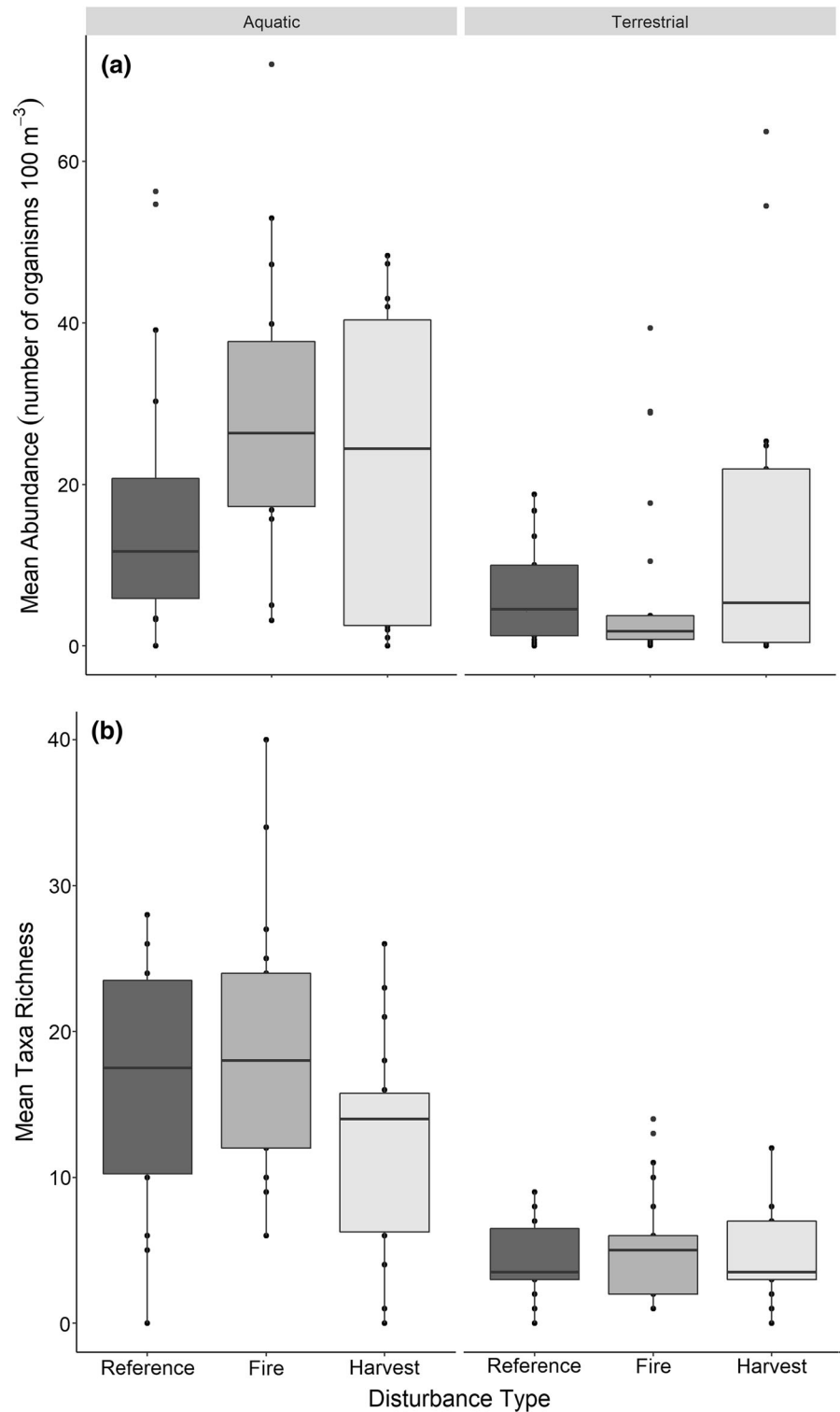


Table 3 PERMANOVA results testing the effect of forest disturbance history and time on aquatic invertebrate drift and terrestrial invertebrate subsidy community composition (Bray–Curtis similarity with a 4th-root transformation on taxa abundances)

Source	df	SS	Pseudo-F	P (perm)	Pairwise contrasts
Aquatic					
Time	2	13067.00	2.85	0.001	Aug & June*, July*
Disturbance	2	8038.80	1.76	0.016	Fire & Ref*, Harv*
Time*disturbance	4	8753.60	0.96	0.582	
Residuals	45	1.03E + 05			
Terrestrial					
Time	2	7058.50	1.24	0.211	
Disturbance	2	5508.70	0.97	0.502	
Time*disturbance	4	8029.30	0.70	0.919	
Residuals	45	1.28E + 05			

Significance tested at $P < 0.05$ and displayed in bold for the overall model test. Significant pairwise comparisons denoted as * for $P < 0.05$

Table 4 SIMPER results showing the macroinvertebrate taxa abundance (# 100 m⁻³) contributing the most to dissimilarity between disturbance types (reference $n = 6$; harvested $n = 6$; fire $n = 7$) detected significant in the PERMANOVA pairwise comparisons

Taxa	Reference	Fire	Individual contrib. %	Cumulative contrib. %
Chironomidae	23.77	31.11	41.92	41.92
<i>Baetis</i>	4.42	12.38	9.78	51.69
<i>Dolophilodes</i>	0.62	110.00	7.43	59.13
Simuliidae	8.32	4.35	6.55	65.68
<i>Amphinemura</i>	15.59	0.79	4.72	70.39
<i>Leuctra</i>	0.31	2.70	2.66	73.05
<i>Lepidostoma</i>	2.74	0.97	2.35	75.41
Ceratopogonidae	0.01	1.41	1.66	77.06
Leptophlebiidae	1.81	0.50	1.66	78.72
Average dissimilarity = 66.69%				
Species	Harvested	Fire		
Chironomidae	175.02	31.11	49.05	49.05
<i>Baetis</i>	0.41	12.38	8.6	57.65
<i>Dolophilodes</i>	0.31	110.00	6.39	64.04
Simuliidae	2.84	4.35	5.17	69.21
<i>Leuctra</i>	1.61	2.70	3.61	72.82
Culicidae	69.19	0.00	2.67	75.49
<i>Lepidostoma</i>	0.51	0.97	2.05	77.54
Ceratopogonidae	0.03	1.41	1.57	79.11
Average dissimilarity = 70.04%				

disturbance types and were found in greater abundances at fire compared to reference and harvested sites. *Dolophilodes* was 177 and 354 X more abundant at fire sites than at reference and harvested sites, respectively (Table 4).

Community composition of aquatic and terrestrial invertebrate drift patterns expressed as biomass showed similar interspersed between disturbance types in the NMDS ordination plots (Online Resource, Figure S1). However, significant differences were detected in the community biomass composition of

Table 5 PERMANOVA results testing the effect of forest disturbance history and time on aquatic invertebrate drift and terrestrial invertebrate biomass (mg 100 m⁻³) subsidy composition (Bray–Curtis similarity with a 4th-root transformation on taxa biomass)

Source	df	SS	Pseudo-F	P(perm)	Pairwise contrasts
Aquatic					
Time	2	12302.00	2.76	0.001	Aug & June*, July*
Disturbance	2	8102.60	1.82	0.024	Fire & Harv*
Time*disturbance	4	8275.20	1.82	0.577	
Residuals	46	1.02E + 05			
Terrestrial					
Time	2	4967.80	2483.90	0.586	
Disturbance	2	6122.60	3061.30	0.361	
Time*disturbance	4	7691.80	1923.00	0.911	
Residuals	46	1.28E + 05			

Significance tested at $P < 0.05$ and displayed in bold for the overall model test. Significant pairwise comparisons denoted as * for $P < 0.05$

aquatic invertebrates among disturbance types ($P = 0.024$) and time ($P = 0.001$). Further pairwise testing found that fire sites statistically differed from harvested sites ($P = 0.014$), but not reference sites ($P = 0.17$) (Table 5). SIMPER analysis was able to identify that greater abundances of Trichoptera, Odonata, and Ephemeroptera at fires sites and greater abundances of Diptera and Coleoptera at harvested sites as the major contributors to the dissimilarity in aquatic invertebrate drift biomass (Table 6). Indicator analysis showed Chironomidae (IndVal $g = 0.96$, $P = 0.016$) were significantly associated with fire sites throughout all months. *Hydatophylax* caddisflies (IndVal $g = 0.648$, $P = 0.005$), *Baetis* mayflies (IndVal $g = 0.87$, $P = 0.014$), and *Paracapnia* stoneflies (IndVal $g = 0.73$, $P = 0.004$) were associated with fire sites in June, July, and August, respectively.

Simuliidae were associated with fire sites in August, but both harvested and reference sites in June and July (IndVal $g = 0.87$, $P = 0.017$). *Lepidostoma* (IndVal $g = 0.84$, $P = 0.004$) and *Limnephilus* (IndVal $g = 0.77$, $P = 0.001$) were associated with reference and fire sites. The only taxa associated exclusively with harvested sites were Dytiscidae (IndVal $g = 0.766$, $P = 0.049$). For drift biomass data, the indicator analysis showed that Amphipoda were significantly associated with fire sites (IndVal $g = 0.535$, $P = 0.007$).

Discussion

We found evidence that drifting aquatic invertebrate communities were different in fire-disturbed streams

Table 6 SIMPER results showing the macroinvertebrate taxa biomass (mg 100 m⁻³) contributing the most to dissimilarity between disturbance types (reference $n = 6$; harvested $n = 6$; fire $n = 7$) detected significant in the PERMANOVA pairwise comparisons

Taxa	Harvested	Fire	Individual contrib. %	Cumulative contrib. %
Trichoptera	2.02	6.76	32.99	32.99
Diptera	3.58	2.40	23.53	56.53
Odonata	0.01	6.57	13.84	70.36
Ephemeroptera	0.24	0.64	7.29	77.66
Coleoptera	1.55	0.36	7.11	84.76
Average dissimilarity = 83.50%				

Taxon-specific contributions (%), cumulative contributions ($\sim 80\%$ cut-off), and average dissimilarity between disturbance type included)

compared to buffer-protected harvest-disturbed streams or reference streams more than a decade after the wildfire event. Aquatic macroinvertebrate drift communities at fire sites contained significantly greater total abundance and biomass, and consistently greater EPT abundance, supporting our hypothesis that wildfire-disturbed forest catchments would create ecological conditions that supported overall increases in abundance and different communities of aquatic macroinvertebrates in drift. These aquatic invertebrate response measures suggest that fire disturbance may have induced long-term changes in stream habitat conditions, supporting production of, or favoring, a drifting macroinvertebrate community with greater overall biomass. The long-term fire effects may result in consequences for secondary consumers in headwaters and downstream reaches such as increased prey resources due to greater post-fire-aquatic invertebrate biomass and production (Nakano et al., 1999; Kawaguchi et al., 2003).

Our findings expand on the results from Musetta-Lambert et al. (2017), where a distinct aquatic macroinvertebrate community composition associated with experimental leaf packs, largely driven by shredders, was detected at fire-disturbed sites compared to reference and harvested sites in the same study area. While we sampled only drift communities and did not sample benthic community composition or macroinvertebrate communities associated with experimental leaf packs, other studies have shown that stream drift and benthic community composition are generally proportional, positively related, and sample similar dominant taxa (Ramirez & Pringle, 1998; Imbert & Perry, 2000; Kennedy et al., 2014). Previous studies have shown that wildfire can have significant short-term impacts, like those of riparian harvesting, on small forested streams due to their dependence on allochthonous subsidies from riparian forests that can be lost during wildfire (Minshall, 2003; Malison & Baxter, 2010a; Studinski & Hartman, 2015). In relation to benthic macroinvertebrate communities, studies have shown a return to or exceedance of pre-fire abundance and biomass between 2- to 10-years following fire as an early successional vegetation community develops in the riparian zone (Roby & Azuma, 1995; Minshall et al., 2001a, b; Minshall, 2003; Mellon et al., 2008). Our study showed that measurable differences in community composition of aquatic macroinvertebrates, as

indicated in the drift, persisted in fire-disturbed boreal forest catchments by 15 years post-disturbance. Over longer time-scales, the effects of wildfire on benthic macroinvertebrate communities are generally restricted to subtle shifts in community composition due to changes in stream and riparian habitat characteristics (Minshall, 2003). Longer term impacts of wildfire on aquatic invertebrate community composition that have previously been observed include a shift towards taxa that are adapted to post-disturbance conditions or to taxa that are trophic generalists (Albin, 1979; Mihuc & Minshall, 1995; Minshall et al., 1997). One study by Albin (1979) in Yellowstone National Park observed greater mean abundance, richness, and Shannon–Wiener diversity in headwater streams of catchments that had burned 36–45 years previously compared to reference streams. The variability in the documented persistence of wildfire effects on aquatic invertebrate communities depends on the location, frequency, and severity of the wildfire (Minshall et al., 1989; Mihuc et al., 1996; Minshall, 2003).

Notably greater abundances of generalist feeders such as the mayfly *Baetis* and caddisfly *Dolophilodes* at fire sites compared to reference and harvested sites were found to contribute the most to dissimilarity between the aquatic invertebrate communities in drift between disturbance types. These trends are consistent with well-documented examples of wildfire increasing populations of opportunistic and generalist feeders (Minshall et al., 1997; Malison & Baxter, 2010a) and rapid reproducing taxa such as *Baetis* (Malison & Baxter, 2010b; Jackson et al., 2012) from both benthic and emergence studies. Other studies have shown increases in baetids following disturbance events that create canopy openings over streams (e.g., full catchment harvesting) and this has been suggested as a response to increased rates of primary productivity within streams no longer sheltered from solar radiation (Wallace & Gurtz, 1986; Stone & Wallace, 1998; Wilson et al., 2014). While we did not see any significant differences in canopy openness between the fire-disturbed streams and streams with undisturbed riparian forest, it would be reasonable to suggest that the canopy openness above streams in the fire-disturbed riparian areas would have been higher in the decade prior to sampling. The increase in baetids observed in this study may be a long-term response to historically greater canopy openness and has been

sustained from increased inputs of high-quality litter subsidies from deciduous vegetation in the riparian zone to the fire-disturbed streams as the canopy has regenerated (Musetta-Lambert et al., 2017). Baetids could be suggested as candidate indicator taxa for forest monitoring programs in light of their responses in both reference and fire-disturbed streams and patterns showing increased abundance in fire-disturbed streams, as they were not associated with long-term post-harvest conditions. The indicator analysis also revealed month-to-month differences in taxa associations with disturbance types. For example, *Hydatophylax* caddisflies were uniquely identified as indicator taxa during June sampling and *Paracapnia* stoneflies were uniquely identified as indicator taxa during August sampling. These month-to-month differences were likely due to differences in life-cycle timing and abiotic conditions (e.g., flow regimes, water temperature), but their propensity to be more abundant in fire-disturbed streams than reference and harvested streams suggests that a potential subset of EPT may be useful in pursuing as a bioindicator in further studies. *Lepidostoma* and *Limnephilus* caddisflies were significantly associated with both reference and fire sites, as indicated by the indicespecies analyses, but they were not associated with harvesting (with traditional riparian buffers) disturbance. Changes in abundance of Chironomidae and Simuliidae may be helpful bio-indicators, showing significant variation in total abundance across disturbances, and well-studied shorter term trends show increases in abundance following wildfire (Mihuc & Minshall, 1995; Malison & Baxter, 2010a; Verkaik et al., 2015). Finally, we found Chironomidae contributed the most overall to differences among disturbances and were found in highest abundances at harvested sites, followed by wildfire and then reference sites. Previous studies investigating the effects of wildfire on aquatic invertebrate communities (Mihuc & Minshall, 1995; Malison & Baxter, 2010b; Jackson et al., 2012) did not also include sites impacted by harvesting in their studies but did find greater Chironomidae at wildfire-disturbed sites than at reference sites. In this study, as in many other studies and biomonitoring programs, Chironomidae were left at the family level because identification at lower taxonomic levels is time-consuming, and requires extensive taxonomic expertise and the ecological information on chironomids remains fragmented (Puntí et al., 2009). Further

research to improve the taxonomic resolution could increase our understanding of the underlying mechanisms of how disturbance influences ecological structure and function in stream ecosystems. For example, Rodríguez-Lozano et al. (2016) found that fish feeding preferences of chironomids were obscured when the family level was used compared to subfamily or genus levels. An overall increase in abundance of trophic generalists, r-strategists, and taxa with high dispersal rates (e.g., Chironomidae, Baetidae, and Simuliidae) may be partly due to shifts in riparian vegetation community composition, timing of leaf litter input, and an interaction between wildfire severity and time since burned (Mihuc & Minshall, 1995; Jackson et al., 2012; Verkaik et al., 2013, 2015). However, our study seems to be first to report this trend in drifting aquatic invertebrate communities, specifically in North American boreal forests.

Our results did not detect any persisting disturbance effect on terrestrial invertebrate community composition or the potential energy subsidies (i.e., biomass) they provide to streams from riparian forests. The lack of any significant finding regarding abundance or biomass inputs of terrestrial invertebrates found in drift suggests that either the riparian conditions required to support terrestrial invertebrates had returned to pre-disturbance conditions or differences in riparian condition were subtle enough not to impact terrestrial invertebrate communities. Based on a previous study in the same area, Musetta-Lambert et al. (2017) found that fire-disturbed riparian forests had more dense and diverse woody-stem vegetation communities of largely early successional species and contributed greater leaf biomass to streams than riparian forests in harvested or reference catchments. We, therefore, had expected that the more dense, richer, early successional woody-stem vegetation in riparian areas of fire-disturbed streams would support a more abundant and potentially distinct terrestrial invertebrate community that would be delivered to streams. We found no evidence that terrestrial invertebrate subsidies entering drift in streams were greater or different from those in streams of harvest-disturbed and reference catchments. While we did not find evidence in support of our second hypothesis, our findings do align with previous studies that found that terrestrial invertebrate subsidies were not greater in streams surrounded by early successional vegetation (Allan et al., 2003; Wilson et al., 2014). Although these studies

measured greater biomass of terrestrial invertebrates in early successional vegetation of riparian zones, they did not find greater biomass of terrestrial invertebrates in subsidies to streams from that vegetation (Allan et al., 2003; Wilson et al., 2014). Wilson et al. (2014) suggested that terrestrial invertebrates may stay within or disperse between early successional habitat; therefore, while greater abundances of terrestrial invertebrates may be present in early successional riparian zones produced post-disturbance, this pattern may not be detectable in headwater streams that make up a small area of the overall catchment. It is possible that the absence of the predicted increase in terrestrial invertebrate in drift from the fire-disturbed early successional riparian vegetation may have resulted from the limited sampling scheme we deployed, or not including other methods to investigate terrestrial invertebrate subsidies such as pan traps (Jackson et al., 2012). We measured terrestrial invertebrates in stream drift on three occasions over 24-h sampling periods but may have missed specific periods or conditions under which terrestrial invertebrate delivery to streams was elevated. Terrestrial invertebrate input to streams is highly variable in time (Hunt, 1975) at yearly, seasonal, and diurnal scales and can be affected by air temperature and humidity patterns. Future work should include sampling terrestrial invertebrate communities within riparian early successional vegetation and include a more intensive sampling method within streams, including using traditional pan trap techniques within riparian forests.

Within the context of applying END principles to riparian and upland forest management, our invertebrate drift results provide further support to our earlier contention (Musetta-Lambert et al., 2017) that wildfire disturbance patterns in boreal forest catchments and riparian areas promote more abundant aquatic invertebrate communities within headwater streams. The overall goal of END is to manage forests in a manner that ensures maintenance of ecological structure and function that falls within the historical natural range of variation in the ecosystem through carefully planned and implemented silviculture practices (Naylor et al., 2012). In areas that are disturbance prone, natural disturbances can initiate critical forest renewal processes such as succession that enhance habitat complexity and support biodiversity (Naylor et al., 2012; Sibley et al., 2012). Emulating those disturbance patterns with END forest harvesting practices in the

riparian zone should produce similar response patterns to our results showing increased total drifting invertebrate abundance and biomass. Future studies should be carried out including streams within watersheds that were harvested under END-based harvesting techniques to determine the effectiveness of these techniques at reproducing post-fire patterns in ecological function and structure. Variable retention harvesting procedures in the riparian zone that mimic the patchy nature of wildfire burns within watersheds are currently in practice to emulate wildfire incursions in riparian forests (OMNR, 2010; Sibley & Gordon, 2010), but should be experimentally studied as a next step to see if they produce observed patterns from this study. Our results contribute management targets to determine if END-based harvesting procedures are achieving the desired outcomes of enhanced aquatic habitats and biodiversity. Although we did not find that wildfire-derived early successional riparian forests delivered greater quantities of terrestrial invertebrate subsidies to streams (quantified as the proportion in drift) than undisturbed riparian forests, our earlier work (Musetta-Lambert et al., 2017) indicated aquatic habitat implications of wildfire disturbance that could be construed as positive under an emulation of natural disturbance regime such as the promotion of early successional riparian forests and an associated increase in leaf subsidies. Our previous work, combined with the results of this study, provides lines of evidence that forest management strategies aimed at emulating wildfire-derived riparian forest conditions through harvesting techniques could conserve long-term aquatic habitat and biodiversity within the historical natural range of variation.

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