



Wildfire severity mediates fluxes of plant material and terrestrial invertebrates to mountain streams

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ABSTRACT

Wildfire effects upon riparian plant community structure, composition, and distribution may strongly influence the dynamic relationships between riparian vegetation and stream ecosystems. However, few studies have examined the influence of fire on these processes. To that end, we compared the quantity and composition of allochthonous inputs of plant material and terrestrial invertebrates among stream tributaries characterized by various degrees of burn severity 5 years post-fire in the Frank Church Wilderness of central Idaho, USA. The magnitude of inputs of coniferous leaf litter to unburned stream reaches was five times that of inputs to severely burned reaches. Deciduous leaf litter inputs to unburned reaches were 1.5 times, and inputs of terrestrial invertebrates were twice, the magnitude of inputs to severely burned reaches. NMS ordination and MRPP analysis indicated that the taxonomic composition of terrestrial invertebrate inputs to unburned stream reaches was significantly different than the composition of invertebrate inputs to either high-severity or low-severity reaches ($A = 0.057$, $p = 0.040$). Unburned and low-severity stream reaches received greater inputs of large-bodied invertebrates belonging to the orders Hymenoptera, Lepidoptera, Orthoptera, and Diptera. Taken as a whole, our results indicate that fire can significantly alter terrestrial–aquatic connectivity via alterations in riparian-to-stream inputs of leaf material and arthropods. Given these findings, wildfire severity might be expected to be a critical factor in shaping stream–riparian food webs in fire-prone areas.

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1. Introduction

Riparian zones are critical ecotonal components of stream ecosystems (Gregory et al., 1991; Naiman and Decamps, 1997). In particular, riparian vegetation is important in mediating lateral fluxes of energy to streams such as leaf litter (Junk et al., 1989) and terrestrial invertebrates (Piccolo and Wipfli, 2002; Allan et al., 2003). In headwater streams, allochthonous inputs of organic matter (i.e. leaf litter) can provide the primary source of energy to stream consumers (Vannote et al., 1980; Finlay, 2001). Terrestrial invertebrates falling into streams can make up a significant portion of the energy budget of some fishes (Wipfli, 1997; Nakano et al., 1999b) and may also drive top-down effects on benthic invertebrate communities, emergence, and terrestrial–aquatic feedback loops (reviewed in Nakano et al. (1999b) and Baxter et al. (2005)).

The role of wildfire in stream–riparian ecosystems is not fully described (Bisson et al., 2003). To date, research has primarily focused on the effects of fire on short-term nutrient flows and stream chemistry (i.e. Stephens et al., 2004; Elliott and Vose, 2005),

sediment inputs (i.e. Benda et al., 2003; Rieman et al., 2003), and aquatic macroinvertebrates and fish (Gresswell, 1999; Dunham et al., 2003; Minshall, 2003). The influence of fire on terrestrial–aquatic food web connectivity is only beginning to receive attention (Spencer et al., 2003; Malison and Baxter, 2010b). However, because of its effects on riparian plant community structure, composition, and distribution, wildfire might be expected to strongly alter the dynamic relationships between riparian vegetation and stream ecosystem functions (Messier et al., 2012).

The objective of the present study was to compare the quantity and composition of allochthonous inputs of organic matter (plant materials and terrestrial invertebrates) among stream tributaries characterized by various degrees of burn severity 5 years post-fire in a wilderness catchment. We predicted that riparian zones associated with severely-burned reaches in the study area, characterized by removal of the conifer canopy and incomplete recovery of the deciduous understory (Jackson and Sullivan, 2009), would contribute less allochthonous material to streams. In addition, we anticipated that the taxonomic composition of terrestrial invertebrate flux to streams would differ between severely burned reaches and unburned reaches, aligning with patterns in vegetation composition and structure reported at the same suite of study sites in a companion study (Jackson and Sullivan, 2009).

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2. Methods

2.1. Study area

We conducted this study in the lower portion of the Big Creek Watershed located within the Frank Church River of No Return Wilderness of central Idaho. The degree of anthropogenic influence on this 13,000-km² roadless area is low. The Frank Church Wilderness was designated as a primitive area in 1931 and inducted under The Wilderness Act in 1980. Since 1985, wildfires within the Frank Church Wilderness have been managed for resource benefits. Wildfires burned within portions of the Big Creek catchment in 1988, 2000, 2005, 2006, 2007 and 2008. The Diamond Peak Wildfire burned 606 km² of the lower portion of the Big Creek watershed with mixed severity in August and September of 2000. This fire is unique in its extent, providing multiple burned stream reaches that all experienced fire at the same time. Our study took place in 2005; 5-years after the Diamond Peak fire.

The Big Creek watershed is characterized by a mixed Douglas-fir (*Pseudotsuga menziesii*) – ponderosa pine (*Pinus ponderosa*) forest. Black cottonwood (*Populus trichocarpa*) and quaking aspen (*Populus tremuloides*) represent the dominant riparian canopy species; red-osier dogwood (*Cornus stolonifera*) and rocky mountain maple (*Acer glabrum*), the mid-story, and thimbleberry (*Rubus parvifloris*) and mallow ninebark (*Physocarpus malvaceus*), the understory (see Jackson and Sullivan, 2009).

Annual precipitation in the catchment is approximately 40 cm, with the majority falling as snow (Minshall et al., 2003). Historical fire regimes for *Pseudotsuga*-dominated mixed conifer forests are highly variable in severity and frequency (Agee, 1993). Estimates of the historical fire return interval in this region are inconsistent. Heyerdahl et al. (2008), using tree-stand age and dendrochronology, estimated an average historic fire-return interval for the area at 13 years, but alluvial sediment deposits from the last 8000 years recorded a much longer return interval for larger fires at 33–80 years (Pierce et al., 2004).

We based all research out of the University of Idaho's Taylor Wilderness Research Station, and used select tributaries of lower Big Creek within a one-day hike (~40 km) from the research station as study streams. We chose three different fire classes based principally on the presence or absence of an intact conifer canopy: (1) Unburned – Riparian vegetation at these tributaries was either unburned or was burned greater than 50 years ago (Fig. 1A); (2) Low-severity burn – Fire removed the riparian understory, but canopy remained largely intact. Riparian undergrowth had recovered since fire. The only visible sign of fire at these reaches was the presence of fire scars on large trees (Fig. 1B); (3) High-severity burn – Fire removed both the riparian understory and the conifer canopy. Riparian undergrowth had returned but conifer canopy remained absent (Fig. 1C).

Of the 12 study sites chosen, we classified six as high-severity burn, three as low-severity burn, and three as unburned (Table 1, Fig. 2). An unbalanced design was unavoidable given the availability of tributaries characterized by differing burn severity within the accessible area. Seven sites were located at stream reaches representing independent tributary catchments (BT, CG, CL, CV, DC, GT, PN); the remaining five sites were located at reaches within three nested drainages (CA, CB, CW, LW, UP) (Fig. 2). We used a hierarchical reach classification approach to identify comparable and representative stream segment types based on channel bankfull width and depth, floodplain width, reach gradient, substrate type, and valley type (Frissell et al., 1986; Montgomery and Buffington, 1997; Bisson et al., 2006). We designated study sites within the selected stream segments by measuring a 100-m length along the stream, which represented at least 10× bankfull width (see Harrelson et al., 1994; Cianfrani et al., 2009). All streams were

2nd or 3rd order (Strahler, 1952) located in alluvial valleys and reaches were characterized by step-pool morphology (Montgomery and Buffington, 1997).

2.2. Allochthonous inputs

We collected allochthonous inputs falling into the stream using four pan traps (1 m × 0.65 m) per reach (Fig. 1D), with the placement of traps representing the average degree of canopy cover. For example, if average canopy cover for the stream reach was 75%, three pan traps were placed under the canopy and the fourth in the open. We distributed traps laterally across the stream to represent multiple points of potential input of organic matter. We partially filled pan traps with water and biodegradable soap to trap invertebrates and kept them open 24 h per day. We collected pan trap contents every four to five days from mid July through late September 2005. Because not all pan traps were deployed at once, and some data points were missing due to pan-trap disruption by wildlife, we collapsed the data into seven sampling periods for leaf litter and three sampling periods for terrestrial invertebrates.

In the laboratory, we first sorted leaf litter and other plant material into deciduous and coniferous leaf litter and materials and then dried all material at 55 °C for 24 h. We sorted all invertebrates and identified all individuals to order or sub-order following previous studies by Wipfli (1997) and Piccolo and Wipfli (2002). Following identification, we identified all invertebrates as either aquatic or terrestrial, based on origin of larval habitat. After enumeration and identification, we dried (105 °C, ≥24 h) and weighed invertebrates by taxonomic group (Wipfli, 1997; Nakano et al., 1999b).

2.3. Geomorphology

We measured a suite of common stream channel geomorphologic measurements at each study site following Cianfrani et al. (2009) (see Table 1). We recorded one cross-sectional transect at a representative riffle or run. Along this transect, we measured bankfull width, bankfull depth, and floodprone width. We also recorded elevation, aspect, and slope.

2.4. Numerical and statistical analysis

We calculated width-to-depth, entrenchment, and incision ratios from geomorphic field measurements (Rosgen, 1996; Sullivan and Watzin, 2008) using the following formulae: (1) width to depth ratio = bankfull width/mean bankfull depth; (2) entrenchment ratio = floodprone width/bankfull width; (3) incision ratio = low-bank height/maximum bankfull depth.

Because upstream observations of terrestrial inputs were not expected to influence downstream observations, we considered study sites located along the same stream to be independent (e.g. Calf, Cow, and upper and lower Cabin sites). However, we screened for potential spatial autocorrelation among our response variables using global Moran's *I* (Moran, 1950; Cliff and Ord, 1972) for each sampling period. Subsequently, we performed a repeated measures analysis of variance (ANOVA) using proc mixed in SAS to test for potential differences in allochthonous input biomass of leaf material and invertebrates among burn-severity treatments. Study sites were included in the model as a random effect nested within burn severity. We performed post-ANOVA linear contrasts to detect pairwise differences among burn severity treatments. In addition, we generated descriptive statistics (mean and standard deviation) for individual terrestrial invertebrate taxonomic groups across burn types.

To identify potential differences in the composition of the terrestrial invertebrate component of allochthonous inputs among

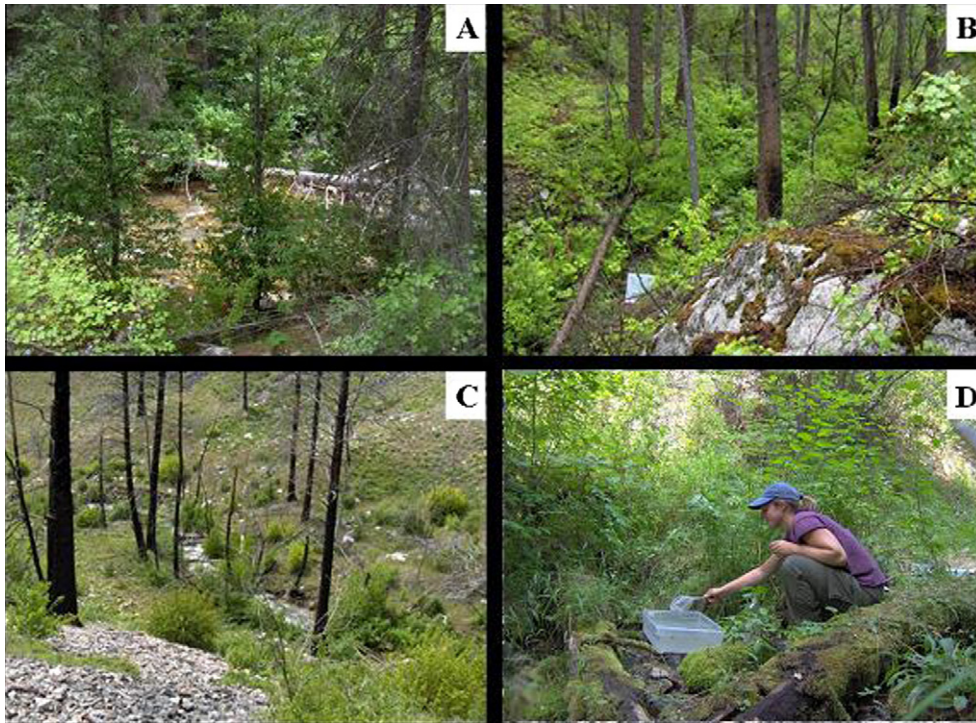


Fig. 1. Pictures of the three fire classes (treatments) based upon the appearance of post-fire vegetation in 2005: (A) Unburned, within the last 50 years. (B) Low-severity burn, where fire burned riparian vegetation, but canopy remained intact. (C) High-severity burn, with both canopy and riparian understory removed by wildfire. (D) Example of a pan trap used for collecting allochthonous inputs. Photo D courtesy of Stephanie Jenkins.

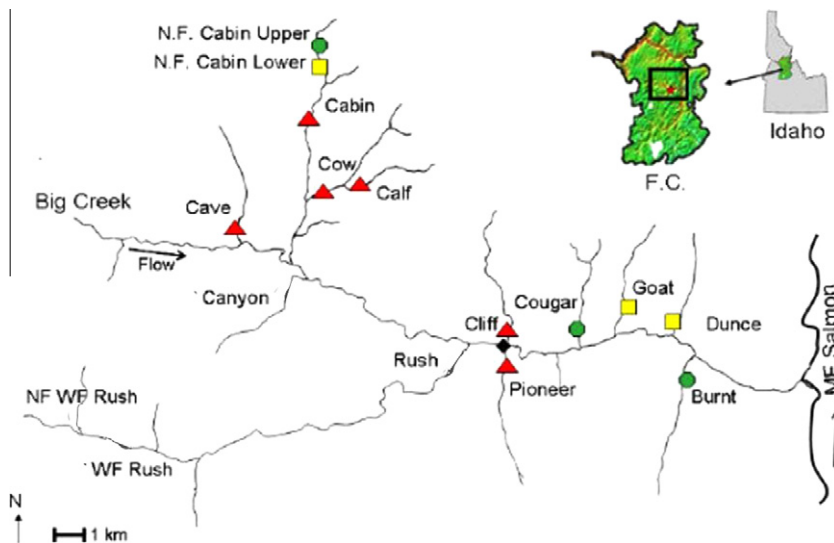


Fig. 2. Study reaches in the Big Creek Watershed, located in the Frank Church River of No Return Wilderness in central Idaho. Reaches are all located on tributaries of Big Creek – a major tributary of the Middle Fork of the Salmon River. Circles represent unburned reaches ($n = 3$); squares, low-severity burn reaches ($n = 3$); and triangles, high-severity burned reaches ($n = 6$). The diamond marks the location of Taylor Wilderness Research Station.

burn types, we used Non-metric Multidimensional Scaling (NMS) and Multi-Response Permutation Procedure (MRPP) ordinations (Kruskal, 1964), following (McCune et al., 2002). We generated Pearson's r rank coefficients for terrestrial invertebrate taxa and for physical and geomorphologic parameters. We followed NMS ordination of each community by MRPP to test for differences in composition and of terrestrial invertebrate inputs among burn types (see Mielke, 1984; Mielke and Berry, 2001 as cited in McCune et al. (2002)). We applied a Bonferroni correction to account for multiple comparisons (Miller, 1981). Sorenson (Bray-Curtis) distances were used for both NMS and MRPP procedures.

All data were transformed where necessary to adhere to assumptions of normality and homogeneity of variance. We used R (R Foundation for Statistical Computing, Vienna, Austria) for Moran's I , SAS (SAS Institute, Inc., Cary, NC) for repeated measures ANOVAs and PC-ORD 5 (McCune and Mefford, 1999) for NMS and MRPP procedures.

3. Results

For all response variables across all sampling periods, results from Moran's I indicated that there was no spatial clustering

Table 1 Physical and geomorphologic characteristics, along with dominant tree species, of all study reaches of the Big Creek watershed. Tree codes: PSME (*Pseudotsuga menziesii*), POTRI (*Populus trichocarpa*).

Reaches by burn severity	Abbrv.	Elevation (m)	Aspect	Stream order	Bankfull width (m)	Bankfull depth (m)	Flood-prone width (m)	Width/depth	Entrenchment	Incision	Stream gradient (m/m)	Dominant tree species (Dominance)
<i>Unburned</i>												
Burnt	BT	1300	N	3	4.50	0.55	10.5	8.26	9.00	0.33	– ^a	PSME (100)
Cougar	CG	1180	S	3	4.50	0.68	9.0	6.67	10.00	0.60	12	PSME (89)
Upper NF Cabin	UP	1601	S	2	2.50	0.34	4.0	7.46	9.00	0.50	18	PSME (94)
Mean		1360		2.7	3.83	0.52	7.8	7.46	9.33	0.48	15	
<i>Low-severity</i>												
Dunce	DC	1165	S	2	1.75	0.46	7.0	3.85	7.75	0.43	26	PSME (96)
Goat	GT	1328	S	2	1.75	0.47	12.0	3.72	15.00	0.00	7	PSME(68)
Lower NF Cabin	LW	1584	S	3	2.50	0.51	5.5	4.90	7.00	0.57	14	PSME (100)
Mean		1359		2.3	2.00	0.48	8.2	4.16	9.92	0.33	16	
<i>High-severity</i>												
Cabin	CB	1406	S	4	6.50	0.89	30.0	7.30	24.43	0.48	5	PSME (61)
Calf	CA	1394	SW	1	3.00	0.37	26.0	8.11	26.00	0.24	14	PSME (100)
Cave	CV	1238	S	3	7.00	0.67	28.0	10.45	26.50	0.60	6	PSME (100)
Cliff	CL	1213	S	2	3.50	0.97	15.0	3.61	14.33	0.53	13	PSME (67)
Cow	CW	1373	SW	2	5.00	0.72	9.5	6.99	9.50	1.70	13	POTRI (85)
Pioneer	PN	1248	N	3	3.00	0.38	5.5	7.89	5.50	0.00	10	PSME (100)
Mean		1312		2.5	4.67	0.67	19.0	7.39	17.71	0.59	10	

^a Data unavailable.

($p > 0.05$ in all cases), suggesting that observations from nearby study sites were independent from one another.

3.1. Leaf litter inputs

Both burn severity and time emerged as influential factors for coniferous and deciduous leaf litter (Table 2; Figs. 3A and B). In addition to significant independent effects of these factors, the interaction of burn severity and time was important in explaining patterns in coniferous leaf litter, with inputs increasing as the summer progressed and trending downward starting in September (Table 2, Fig. 3A). Severely-burned study reaches ($0.11 \pm 0.32 \text{ g/m}^2$) contributed 4–5 times less coniferous leaf litter to the stream than either low-severity burned ($0.41 \pm 0.61 \text{ g/m}^2$) or unburned ($0.56 \pm 0.96 \text{ g/m}^2$) reaches, which were not significantly different from one another (Fig. 3A).

Likewise, differences in deciduous inputs to streams were also explained by burn severity and time, although the interaction of these two factors was not significant (Table 2). Again, inputs increased throughout the summer months with a decrease observed at the beginning of September (Fig. 3B). We observed a gradient of decreasing deciduous leaf litter from unburned to high-severity burned reaches. Riparian vegetation in high-severity burned reaches contributed the least deciduous leaf litter to the stream ($0.34 \pm 0.32 \text{ g/m}^2$), riparian vegetation in unburned reaches contributed the most ($0.57 \pm 0.96 \text{ g/m}^2$), and riparian vegetation in low-severity burned reaches contributed an intermediate amount ($0.42 \pm 0.61 \text{ g/m}^2$). Post-hoc comparisons revealed that deciduous inputs to high-severity burned reaches were significantly less than inputs to unburned reaches ($F = 5.28$; $p = 0.028$). Riparian contributions of leaf litter to low-severity burned reaches were indistinguishable from either of the other two treatment groups.

3.2. Terrestrial-to-aquatic invertebrate flux

We observed differences in both the biomass and taxonomic composition of terrestrial invertebrate inputs to streams with varying burn severity, even at a coarse taxonomic resolution. Specifically, we observed a significant effect of burn severity, reach, and time on the biomass of terrestrial invertebrate inputs (Table 2). Post-hoc comparisons revealed that the magnitude of terrestrial invertebrate inputs at unburned reaches were significantly different than either of the other treatment groups ($F = 11.32$; $p = 0.002$ for unburned versus low, $F = 17.40$; $p < 0.001$ for unburned versus high). Unburned reaches had roughly twice the terrestrial invertebrate inputs ($245.6 \pm 29.7 \text{ mg/m}^2$) compared to both low-severity burned reaches ($125.9 \pm 28.8 \text{ mg/m}^2$) and high-severity burned reaches ($114.0 \pm 23.7 \text{ mg/m}^2$). In contrast to leaf litter patterns, terrestrial invertebrate inputs increased from July to September with no observed decrease at the end of the sampling period (Fig. 3C).

We observed substantial differences in inputs of invertebrates belonging to the orders Diptera (flies), Hymenoptera (ants and wasps), Orthoptera (grasshoppers), and Lepidoptera adults (butterflies and moths) among treatment groups. Mean inputs of invertebrates of the order Diptera to unburned stream reaches ($132.2 \pm 31.9 \text{ mg/m}^2$) were twice those to low-severity burned reaches ($68.5 \pm 25.8 \text{ mg/m}^2$) and eight times those to high-severity burned reaches ($16.2 \pm 0.6 \text{ mg/m}^2$). Inputs of the order Orthoptera to unburned stream reaches ($63.2 \pm 77.4 \text{ mg/m}^2$) was twelve and three times the inputs to low-severity ($5.0 \pm 7.5 \text{ mg/m}^2$) and high-severity ($22.6 \pm 38.8 \text{ mg/m}^2$) stream reaches, respectively. Flux of Lepidoptera adults to low-severity burned reaches was 1.5-times the flux to unburned reaches ($30.0 \pm 4.3 \text{ mg/m}^2$ and $21.3 \pm 3.0 \text{ mg/m}^2$ respectively) and three times the flux to high-severity burned reaches ($10.6 \pm 2.9 \text{ mg/m}^2$). Inputs of the order

Table 2

Repeated measures analysis of variance (ANOVA) results for (1) coniferous leaf litter; (2) deciduous leaf litter; and (3) terrestrial invertebrate inputs.

	$df_{(num)}$	$df_{(den)}$	F	p
<i>Coniferous litter</i>				
Reach (burn severity)	9	36	2.00	0.068
Burn severity	2	36	11.77	<0.001
Time	6	36	10.88	<0.001
Time * burn severity	12	36	2.53	0.016
<i>Deciduous litter</i>				
Reach (burn severity)	9	36	2.16	0.049
Burn severity	2	36	2.64	0.085
Time	6	36	7.38	<0.001
Time * burn severity	12	36	1.62	0.129
<i>Terrestrial invertebrate biomass</i>				
Reach (burn severity)	9	35	6.44	<0.001
Burn severity	2	35	9.59	0.001
Time	2	35	5.08	0.012
Time * burn severity	4	35	1.93	0.127

Hymenoptera was comparable among unburned and low-severity burned stream reaches ($35.3 \pm 18.1 \text{ mg/m}^2$ and $35.5 \pm 6.8 \text{ mg/m}^2$ respectively) but nearly 1.5-times inputs to high-severity burned reaches ($22.5 \pm 14.4 \text{ mg/m}^2$). We observed substantial inputs of Diplopoda (millipedes) and Lepidoptera larvae (caterpillars) to Burnt Creek during the later sampling periods. Mean Diplopoda inputs to Burnt Creek from the fourth week of August and first week of September was $55.1 \pm 12.5 \text{ mg/m}^2$ and we observed a one-time input of 516.6 mg/m^2 of Lepidoptera larvae to Burnt Creek during the first week of September.

We included sixteen taxonomic groups of terrestrial invertebrates in NMS and MRPP analyses. MRPP showed that the composition of the terrestrial-to-aquatic invertebrate flux differed among the three burn types ($A = 0.06$, $p = 0.040$) (Table 3). Based on multiple MRPP comparisons, the greatest difference in riparian terrestrial invertebrate community composition resulted from differences between low-severity and high-severity burn reaches. NMS ordination echoed these results. The three-axis NMS solution (stress = 2.45, $p = 0.020$) represented 93.0% of the total compositional variation; 24.1% on axis 1, 28.9% on axis 2, and 39.9% on axis 3 (Fig. 4A–C).

Diplopoda and Lepidoptera larvae, both ground or canopy dwellers and comprised of relatively large individuals, were positively correlated with axis 2 ($r = 0.91$, 0.91 ; respectively) (Fig. 4A). Diptera, Hymenoptera, and Psocoptera (booklice) were positively correlated with axis 1 ($r = 0.79$, 0.73 , 0.67 ; respectively) (Fig. 4B). Orthoptera were negatively correlated with axis 3 ($r = -0.73$) (Fig. 4C). Of the physical parameters, only gradient ($r = 0.56$) and elevation ($r = 0.54$) were notably correlated with the model (axis 1).

4. Discussion

To our knowledge, our wilderness catchment study is one of the only investigations to directly quantify the effects of wildfire on fluxes of food resources from riparian zones to streams (but see Spencer et al., 2003). Our study builds on previous work in the greater Big Creek study area (Minshall et al., 2001; Malison, 2008; Jackson and Sullivan, 2009) to provide additional evidence that the severity of wildfire exerts strong influences on riparian-to-stream energy fluxes.

4.1. Leaf litter inputs

Our leaf litter results add additional nuance to the current understanding of the influences of wildfire on linked stream–riparian food webs. In particular, burn severity has been shown to correlate with changes in aquatic benthic invertebrate communities (Minshall,

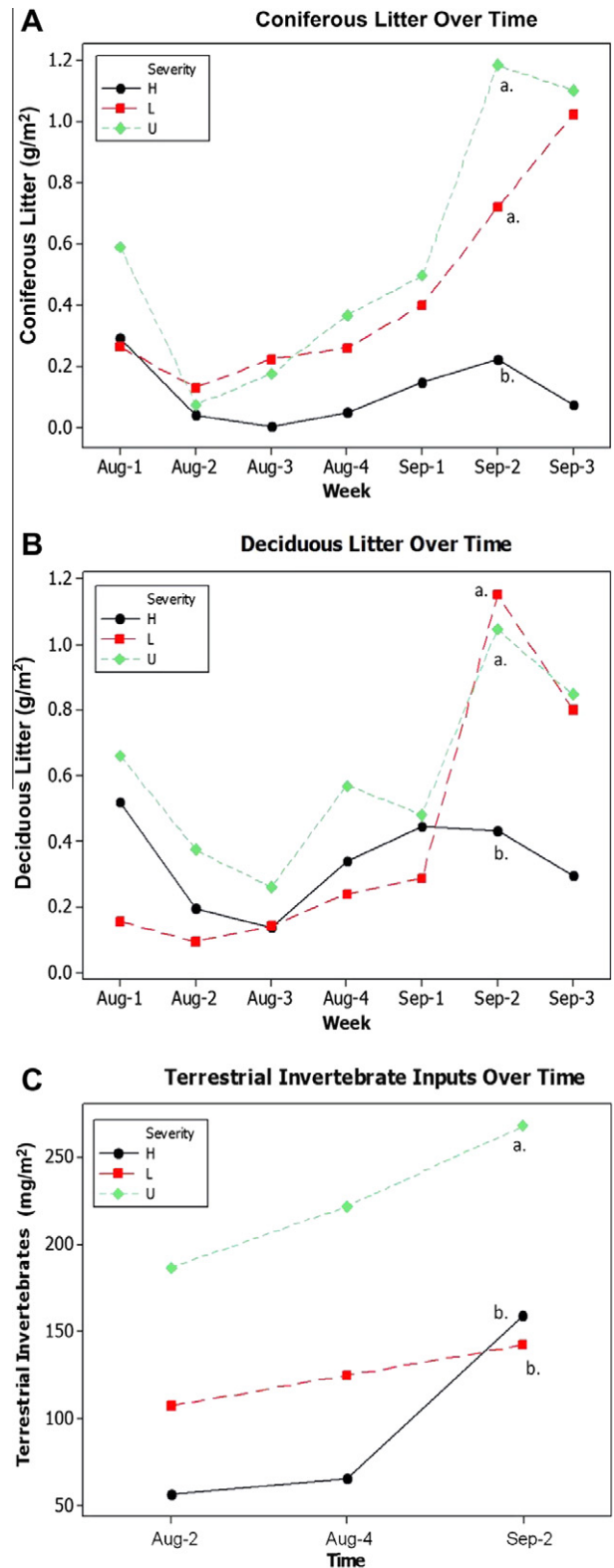


Fig. 3. Inputs from the riparian zone to the stream of: (A) coniferous leaf litter, (B) deciduous leaf litter, and (C) terrestrial invertebrates. All parameters are expressed as mean biomass per square meter. Black diamonds represent high-severity burned reaches, red squares represent low-severity burned reaches, and green diamonds represent unburned reaches. Differing lower-case letters represent significant differences ($\alpha = 0.05$) among burn types based on linear contrasts following ANOVA. For leaf material, dates are month and week. For terrestrial invertebrates, the data are collapsed into three sampling periods each representing two weeks of sampling. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2003) but the mechanisms by which wildfire influences benthic invertebrates has yet to be fully explained. Also working in Big Creek, Minshall et al. (2001) showed that invertebrate scraper densities (feeding on algae) increased in streams affected by the 1979 Mortar Creek Fire and that shredder densities (feeding on allochthonous leaf material) initially fell dramatically (1st two months), then gradually increased but never reached reference conditions even after 10 years time. Examination of stable carbon and nitrogen isotope ratios in benthic consumers in Glacier National Park following wildfire indicated a shift from reliance on allochthonous to autochthonous food sources (Spencer et al., 2003). Our results show a reduction in both coniferous and deciduous leaf litter inputs to streams exposed to high-severity wildfire, supporting the hypothesis that changes in food availability in fire-impacted streams is one mechanism driving changes in aquatic invertebrate populations.

The timing of leaf litter inputs to stream reaches also likely mediates effects on aquatic consumers (Richardson, 1991; Gjerlov and Richardson, 2004). In our study, time was a significant factor explaining both coniferous and deciduous leaf litter inputs with increased inputs toward the end of summer (Fig. 3A and B). In addition, the interaction between time and burn severity was an important predictor of coniferous leaf litter flux indicating that severe wildfire may alter the timing of riparian-to-aquatic fluxes of plant materials. Fire-induced shifts in the timing of inputs of coniferous and deciduous leaf litter to streams may partly contribute to increased dominance by trophic generalists as well as more temporal variability of benthic invertebrate community composition. For example, following the 1989 Yellowstone fires, Mihuc and Minshall (1995) found that trophic generalists were common stream food-web components in Cache Creek, MT. Similarly, Malison and Baxter (2010a) found that opportunistic species (i.e. *r*-selected) such as Chironomidae and *Baetis* made up a greater proportion of benthic invertebrate biomass and emergence in Big Creek tributary reaches affected by high-severity fire compared with both low-severity and unburned reaches. In addition, Arckle et al. (2010) found that post-fire benthic invertebrate communities were characterized by inter-annual variability in contrast to relatively stable communities in unburned streams (Robinson et al., 2000) and that macroinvertebrate community composition correlated with changes in organic matter (i.e. when organic matter was present, communities had a greater proportion of collector-gatherers whereas scrapers dominated when organic matter was absent).

We measured the magnitude of leaf litter inputs to streams, however the effects of alterations in inputs of riparian leaf litter on benthic consumers may be mediated by a number of factors that have not been examined within the context of wildfires. Characteristics influencing leaf litter quality such as nutrient composition, allelopathic chemical production, and waxy leaf protection varies both within and among species and can be influenced by environmental factors subject to change following severe wildfire such as available soil nutrients, sun and shade, and soil moisture (e.g. Volk et al., 2003).

4.2. Invertebrate inputs

We expected terrestrial-to-aquatic fluxes of invertebrates to mirror patterns in vegetation composition given that other studies

Table 3
Multiple response permutation procedure (MRPP) of terrestrial invertebrate input taxonomic composition among reaches characterized by different burn severities.

	A	p
Burn severity	0.057	0.040
Unburned vs. low-severity	0.077	0.037
Unburned vs. high-severity	-0.001	0.480
Low-severity vs. high-severity	0.086	0.011

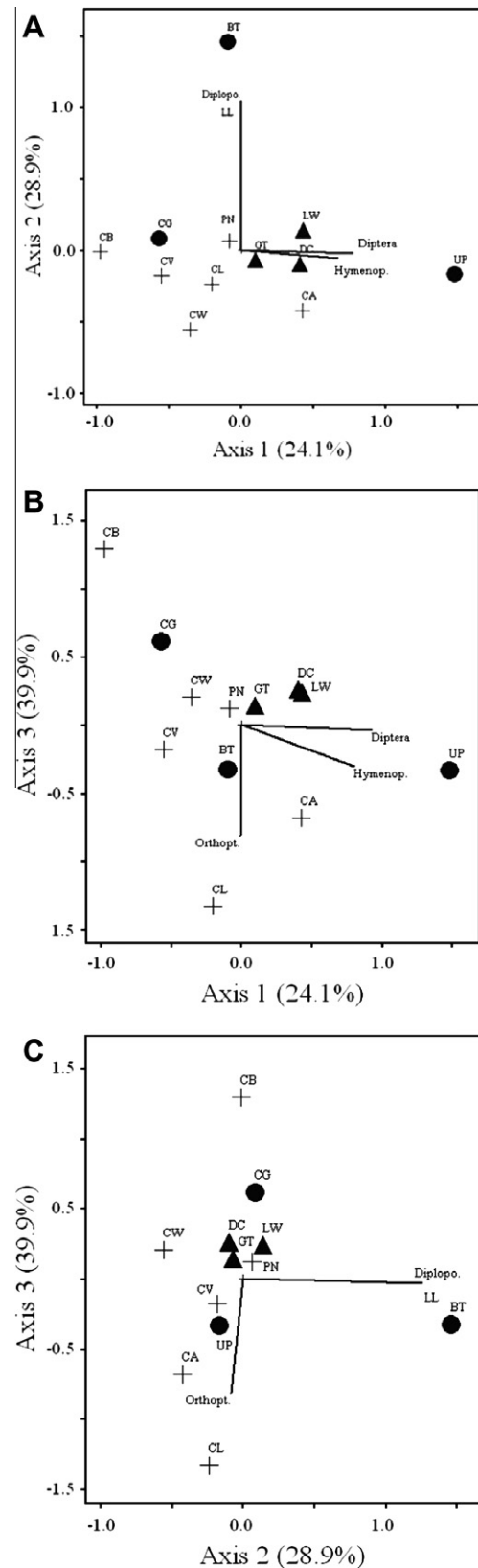


Fig. 4. NMS ordination of terrestrial invertebrates. Unburned reaches are represented by circles, low-severity reaches by triangles, and high-severity reaches by crosses. The amount of variation represented by each axis is indicated in parentheses. Joint plots have been included to show correlations of select taxonomic groups with NMS axes. Abbreviations are: LL – Lepidoptera larvae; Diplopo. – Diplopoda; Hymenop. – Hymenoptera; Orthopt. – Orthoptera.

report variable fluxes of terrestrial invertebrates in relation to the species composition and structure of riparian vegetation (Hetrick et al., 1998; Allan et al., 2003). In our study, both the magnitude and composition of terrestrial invertebrate inputs to streams differed between high-severity burned reaches and both other treatment groups. This result aligned with findings by Jackson and Sullivan (2009), who found that high-severity fire altered riparian vegetation structure and composition at the same study locations. However, we also found differences in terrestrial invertebrate inputs between low-severity and unburned streams whereas Jackson and Sullivan (2009) found no difference in riparian vegetation structure or composition between these treatment groups. Together these results point to a possible functional attribute of riparian vegetation following low-severity fire that influences riparian invertebrate communities. Subtle differences in foliar nutrient composition or litter layer recovery (e.g. Bess et al., 2002) may partly explain differences in terrestrial invertebrate inputs between low-severity and unburned streams. For instance, at these same study sites Jackson (2009) observed that nitrogen concentrations in plant tissues from low-severity burned reaches were low whereas $\delta^{15}\text{N}$ values remained high when compared to unburned sites. This is consistent with work by Grogan (2000), who compared nitrogen concentrations and $\delta^{15}\text{N}$ values for soils and plant tissue between mature forest and burned reaches.

Although streams have been viewed traditionally as recipients versus sources of energy to food webs, this view has shifted in recent years as research has highlighted the importance of emergent aquatic insects to riparian and terrestrial consumers (reviewed in Baxter et al. (2005)). In fact, the direction of invertebrate food fluxes may be temporally offset in temperate climates resulting in a pattern in which fluxes are greater from the forest to the stream during the summer but fluxes from the stream to the forest are relatively greater in other parts of the year (Power, 2001; Baxter et al., 2005). In our study, inputs of both leaf litter and terrestrial invertebrates to streams where fire had occurred were less than to unburned streams. Conversely, in a collaborative study at the same study locations, Malison and Baxter (2010b) found that emergence of adult aquatic insects was as much as five times greater from severely-burned reaches relative to both low-severity burned and unburned reaches in this study area. In part, the contrasting results between aquatic and terrestrial invertebrates may be explained by the following: (1) As a group, benthic invertebrates are highly disturbance-adapted and may recover more quickly than terrestrial invertebrates following wildfire (Minshall, 2003) and (2) Recovery of riparian vegetation is much slower than recovery of periphyton, which may be amplified in the years following wildfire because of increased concentrations of nitrogen and phosphorus entering the stream (Hauer and Spencer, 1998; Spencer et al., 2003). In a similar fashion as the effects of seasonality on reciprocal terrestrial–aquatic exchanges of invertebrates, these linked results may collectively point to a dynamic balance of aquatic-to-terrestrial and terrestrial-to-aquatic invertebrate fluxes along streams in fire-prone landscapes.

In addition to the overall magnitude of inputs of terrestrial invertebrates to stream reaches, the association of larger prey items such as caterpillars, millipedes, grasshoppers, ants and wasps, and black flies with unburned and low-severity burned stream reaches may be an important consideration. Many salmonids selectively forage for larger prey items (Nakano et al., 1999a), so donation of prey items that are larger and more accessible (i.e. Lepidoptera, Diplopoda, Orthoptera, and Hymenoptera) by unburned and low-severity burned riparian zones may provide disproportionately more energetic value to fish (Kawaguchi and Nakano, 2001). Although we detected taxonomic differences across reaches affected by varying degrees of burn severity, the manner in which this information relates to prey availability requires further

study. For example, gut-content analysis by Koetsier et al. (2007) revealed that rainbow trout (*O. mykiss*) in burned streams relied more heavily on autochthonous prey and although trout density between unburned, scorched, and severely burned streams in the Boise River Basin was indistinguishable, trout biomass and average length were significantly greater in both scorched and severely burned streams 10 years post-fire. Therefore, although fish biomass might be expected to decline in areas where terrestrial invertebrate inputs are diminished, increased benthic productivity following wildfire may offset these effects.

Further inquiry into the effects of post-fire shifts in allochthonous resources on aquatic consumers (i.e. fish and macroinvertebrates) will be of considerable importance to our understanding of terrestrial–aquatic food webs in fire-prone landscapes. This understanding would be greatly enhanced by holistic food web studies, and in particular, research that explicitly addresses mechanisms driving changes in food-web properties. In addition, considering the spatial distribution of riparian burn patterns could yield important information relative to the composite influences of wildfire on coupled terrestrial–aquatic dynamics along the drainage network.

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