

# Long-term impact of severe wildfire and post-wildfire salvage logging on macroinvertebrate assemblage structure in Alberta's Rocky Mountains

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**Abstract.** Wildfire is an important natural disturbance on forested landscapes influencing both physical and biological processes. The Lost Creek wildfire was one of the most severe on Alberta's eastern slopes and provided a unique opportunity to assess the long-term impacts of wildfire and post-wildfire salvage logging on northern Rocky Mountain catchments. Macroinvertebrate sampling conducted 8 years after the wildfire indicated distinct macroinvertebrate assemblages in reference, burned, and burned and salvage-logged catchments. Reference catchments were characterised by more sensitive taxa (e.g. stoneflies) and had the lowest abundance of macroinvertebrates. Burned catchments had the greatest abundance of macroinvertebrates and were characterised by greater abundance of chironomids and caddisflies. Burned and salvage-logged catchments supported high numbers of riffle beetles and crane flies. The unique assemblage structures between catchments indicate different mechanisms drive the ecological response in wildfire-affected catchments. Resource availability was an important driver of assemblage structure in the more productive burned catchments and habitat quality was a dominant driver in the burned and salvage-logged catchments. Despite the legacy effects observed in this study, fire-affected catchments still supported sensitive taxa and functional macroinvertebrate assemblages.

**Additional keywords:** natural disturbance, stream ecology.

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## Introduction

Wildfire is an important natural disturbance that can strongly influence both physical and biological environmental processes (Gresswell 1999; Moody and Martin 2001; Hauer *et al.* 2007). Since the 1980s, increases in wildfire frequency, severity, duration and season length in the western United States have been correlated with warming atmospheric temperatures (Schoennagel *et al.* 2004; Westerling *et al.* 2006). Between 1970 and 2003, 60% of the observed increases in wildfire activity occurred in the Rocky Mountains (Westerling *et al.* 2006). These ecosystems will be particularly susceptible to climate change-induced shifts in wildfire behaviour and it is expected that by the end of the 21st century, the annual area burned in Canada will increase by 74 to 118% compared with the latter half of the 20th century (1959–97) (Flannigan *et al.* 2005). Such

increases in area burned will have strong effects on both terrestrial and freshwater ecosystems (Romme *et al.* 2011). Post-fire landscape management such as salvage logging can also influence or compound the effects of fire on aquatic ecosystems by increasing ground disturbance and adding linear features (e.g. skid trails, haul roads and stream crossings) (Beschta *et al.* 1995; Wagenbrenner *et al.* 2016).

Forested mountain catchments provide critical habitat for many species, including macroinvertebrates and salmonid fishes (Hauer *et al.* 2007; Isaak *et al.* 2016). These streams typically have higher water quality than lowland streams (Hauer *et al.* 2007), and are sensitive to the changes in vegetation and soils caused by wildfire (Hynes 1975; Hauer *et al.* 2016). Wildfire alters rainfall-runoff dynamics, which can change sediment and nutrient regimes, channel morphology and water temperature

(Gresswell 1999). Elevated sediment loading, export of nutrients (nitrogen, phosphorus and dissolved organic carbon), export of heavy metals (e.g. mercury and methyl mercury) and stream temperature are commonly reported after wildfire in mountain catchments (Hauer and Spencer 1998; Kelly *et al.* 2006; Shakesby and Doerr 2006; Writer *et al.* 2012; Wagner *et al.* 2014). Increased nutrients stimulate microbial activity and autochthonous (in-stream) primary productivity (Spencer *et al.* 2003; Mihuc and Minshall 2005) while the influx of fine sediment can affect the availability and quality of in-stream habitat and food resources (Bjornn *et al.* 1977; Jones *et al.* 2012). Macroinvertebrate assemblages invariably respond to the water-quality changes associated with wildfire (Barbour *et al.* 1999; Minshall 2003). Assemblage composition often shifts to favour disturbance-adapted taxa, while more sensitive taxa can decline in abundance or be excluded entirely (Mihuc *et al.* 1996; Minshall *et al.* 2001a, 2001b; Malison and Baxter 2010b). Changes in biomass and density are less predictable but are often related to factors such as primary productivity, water chemistry and the occurrence of drought or flooding in the months or years following wildfire (Verkaik *et al.* 2015). Rinne (1996) documented large declines (70–90%) in invertebrate density following high-flow events with heavy sediment loads after a wildfire in Arizona. In contrast, Malison and Baxter (2010b) reported greater invertebrate productivity in severely burned reaches following the Diamond Peak wildfire in Idaho and associated this with increases in food resources. The extent of wildfire effects on macroinvertebrate assemblages depends on fire severity, local catchment characteristics including the hydroclimatic setting, vegetation type, topography, soils and geology, as well as the influences of climate change, including warming and changes in precipitation patterns (Moody and Martin 2001; Shakesby and Doerr 2006; Rugenski and Minshall 2014).

Macroinvertebrates are an important component of Rocky Mountain stream ecosystems. They contribute to nutrient cycling and provide a critical food source for fish and riparian insectivores (Mihuc *et al.* 1996; Rinne 1996; Minshall 2003; Malison and Baxter 2010a). Despite their importance in the trophic structure of stream ecosystems, very little is known about the long-term effects of wildfire on macroinvertebrate assemblages. Previous post-fire invertebrate studies report on shorter-term (1–5-year) impacts (Rinne 1996; Minshall *et al.* 1997; Spencer *et al.* 2003; Malison and Baxter 2010a; Malison and Baxter 2010b). However, fire can produce longer-term changes in the physical stream environment and water-quality conditions regulating stream ecology (Silins *et al.* 2014; Emelko *et al.* 2016). Although several studies in the United States have reported wildfire impacts on macroinvertebrate assemblages lasting as long as 5–10 years (Minshall *et al.* 1989; Roby 1989; Mihuc *et al.* 1996; Vieira *et al.* 2004; Malison and Baxter 2010b), both the longevity of fire effects on macroinvertebrates and factors regulating longer-term patterns of ecosystem recovery are presently not well understood across more northern mountain environments (Bixby *et al.* 2015).

The Lost Creek wildfire was one of the more severe fires in recent decades on the eastern slopes of Alberta's Rocky Mountains and provided an opportunity to assess the short-, mid- and long-term effects of wildfire on northern Rocky Mountain catchments. The Southern Rockies Watershed Project (SRWP)

was established to document the effects of the wildfire and post-wildfire salvage logging on hydrology, biochemistry and aquatic ecology (Silins *et al.* 2016). As reported elsewhere, 11 years of continuous monitoring have demonstrated that wildfire effects on water quality and biogeochemistry are persistent in the study catchments, with many parameters including sediment production, nutrient (phosphorus and dissolved organic carbon) export and primary productivity showing no sign of return to reference conditions over a decade post wildfire (Silins *et al.* 2009; Emelko *et al.* 2011; Silins *et al.* 2014; Wagner *et al.* 2014; Emelko *et al.* 2016; Silins *et al.* 2016). Given these persistent impacts on hydrology and water quality, disturbance-associated effects on macroinvertebrate abundance and assemblage structure between reference and wildfire-affected catchments also were expected. We expected greater abundance in the more productive wildfire-affected catchments, and greater diversity in the unburned systems. Thus, the objectives of the present study were to assess the long-term (8 years post fire) impacts of the Lost Creek wildfire on macroinvertebrates by:

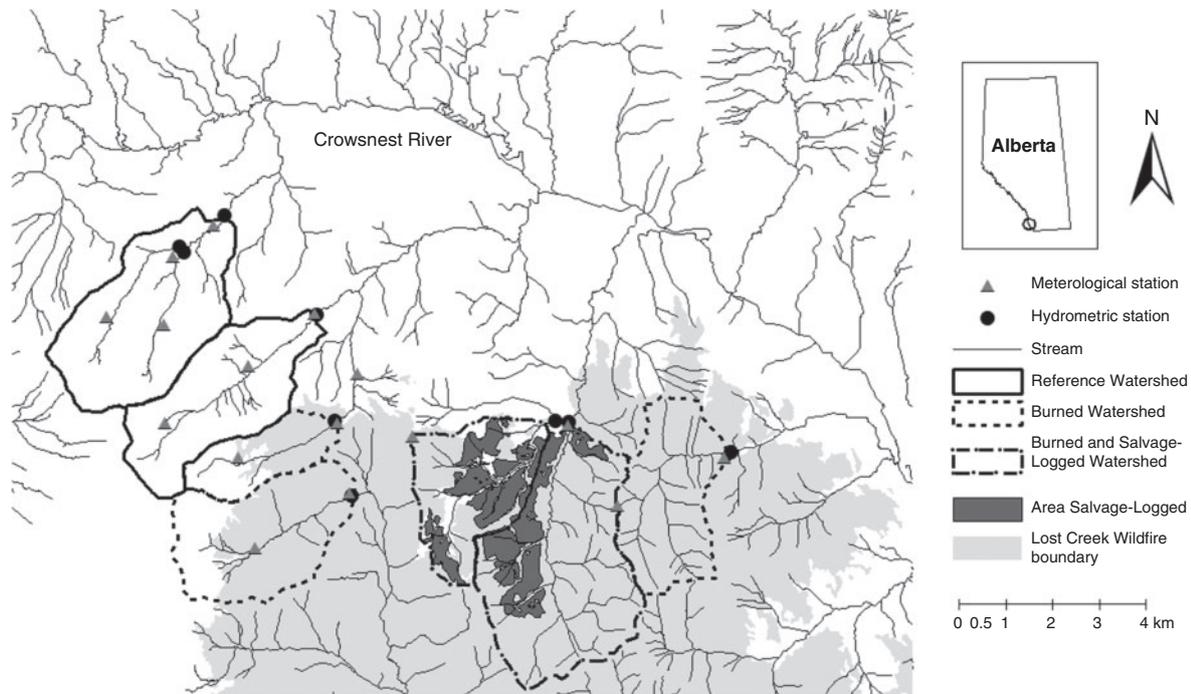
- (1) quantifying differences in macroinvertebrate abundance and assemblage structure in streams draining three types of catchments: reference (unburned), burned, and burned and salvage-logged,
- (2) determining the environmental parameters (water quality, streamflow and periphyton productivity) that best explain variation in macroinvertebrate assemblage structure, and
- (3) analysing a selection of ecological traits of more abundant taxa along a disturbance gradient (reference, burned, and burned and salvage-logged) to infer mechanisms that influence the response of macroinvertebrate assemblages after wildfire.

## Methods

### Site description

The Lost Creek wildfire burned 211.6 km<sup>2</sup> in the forested region of the Crowsnest and Castle River catchments in southern Alberta, Canada, from July to September 2003. The high-severity fire effectively consumed all of the forest cover (closed canopy, mature or old growth), understorey vegetation and forest floor organic material. The upper portions of the study catchments that did not burn (particularly South York and Lynx Creeks) were treeless alpine zones with little available fuel (Fig. 1, Table 1). Seven research catchments were established, including three burned catchments (South York, Lynx and Drum Creeks) and two reference (unburned) catchments (Star and North York Creeks) (Fig. 1, Table 1). Two catchments (Lyons East and Lyons West Creeks) were salvage-logged and instrumented in 2005. Clear-cut salvage harvest occurred over the winters of 2004 and 2005; 2.6 and 2.4 km<sup>2</sup> (19.9 and 33.6% of the catchment area) were harvested in Lyons East and Lyons West respectively (Fig. 1, Table 1). Forest regeneration was slow in wildfire-affected catchments; canopy cover did not recover in the 8 years before sampling and no subsequent fires occurred in research catchments during the study period.

The hydrologic regime of these catchments is snowmelt-dominated. The highest flows occur in late May to early June during the peak of spring snowmelt. Mean annual precipitation



**Fig. 1.** Southern Rockies Watershed Project research catchments (west to east: Star Creek, North York Creek, South York Creek, Lynx Creek, Lyons West Creek, Lyons East Creek and Drum Creek). Lines indicate catchment boundaries; solid: reference, dash: burned, dot-dash: burned and salvage-logged. Shading indicates forest disturbance; light grey: northern boundary of the Lost Creek Wildfire, dark grey: area salvage-logged.

**Table 1.** Characteristics of Southern Rockies Watershed Project research catchments

Catchment	Catchment area (km <sup>2</sup> )	Area burned (km <sup>2</sup> )	Area salvage-logged (km <sup>2</sup> )	Elevation (m)	Slope (%)	Aspect
<i>Reference (Unburned)</i>						
Star	10.59	0 (0%)	0	1479–2627	45	North-east
North York	8.29	0.02 (0.2%)	0	1562–2633	48.8	North-east
<i>Burned</i>						
South York	3.59	1.91 (53.2%)	0	1691–2635	42.1	North-east
Lynx	8.21	5.53 (67.4%)	0	1632–2629	43.3	North-east
Drum	7.13	7.12 (99.9%)	0	1432–2156	47.5	North-east
<i>Burned and salvage-logged</i>						
Lyons East	13.15	10.72 (81.5%)	2.62	1441–2027	31.8	North
Lyons West	7.07	4.13 (58.4%)	2.38	1449–2059	24.8	North-east

in the reference, burned, and burned and salvage-logged catchments was 1087 (898–1398), 1146 (950–1431) and 775 mm (582–971 mm) respectively (2004–2014), most of which fell as snow or as rain during summer storm events. Mean annual area-weighted discharge in the reference, burned, and burned and salvage-logged catchments over the same period was 744 (483–1080), 871 (571–1091) and 592 mm (373–887 mm) respectively. Forest cover before the fire was similar between catchments and consisted predominantly of lodgepole pine (*Pinus contorta* var. *latifolia*) at lower elevations (upper Montane ecozones), Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at mid elevations (subalpine ecozones), and treeless alpine meadow vegetation and bare rock at higher elevations, characteristic of the upper

alpine ecozones. Although no predisturbance hydrologic, water quality or aquatic ecological data existed from the study area (as is typical for most wildfire studies), modest replication (2–3) of undisturbed (reference) and disturbed (burned, and burned and salvage-logged) catchments with similar physical and environmental characteristics have been previously used to support broader inferences on wildfire and salvage-logging impacts (Spencer *et al.* 2003; Reid *et al.* 2010). This assumes that disturbed catchments would behave similarly to reference catchments had the disturbance not occurred.

#### *Environmental parameters*

All parameters used in this analysis were calculated from data collected 8 years after the fire, during the ice-free period from

April to October 2011 (Table 2). Water samples were collected every 2 weeks and analysed according to standard methods (Rice 2012; US Environmental Protection Agency (EPA) 2012) for ammonium ( $\text{NH}_4^+$ ), nitrate + nitrite ( $\text{NO}_3^- + \text{NO}_2^-$ ), soluble reactive phosphorous (SRP), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), alkalinity (as  $\text{CaCO}_3$ ), total suspended solids (TSS) and total dissolved solids (TDS). Total inorganic nitrogen (TIN) was determined by the sum of ammonium, nitrate and nitrite.

Stream discharge ( $\text{m}^3 \text{s}^{-1}$ ) was measured every 2 weeks using a Sontek acoustic Doppler velocity meter (Flow Tracker ADV, Sontek/YSI). Stage was recorded every 10 min using HOBO water level loggers suspended in PVC stilling wells (U20-001-04; Onset Computer Corporation) or with a dry gas bubbler and pressure transducer (Waterlog Model H-350 Lite and H-355, Design Analysis Associates Inc.) connected to a measurement and control data logger (CR1000, Campbell Scientific). Discharge and manual stage measurements were used to develop rating curves for each stream and calculate mean daily discharge. Stream temperature was recorded either every 60 min using HOBO temperature data loggers or every 10 min using HOBO temperature and water level loggers (H08-001-02 or U20-001-04; Onset Computer Corporation). Mean daily stream temperature (AVDT) was calculated and used for this analysis.

Periphyton samples were collected using three replicate unglazed ceramic tiles ( $155 \text{ cm}^2$ ) anchored to the streambed in riffle sections of all seven catchments in late April–early May after ice-out. Tiles were scrubbed clean in running stream water before deployment and periphyton was allowed to colonise naturally. Samples were collected monthly for 5 months (June to October) by scraping and rinsing periphyton from the tile surface into acid-washed (10% HCl) Nalgene high-density polyethylene (HDPE) sample bottles. Ash-free dry mass (AFDM) was used as a surrogate for primary productivity (Aloi 1990); samples were frozen before analysis.

#### Macroinvertebrate sampling

Macroinvertebrate sampling was conducted at the end of the growing season in October 2011. A Surber sampler ( $500\text{-}\mu\text{m}$  mesh,  $0.096 \text{ m}^2$ ) was used to collect invertebrates from eight randomly chosen riffle sections along a 100-m transect upstream of each hydrometric gauging station. The sampler was placed on the streambed facing upstream. Large rocks within the sampling area were rubbed clean and removed, then the bed material was vigorously disturbed for 2 min. Sampler contents were placed in a white plastic basin and large debris (e.g. whole leaves, twigs and rocks) were rinsed and removed. Macroinvertebrates, associated plant material and detritus were transferred to Nalgene HDPE sample bottles and preserved in 95% ethanol. The  $500\text{-}\mu\text{m}$  mesh of the Surber sampler permitted the collection of larger-bodied water mites and later insect instars. Macroinvertebrates were sorted, enumerated and identified to the lowest practical taxonomic unit (usually family) using a dissecting microscope and the following keys: Clifford (1991) and Thorp and Covich (2009). Identification of freshwater macroinvertebrates to the level of family has been shown to be sufficient for multivariate analyses comparing assemblage structure between disturbed and undisturbed systems (Bowman and Bailey 1997; Bailey *et al.* 2001).

Table 2. Environmental predictors (average  $\pm$  standard error) for redundancy analysis

Catchment	Stream discharge $Q$ ( $\text{m}^3 \text{ s}^{-1}$ )	Stream temperature AVDT (mean daily stream temperature) ( $^\circ\text{C}$ )	Periphyton productivity AFDM (ash-free dry mass) ( $\text{mg cm}^{-2}$ )	Alkalinity (as $\text{CaCO}_3$ ) ALK ( $\text{mg L}^{-1}$ )	Dissolved organic carbon DOC ( $\text{mg L}^{-1}$ )	Dissolved inorganic carbon DIC ( $\text{mg L}^{-1}$ )	Soluble reactive phosphorous SRP ( $\mu\text{g L}^{-1}$ )	Total dissolved solids TDS ( $\text{mg L}^{-1}$ )	Total inorganic nitrogen TIN ( $\mu\text{g L}^{-1}$ )	Total suspended solids TSS ( $\text{mg L}^{-1}$ )
<i>Reference (unburned)</i>										
Star	$0.32 \pm 0.02$	$4.00 \pm 0.17$	$0.06 \pm 0.02$	$158.13 \pm 4.67$	$1.89 \pm 0.58$	$34.53 \pm 1.35$	$2.58 \pm 0.24$	$173.13 \pm 7.02$	$118.39 \pm 6.42$	$0.83 \pm 0.46$
North York	$0.40 \pm 0.03$	$3.15 \pm 0.13$	$0.12 \pm 0.06$	$120.84 \pm 4.19$	$1.07 \pm 0.17$	$26.67 \pm 1.10$	$2.42 \pm 0.19$	$133.48 \pm 5.29$	$100.42 \pm 7.96$	$0.47 \pm 0.12$
<i>Burned</i>										
South York	$0.18 \pm 0.01$	$4.04 \pm 0.21$	$0.19 \pm 0.08$	$108.67 \pm 4.81$	$1.68 \pm 0.28$	$24.19 \pm 1.41$	$2.67 \pm 0.33$	$116.08 \pm 7.37$	$77.63 \pm 17.56$	$5.63 \pm 2.83$
Lynx	$0.51 \pm 0.05$	$4.39 \pm 0.19$	$0.24 \pm 0.13$	$127.64 \pm 3.46$	$1.65 \pm 0.32$	$29.17 \pm 0.85$	$2.63 \pm 0.25$	$135.63 \pm 4.85$	$105.75 \pm 11.67$	$1.24 \pm 0.35$
Drum	$0.20 \pm 0.02$	$5.49 \pm 0.14$	$0.18 \pm 0.05$	$148.67 \pm 10.35$	$2.03 \pm 0.41$	$32.20 \pm 2.64$	$5.08 \pm 0.56$	$165.5 \pm 9.89$	$87.25 \pm 16.74$	$4.27 \pm 2.01$
<i>Burned and salvage-logged</i>										
Lyons East	$0.41 \pm 0.06$	$7.11 \pm 0.36$	$0.40 \pm 0.13$	$100.16 \pm 12.12$	$3.69 \pm 0.56$	$22.26 \pm 2.78$	$8.42 \pm 0.91$	$124.00 \pm 10.32$	$24.83 \pm 9.79$	$8.49 \pm 4.74$
Lyons West	$0.30 \pm 0.02$	$5.90 \pm 0.31$	$0.17 \pm 0.06$	$104.46 \pm 10.33$	$3.61 \pm 0.68$	$23.26 \pm 2.34$	$6.25 \pm 0.68$	$127.58 \pm 8.89$	$26.54 \pm 8.90$	$12.08 \pm 6.07$

Roundworms (Nematoda) and the water mite family Feltriidae were excluded from the analysis as the large mesh size (500  $\mu\text{m}$ ) prevented consistent collection of a representative sample. Specimens that could not be identified to class were also excluded. Individuals from the stonefly families Capniidae and Leuctriidae were too young to be distinguished from each other and were grouped for this analysis as Capniidae + Leuctriidae. Excluded specimens represented 2.61% of the total specimens collected.

Parameters describing community composition (taxonomic richness, diversity and evenness) were calculated using formulae from Morris *et al.* (2014). Taxonomic richness ( $S$ ) is the total number of taxa observed in each catchment (Eqn 1). Diversity ( $D$ ) was calculated using Simpsons Index of Diversity where  $p_i$  is the proportion of individuals of taxon  $i$  (Eqn 2). Evenness ( $E$ ) was calculated using Simpson's Evenness (Eqn 3):

$$S = \text{number of unique taxa} \quad (1)$$

$$D = 1 - \sum p_i^2 \quad (2)$$

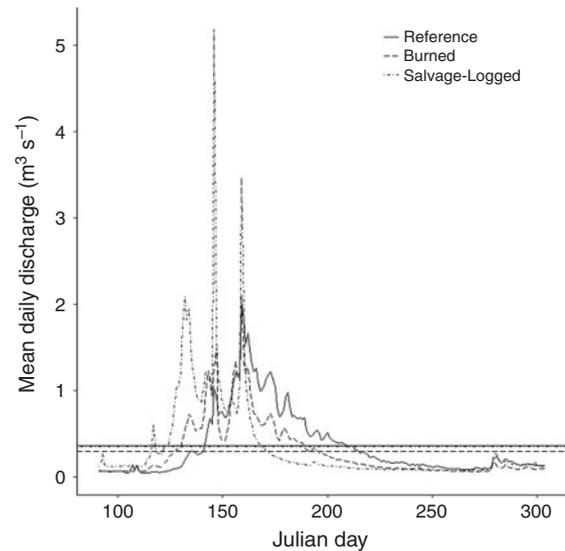
$$E = D/S \quad (3)$$

### Statistical analysis

Statistical analyses were conducted using *R* (R Core Team 2018). Community ordination and analysis were conducted using the *vegan* package (Oksanen *et al.* 2019). One-way analysis of variance (ANOVA) was used to test for an effect of disturbance category on univariate environmental predictors (streamflow, temperature, water chemistry and primary productivity). Parameters that did not meet the assumptions of parametric tests (normal distribution and equal variance) were either log-transformed or analysed using a non-parametric Kruskal–Wallis rank sum test. Post-hoc comparisons between treatments were conducted following one-way ANOVA using Tukey's honest significant difference (Tukey's HSD) test or following Kruskal–Wallis rank sum test using Fisher's least significant difference test. Permutational multivariate analysis of group dispersions (PERMDISP2) was used to test for multivariate homogeneity of group dispersions. Tukey's HSD test was used to conduct post-hoc pairwise comparisons of dispersion between treatments. A multivariate analysis of variance (mANOVA) was conducted on the Bray–Curtis dissimilarity matrix to test for significant differences in taxonomic composition between catchments and treatments.

Non-metric multidimensional scaling (NMDS) using Bray–Curtis dissimilarity matrices was used to visualise the variability of invertebrate taxa in multidimensional space and evaluate the similarity of invertebrate assemblages among catchments within disturbance categories. NMDS ordinations were conducted using both raw counts and  $\log(x + 1)$  transformed data. As invertebrate abundance was considerably higher in the burned catchments, ordinations using counts were heavily influenced by burned catchments. To reduce this effect, ordinations were also conducted using relative abundances instead of counts to compute the dissimilarity matrix.

Redundancy analysis (RDA) was used to determine the strongest environmental correlates of macroinvertebrate



**Fig. 2.** Mean daily discharge ( $\text{m}^3 \text{s}^{-1}$ ) in reference, burned, and burned and salvage-logged catchments in 2011. Horizontal lines indicate mean discharge for the ice-free period (April–October 2011); solid: reference, dash: burned, dot-dash: burned and salvage-logged.

assemblage structure among disturbance categories. Environmental variables used in the RDA are summarised in Table 2. Detrended correspondence analysis (DCA) indicated RDA was the appropriate model, as axis lengths were less than 3 standard deviations (between 1.75 and 2.34) (Borcard *et al.* 2011). Variables with high multicollinearity (variance inflation factor  $>10$ ) were removed before the selection of the most important environmental parameters using a forward stepwise selection procedure (ordiR2step). A Hellinger transformation was applied to the species counts and environmental parameters were standardised to mean zero and unit variance before fitting the RDA model (Legendre and Gallagher 2001).

## Results

### Environmental parameters

Stream discharge ( $Q$ ) in 2011 was similar between reference, burned, and burned and salvage-logged catchments ( $Q_{\text{daily}} = 0.36 \pm 0.02, 0.30 \pm 0.02$  and  $0.35 \pm 0.03 \text{ m}^3 \text{ s}^{-1}$  respectively;  $\chi^2 = 7.8498, P = 0.0197$ ). The annual flow regime (range of flows) varied more between treatments than did mean discharge (Fig. 2). Reference catchments were the least variable, with the least pronounced snowmelt and stormflow peaks and the lowest peak discharge ( $2.03 \text{ m}^3 \text{ s}^{-1}$ ). The burned catchments were intermediate, with peak discharge of  $2.11 \text{ m}^3 \text{ s}^{-1}$ . Burned and salvage-logged catchments were the most variable, with steeper snowmelt and stormflow limbs and the highest peak discharge ( $5.18 \text{ m}^3 \text{ s}^{-1}$ ). Mean daily stream temperature was significantly different between treatments ( $\chi^2 = 38.492, P < 0.001$ ). Stream temperature was highest and most variable in the burned and salvage-logged catchments ( $6.51 \pm 0.24^\circ\text{C}$  compared with  $4.64 \pm 0.11$  and  $3.58 \pm 0.11^\circ\text{C}$  in the reference and burned catchments respectively).

Periphyton productivity (AFDM) varied throughout the growing season in all catchments; mean seasonal AFDM was

**Table 3. Macroinvertebrate counts and relative abundances (in brackets)**

Abbreviations are shown in brackets for taxa included in the non-metric multidimensional scaling (NMDS) ordination (Fig. 5)

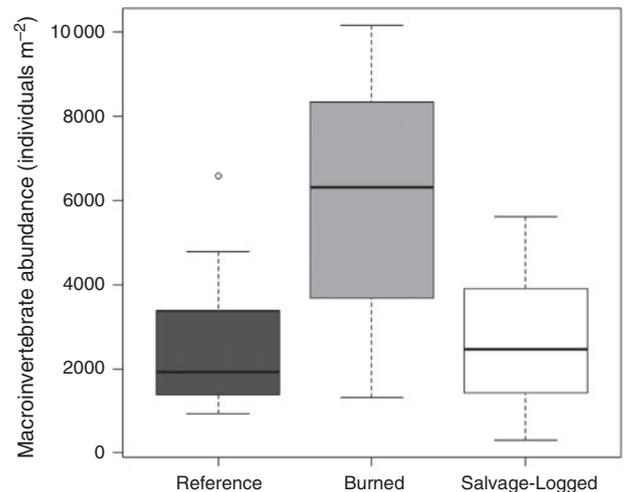
Taxon		Reference	Burned	Burned and salvage-logged	Total
Arachnida: Trombidiformes	Hydryphantidae	17 (0.45%)	3 (0.02%)	3 (0.07%)	23 (0.11%)
	Hygrobatidae	5 (0.13%)	2 (0.01%)	0 (0%)	7 (0.03%)
	Lebertiidae	5 (0.13%)	20 (0.15%)	15 (0.37%)	40 (0.19%)
	Sperchontidae	18 (0.47%)	101 (0.75%)	5 (0.12%)	124 (0.58%)
	Torrenticolidae	0 (0%)	0 (0%)	5 (0.12%)	5 (0.02%)
Crustacea	Ostracoda	113 (2.97%)	160 (1.18%)	64 (1.57%)	337 (1.57%)
Insecta: Coleoptera	Elmidae (ELMI)	29 (0.76%)	543 (4.01%)	1167 (28.63%)	1739 (8.12%)
Insecta: Diptera	Ceratopogonidae	3 (0.08%)	37 (0.27%)	6 (0.15%)	46 (0.21%)
	Chironomidae (CHIRO)	418 (10.99%)	2253 (16.65%)	346 (8.49%)	3017 (14.09%)
	Empidiidae	4 (0.11%)	59 (0.44%)	3 (0.07%)	66 (0.31%)
	Psychodidae (PSYCH)	12 (0.32%)	561 (4.15%)	31 (0.76%)	604 (2.82%)
	Tipulidae (TIPUL)	5 (0.13%)	40 (0.30%)	65 (1.59%)	110 (0.51%)
Insecta: Ephemeroptera	Other Diptera	5 (0.13%)	22 (0.16%)	1 (0.02%)	28 (0.13%)
	Baetidae (BAET)	22 (0.58%)	1239 (9.16%)	73 (1.79%)	1334 (6.23%)
	Ephemereillidae	16 (0.42%)	205 (1.52%)	129 (3.16%)	350 (1.63%)
	Heptageniidae (HEPTA)	195 (5.13%)	76 (0.56%)	1 (0.02%)	272 (1.27%)
	Siphonuridae (SIPHL)	78 (2.05%)	31 (0.23%)	51 (1.25%)	160 (0.75%)
Insecta: Plecoptera	Other Ephemeroptera	886 (23.3%)	4540 (33.56%)	946 (23.21%)	6372 (29.76%)
	Capniidae + Leuctridae (CA_LE)	158 (4.15%)	97 (0.72%)	19 (0.47%)	274 (1.28%)
	Chloroperlidae (CHLOR)	367 (9.65%)	416 (3.07%)	453 (11.11%)	1236 (5.77%)
	Peltoperlidae (PELTO)	50 (1.31%)	255 (1.88%)	5 (0.12%)	310 (1.45%)
	Perlidae	42 (1.1%)	18 (0.13%)	74 (1.82%)	134 (0.63%)
Insecta: Trichoptera	Perlodidae	19 (0.5%)	58 (0.43%)	14 (0.34%)	91 (0.43%)
	Other Plecoptera	959 (25.22%)	920 (6.8%)	423 (10.38%)	2302 (10.75%)
	Brachycentridae (BRAC)	151 (3.97%)	769 (5.68%)	34 (0.83%)	954 (4.46%)
	Hydropsychidae	14 (0.37%)	41 (0.3%)	2 (0.05%)	57 (0.27%)
	Rhyacophilidae	88 (2.31%)	508 (3.75%)	67 (1.64%)	663 (3.1%)
Platyhelminthes	Other Trichoptera	54 (1.42%)	75 (0.55%)	72 (1.77%)	201 (0.94%)
	Turbellaria (TURB)	70 (1.84%)	481 (3.56%)	2 (0.05%)	553 (2.58%)
Total		3803	13 530	4076	21 409

lowest in the reference catchments and greatest in the burned and burned and salvage-logged catchments ( $0.09 \pm 0.03$ ,  $0.21 \pm 0.05$  and  $0.28 \pm 0.07$  mg cm<sup>-2</sup> in the reference, burned, and burned and salvage-logged catchments respectively;  $F_{1,61} = 7.504$ ,  $P < 0.01$ ). AFDM was significantly lower in the reference catchments compared with the burned and burned and salvage-logged catchments.

Water chemistry values are summarised in Table 2. TIN, TDS, DIC and alkalinity were greatest in the reference and lowest in the burned and salvage-logged catchments, showing a generally monotonic pattern across disturbance categories. In contrast, SRP, TSS and DOC were greatest in the burned and salvage-logged catchments, following a pattern of burned and salvage-logged > burned > reference.

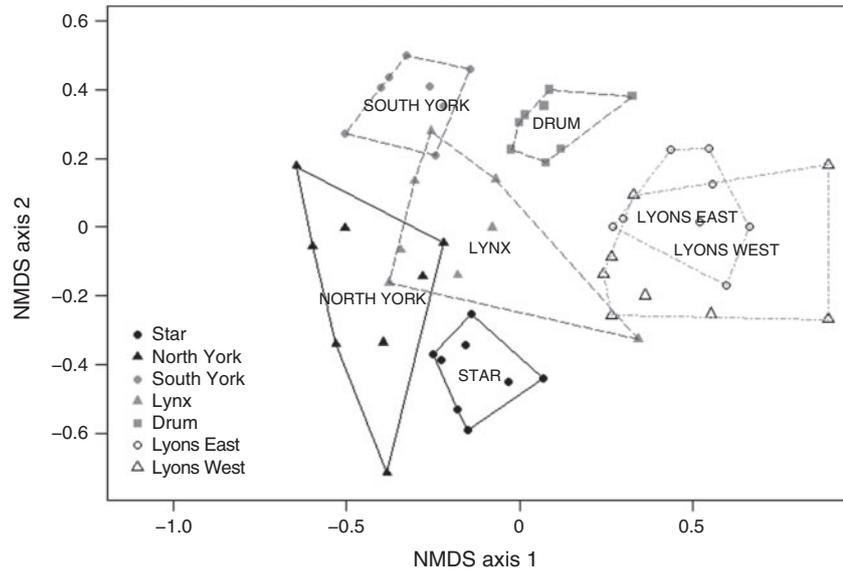
#### Macroinvertebrate assemblage structure

A total of 21 409 individuals from 29 taxonomic groups were identified, enumerated and included in this analysis (Table 3). Insects (Ephemeroptera, Plecoptera, Trichoptera, Diptera and Coleoptera) made up the majority of the macroinvertebrate assemblages (94.0, 94.3 and 97.7% in the reference, burned, and burned and salvage-logged catchments respectively). Flatworms (Platyhelminthes: Turbellaria), aquatic mites (Acariformes: Prostigmata: Parasitengonina: Hydrachnididae) and ostracods (Crustacea) comprised the remainder of the assemblages.



**Fig. 3.** Macroinvertebrate abundance (number of individuals m<sup>-2</sup>) in reference ( $n = 16$ ), burned ( $n = 24$ ), and burned and salvage-logged ( $n = 16$ ) catchments.

Macroinvertebrates were most abundant in burned streams, with a mean density of  $5959.6 \pm 577.1$  individuals m<sup>-2</sup> (Fig. 3). Abundance was similar between reference and burned and



**Fig. 4.** Non-metric multidimensional scaling (site scores). Ordination was performed using a Bray–Curtis dissimilarity matrix calculated with taxa counts. Black: reference, grey: burned, white: burned and salvage-logged. Lines form a polygon encompassing all site scores for a given catchment (solid: reference, dash: burned, dot-dash: burned and salvage-logged).

salvage-logged streams with densities of  $2529.5 \pm 405.5$  and  $2731.1 \pm 421.5$  individuals collected per sample respectively. Taxonomic richness ( $S$ ) was similar across catchments ( $S = 25.0 \pm 3.0$ ,  $26 \pm 0.0$  and  $23.5 \pm 0.5$  in the reference, burned, and burned and salvage-logged catchments respectively). All taxa sampled were represented at least once in each of the reference, burned, and burned and salvage-logged catchments with the exception of two aquatic mite families. The family Hygrobatidae was absent from the burned and salvage-logged catchments and the family Torrenticolidae was absent from the reference and burned catchments; both families were relatively rare across catchments, accounting for 0.03 and 0.02% of the total individuals sampled respectively. Diversity ( $D$ ) and evenness ( $E$ ) were moderately higher in reference catchments and similar across the wildfire-affected catchments ( $D = 0.85 \pm 0.01$ ,  $0.80 \pm 0.05$  and  $0.79 \pm 0.01$  and  $E = 0.28 \pm 0.06$ ,  $0.22 \pm 0.05$  and  $0.21 \pm 0.01$  in the reference, burned, and burned and salvage-logged catchments respectively). Counts and relative abundances of all taxonomic groups are summarised by disturbance category in Table 3.

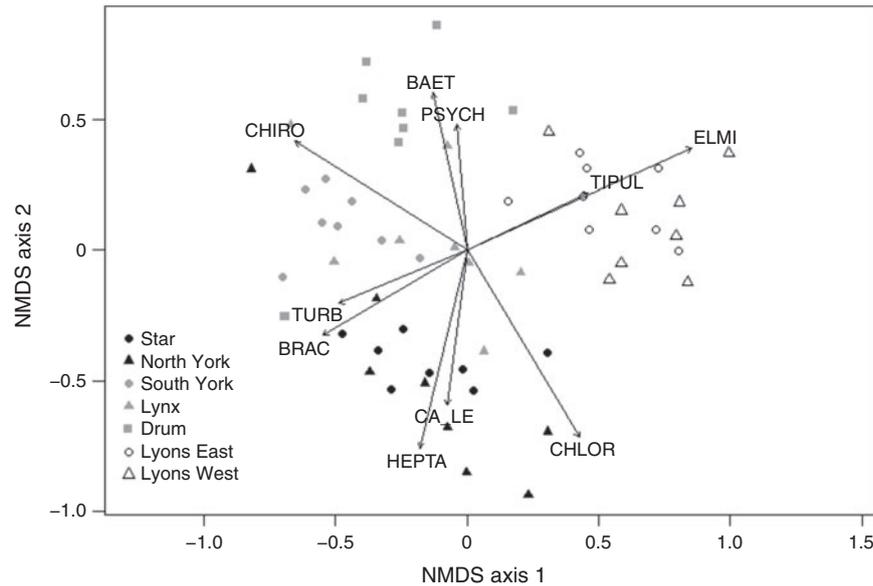
Reference catchments were characterised by high relative abundances of stoneflies (Plecoptera) (41.9% compared with 13.1 and 24.2% in the burned and burned and salvage-logged catchments respectively). In particular, the relative abundance of Capniidae + Leuctridae was high (4.15% compared with 0.72 and 0.47% in the burned and burned and salvage-logged catchments). Burned catchments showed high relative abundances of both true flies (Diptera) and mayflies (Ephemeroptera) (22.0 and 45.1% compared with 11.8 and 31.5%, and 11.1 and 29.44% in the reference and burned and salvage-logged catchments respectively). In particular, the true fly families Chironomidae and Psychodidae and the mayfly family Baetidae were abundant in burned catchments. The

burned and salvage-logged catchments were characterised by particularly high abundances of riffle beetles (Coleoptera: Elmidae) (28.63% compared with 0.76 and 4.01% in the reference and burned catchments respectively) as well as crane flies (Diptera: Tipulidae) (1.59% compared with 0.13 and 0.30% in the reference and burned catchments respectively). The burned and salvage-logged catchments had particularly low numbers of flatworms; only two individuals were collected, representing 0.05% of the macroinvertebrate assemblage compared with 1.84 and 3.56% in the reference and burned catchments respectively.

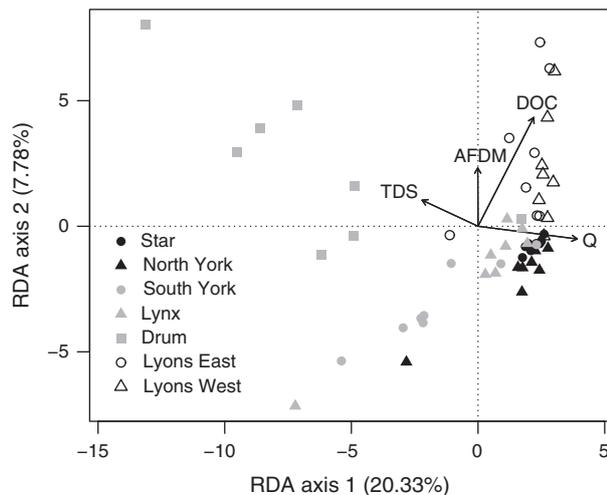
#### *Multivariate analysis of macroinvertebrate assemblage structure*

Invertebrate assemblages formed distinct groups according to catchment and disturbance category in NMDS ordinations (Fig. 4). Multivariate ANOVA of the Bray–Curtis dissimilarity matrices confirmed significant differences in assemblage structure between catchments ( $F = 7.845$ ,  $P < 0.01$ ) and treatments ( $F = 11.403$ ,  $P < 0.01$ ). The test of homogeneity of multivariate dispersions (PERMDIPS2) indicated that  $\beta$  diversity was homogeneous between disturbance category (number of permutations = 999,  $F = 2.821$ ,  $P = 0.07$ ) as confirmed with Tukey's HSD test ( $P > 0.12$ ).

Several taxonomic groups were strongly associated ( $P < 0.01$ ) with study catchments across disturbance categories (Fig. 5). Heptageniidae and Capniidae + Leuctridae were strongly associated with reference catchments. Burned catchments were positively associated with the families Baetidae, Psychodidae and Chironomidae whereas Tipulidae and Elmidae were strongly associated with burned and salvage-logged sites. Several taxa were also associated with catchments in two disturbance categories including Peltoperlidae, Brachycentridae and Turbellaria associated with both reference and burned



**Fig. 5.** Non-metric multidimensional scaling (taxon vectors). Ordination performed using a Bray–Curtis dissimilarity matrix calculated with relative abundances. Points show site scores and vectors show highly correlated taxa ( $P \leq 0.0005$ ); taxon abbreviations are defined in Table 3. Black: reference, grey: burned, white: burned and salvage-logged.



**Fig. 6.** Redundancy analysis (RDA) bi-plot. Points show site scores, vectors show environmental parameters significantly correlated with macroinvertebrate assemblages. Parameter abbreviations are explained in Table 2. Black: reference, grey: burned, white: burned and salvage-logged.

catchments and Chloroperlidae, which was characteristic of both reference and burned and salvage-logged catchments.

The RDA model explained 34.4% of the variance in invertebrate assemblage structure ( $P < 0.01$ , Fig. 6). The first two RDA axes explained 20.3 and 7.8% of the variation respectively. The variables selected by the model in decreasing order of strength were: DOC, stream discharge ( $Q$ ), periphyton productivity (AFDM) and TDS. Reference reaches were characterised by higher discharge and lower periphyton productivity. The burned

catchments were highly variable; Drum Creek had particularly high TDS, South York Creek was characterised by low discharge and DOC, and Lynx Creek was more similar to the reference sites, having high discharge and low DOC. Burned and salvage-logged sites were characterised by high DOC and elevated periphyton productivity. Environmental predictors are summarised in Table 2.

## Discussion

Persistent wildfire effects on macroinvertebrate assemblages were observed in both burned and burned and salvage-logged catchments 8 years after the Lost Creek wildfire (Fig. 4). This observation is consistent with the slow post-wildfire recovery of biogeochemical and biological factors (including increased sediment, phosphorus and carbon export and increased periphyton productivity) observed in these wildfire-affected watersheds (Bladon *et al.* 2008; Silins *et al.* 2009; Emelko *et al.* 2011; Silins *et al.* 2014; Wagner *et al.* 2014; Emelko *et al.* 2016; Silins *et al.* 2016). Previous reports on the duration of wildfire impacts to water quality and stream biology have focused on shorter time-scales (2–3 years) than those described here (Moody and Martin 2001; Robson *et al.* 2018). Results of the present study demonstrate that the effects of both wildfire and post-fire salvage logging on macroinvertebrate assemblages (the latter effects have not been previously described) can be long-lasting (Fig. 6) and these effects are strongly associated with the persistence of fire effects on the chemical and biological stream environments. In particular, DOC and periphyton productivity (AFDM) were closely associated with variation in invertebrate assemblage structure among disturbance categories and continue to be influenced by wildfire-related changes to runoff and water quality (Emelko *et al.* 2016; Silins *et al.* 2016). It is important to

recognise that multiple stream water quality and physical variables after wildfire were strongly correlated, thus although redundancy analysis identified DOC and AFDM as the dominant fire-associated variables, sediment, phosphorus, carbon and periphyton productivity are all likely key drivers regulating the persistence of wildfire effects. The glacial history of these research catchments contributes to long-lasting wildfire effects compared with mountain ecosystems in the western United States (e.g. Yellowstone; Minshall *et al.* 1997) owing to the presence of highly erodible glacial-fluvial deposits that provide a source of bioavailable phosphorus (Emelko *et al.* 2016).

The differences in ecological response (Fig. 5) of the macroinvertebrate assemblages in the burned and burned and salvage-logged catchments were unexpected (Table 2). Sediment export, phosphorus and DOC concentrations (biogeochemical) and periphyton productivity (biological) consistently follow the pattern burned and salvage-logged > burned > reference. Accordingly, it would be expected that the response of macroinvertebrate assemblages in burned and burned and salvage-logged catchments would follow the same pattern. Notably, assemblage structure differed between burned and burned and salvage-logged watersheds (Figs 4, 5) and macroinvertebrate abundance was 2× greater in burned catchments whereas abundance in burned and salvage-logged catchments did not differ significantly from reference assemblages (Fig. 3). Chironomidae and Baetidae were predominant in burned catchments whereas Tipulidae and Elmidae were indicative of burned and salvage-logged systems (Fig. 5; Table 3). These unique assemblage structures and macroinvertebrate abundances between disturbance categories suggest that different mechanisms are driving the ecological responses in wildfire-affected catchments.

Wildfire can affect macroinvertebrate assemblages through several biophysical mechanisms; in this study, we consider the influence of resource limitation and habitat quality. Macroinvertebrate responses to wildfire can also be influenced by other factors including life stage and physiology, which were not accounted for in this study. The resource-limitation mechanism occurs when macroinvertebrates respond to changes in the availability (quantity and quality) of both allochthonous (terrestrial) and autochthonous (in-stream) food resources (Minshall *et al.* 1989; Spencer *et al.* 2003; Mihuc and Minshall 2005). Food webs in undisturbed forested headwater streams will be supported primarily by allochthonous sources of energy as low nutrient concentrations and shading from the riparian canopy prevent significant in-stream primary productivity (Vannote *et al.* 1980). Unburned research catchments consistently fit this pattern, having low primary productivity compared with nearby disturbed, both burned (Emelko *et al.* 2016) and harvested (Hawthorn 2014) catchments. The habitat quality mechanism is related to physical habitat characteristics, where increases in runoff, erosion, sediment and nutrient loading alter both habitat availability and suitability (Hauer and Spencer 1998; Shakesby and Doerr 2006). Considering the reference and burned disturbance categories, both periphyton productivity and macroinvertebrate abundance were greater in the burned catchments, suggesting that resource availability was likely the primary mechanism regulating macroinvertebrate assemblage response. However, the burned and salvage-logged catchments (influenced by two consecutive disturbances) consistently

showed disturbance metrics (suspended sediment, DOC, phosphorus and periphyton productivity) higher than catchments affected by the wildfire only (Table 2). The unique invertebrate assemblage structure in the burned and salvage-logged catchments, and the pattern of high primary productivity but low macroinvertebrate abundance suggest that habitat quality had a greater influence on the ecological response in these systems. The increased sediment loading and more variable flow regime in the burned and salvage-logged catchments likely reduced habitat quality to the point that few taxa were able to take advantage of the increased productivity. These observations are consistent with a previous study that reported differential effects of wildfire on invertebrate assemblages in low- and high-severity burns (Malison and Baxter 2010b); these differences were not interpreted in the context of broader ecological limitations proposed here.

The macroinvertebrate assemblage of the reference catchments was consistent with streams with high water quality and a more stable flow regime. Taxa known to be sensitive to environmental perturbation including stoneflies (Plecoptera) and flatheaded mayflies (Ephemeroptera: Heptageniidae) (Barbour *et al.* 1999; Voshell 2002) were relatively abundant in the reference catchments (Fig. 5, Table 3). Stoneflies are particularly sensitive to sedimentation and excess periphyton (Zwick 1992; Barbour *et al.* 1999; Voshell 2002). Diversity and evenness were moderately higher in reference catchments, likely owing to greater stability of the flow regime and high-quality habitat compared with burned and burned and salvage-logged catchments.

Macroinvertebrate assemblages in the burned catchments included greater abundance of disturbance-adapted taxa as well as taxa adapted to capitalise on increased food availability. Invertebrate families in burned catchments included the true flies Chironomidae and Psychodidae and the mayfly family Baetidae (Fig. 5). Many species within Chironomidae and Baetidae are widely considered to be disturbance-adapted taxa and increase in abundance post fire as they have short generation times and can reproduce quickly (Richards and Minshall 1992; Malison and Baxter 2010b). The family Baetidae contains several genera specialised for consuming periphyton (Minshall *et al.* 2001b); their high abundance suggests that individuals were able to capitalise on increased periphyton productivity in the burned catchments. The abundance of a given taxon will be greatest in the area that provides the most suitable habitat (Brittain and Eikeland 1988); the wildfire alone did not compromise habitat quality to the point that invertebrate taxa were unable to take advantage of the excess periphyton resources.

In contrast, salvage logging contributed to greater deterioration in water quality and stream habitat compared with catchments affected by the fire alone, preventing invertebrates from utilising the additional periphyton productivity. Streamflow was very responsive to rainfall and snowmelt events, resulting in higher peak streamflows than in reference catchments. Suspended sediment and turbidity were consistently higher during these periods of high flows and considerable amounts of fine sediment were deposited on and intruded into gravel interstices in the streambed. The reduced invertebrate abundance observed in these catchments is consistent with the observations of Wood

and Armitage (1997) and Bjornn *et al.* (1977), who showed that increased fine sediment reduced invertebrate density and abundance. Although sediment is an important natural component of stream ecosystems, excess fine sediment can fill pore spaces and reduce oxygen availability in gravel bed streams, compromising habitat and food resources and altering macroinvertebrate behaviour including foraging, respiration and drift (Bjornn *et al.* 1977; Brittain and Eikeland 1988; Wood and Armitage 1997; Jones *et al.* 2012). Crane flies (Diptera: Tipulidae) and riffle beetles (Coleoptera: Elmidae) were strongly associated with burned and salvage-logged catchments (Fig. 5). Crane flies have a burrowing lifestyle and are well adapted to high-sediment environments (Giller and Malmqvist 1998; Voshell 2002). As well, riffle beetle larvae can grip substrate during high flows and protect themselves from sediment abrasion by withdrawing their gills (Bjornn *et al.* 1977; Brown 1987; Voshell 2002; Yee and Kehl 2015). Fine sediment deposition likely contributed to the low abundance of caddisflies (Trichoptera) as some taxa require clean substrate to attach their cases and retreats (Bjornn *et al.* 1977; Voshell 2002). The low abundance of baetid mayflies in the burned and salvage-logged catchments is further evidence of the habitat-limitation mechanism overriding the resource mechanism. Many genera of Baetidae are disturbance-adapted scrapers (consume periphyton) and do well in post-fire environments with high periphyton productivity (Vieira *et al.* 2004; Malison and Baxter 2010b). High suspended sediment loads, however, can be detrimental as many genera are also clingers (Bjornn *et al.* 1977); impact from moving sediment dislodges individuals from rocks, causing injury and reducing abundance (Naman *et al.* 2016).

## Conclusion

The clear differences in macroinvertebrate assemblage structure between reference, burned, and burned and salvage-logged catchments 8 years after the Lost Creek wildfire indicate that the effects of wildfire on aquatic communities in this northern Rocky Mountain ecosystem are persistent. However, despite clear differences in the relative abundance of taxa between disturbance categories, taxonomic richness and diversity did not vary strongly. Only 2 of 29 taxa were missing from one or more disturbance categories; both these families (Hygrobatidae and Torrenticolidae) were locally rare across disturbance categories. It is clear that despite the legacy effects observed in this study, fire-affected catchments still support sensitive taxa and functional macroinvertebrate assemblages 8 years after severe wildfire. The cumulative impacts of wildfire and forest harvest should be considered when making post-wildfire management decisions related to salvage logging. Macroinvertebrates provide many important ecosystem services including sediment mixing, breakdown of organic matter, and nutrient and energy cycling (Covich *et al.* 1999) and are an important energy source for salmonid fishes (Rinne 1996; Malison and Baxter 2010b). Salvage logging had an additive effect on the severity of the wildfire disturbance, the burned and salvage-logged catchments had poorer water quality and higher sediment loads than burned catchments. If the decision is made to apply management treatments following wildfire, best practices should be followed to minimise habitat degradation and sediment inputs, particularly in sensitive catchments (Wagenbrenner *et al.* 2016).

## Conflicts of interest

The authors declare no conflicts of interest.

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